Mammal Rev. 2002, Volume 32, No. 2, 179–198. *Printed in Great Britain*.

Habitat use, diet and roost selection by the Big Brown Bat (*Eptesicus fuscus*) in North America: a case for conserving an abundant species

SALVATORE J. AGOSTA
Department of Biology, Frostburg State University, Frostburg, MD 21532–1099, USA

ABSTRACT

Insectivorous bats are integral components of terrestrial ecosystems. Despite this, a growing number of factors causing world-wide declines in bat populations have been identified. Relatively abundant species are important for bat conservation because of their role in ecosystems and the research opportunities they offer. In addition, species that have been well-studied present unique opportunities to synthesize information and highlight important areas of focus for conservation and research. This paper focuses on a well-studied abundant bat, *Eptesicus fuscus*. I review the relevant literature on habitat use, diet and roost selection by *E. fuscus* in North America, and highlight important areas of conservation and research for this species, including the effects of roost disturbance, control of economically important insect pests, exposure to pesticides, long-term monitoring of populations, and the potential consequences of expanding populations. These issues have broad implications for other species and can be used to focus future research and conservation efforts.

Keywords: bat conservation, *Eptesicus fuscus*, food habits, North America, research needs, roosts

CONTENTS

Correspondence: Salvatore J. Agosta, Department of Biology, University of Pennsylvania, Philadelphia, PA 19104–6018, USA (E-mail: sjagosta@hotmail.com)

INTRODUCTION

Bat populations are declining world-wide as a result of a growing number of factors, including habitat loss and fragmentation, disturbances to roosts, exposure to toxins, human hunting pressures and introduced predators (McCracken, 1989; Fenton, 1997; Arita & Ortega, 1998; Fenton & Rautenbach, 1998; Marinho-Filo & Sazima, 1998; Pierson, 1998; Racey, 1998; Rainey, 1998; Richards & Hall, 1998; Utzurrum, 1998; O'Donnell, 2000). This makes it difficult to draw general conclusions about bat conservation, which may require species-specific conservation plans (Fenton, 1997). Insectivorous bats are major consumers of nocturnal insects, many of which are economically important pests. This presents both ecological and economic rationales for their protection (Grinnell, 1918; Constantine, 1970; Whitaker, 1995; Pierson, 1998). In addition, bat guano is rich in nitrogen and other nutrients. Bats may transfer significant amounts of nutrients in ecosystems as guano accumulates at roosts (e.g. tree hollows; Kunz, 1982; Rainey *et al*., 1992; Zielinski & Gellman, 1999) and is spread across the landscape while bats forage (Pierson, 1998). Bats are also important components of cave environments, where the accumulation of guano supports a diverse invertebrate community (Poulson, 1972; Culver *et al*., 2000). Some bat assemblages may be useful indicators of habitat disturbance and quality (Fenton *et al*., 1992; Medellin, Equihua & Amin, 2000).

Like most conservation efforts in North America, bat conservation has focused primarily on rare and endangered taxa (Pierson, 1998). However, because of their potential role in controlling insect populations and distributing nutrients across landscapes, Pierson (1998: 318) argued that widespread, abundant, species may be the most ecologically and economically important. In the UK, recent attention has been directed towards a national landscape-level bat conservation and management plan (Racey, 1998). The broad strategies gleaned from this effort have centred mainly around data collected from the Common Pipistrelle (*Pipistrellus pipistrellus*), one of the most widespread and abundant bats in Europe (Racey, 1998). This work illustrates the importance of abundant species, not only because of their numerical abundance and ecological impact, but also because of the research opportunities they present. In North America, several of the most abundant bats (e.g. *Eptesicus fuscus* and *Myotis lucifugus*) readily roost in buildings and artificial bat boxes (Tuttle & Hensley, 2000), presenting a practical means for ensuring their continued abundance.

Fenton (1997) and Pierson (1998) identified several components of bat conservation. These include (i) protection of foraging habitat; (ii) protection of the prey base; and (iii) protection of roosts. The objective of this paper is to review the relevant literature on habitat use, diet and roost selection by a relatively abundant bat species, *E. fuscus* (Chiroptera: Vespertilionidae), in North America. I focus on these broad components of bat conservation, using a well-studied species to illustrate the importance of species-specific information for determining conservation goals. In addition, I address the importance of conserving abundant bat species, because of both their role in ecosystems and the research opportunities they present. Finally, I identify some specific areas of research that relate directly to the conservation of *E. fuscus* and more broadly to bats in general.

THE BIG BROWN BAT

The Big Brown Bat (*Eptesicus fuscus*) is one of the most widespread mammals in North America, ranging from Canada throughout the United States and Central America, and into north-western South America (Kurta & Baker, 1990). It also occurs on several islands, including Cuba, Jamaica and Puerto Rico. This bat is the only North American representative of the genus *Eptesicus* north of Mexico, and probably has been widespread throughout the Pleistocene (Kurta & Baker, 1990). *Eptesicus fuscus* exhibits significant morphological variation across its range (Burnett, 1983) and is represented by 11 subspecies (Kurta & Baker, 1990). Across its range, it is distinguished from sympatric species by its relatively large size (14–30 g; Nowak, 1999), bi-coloured pelage (blackish-brown to pinkish-tan above, paler underneath), short blunt tragus and long fur (Kurta & Baker, 1990). Because of its widespread distribution and relatively high abundance, *E. fuscus* may play a particularly important role in many ecosystems. Compared with other species, *E. fuscus* has been well-studied (Kurta & Baker, 1990). This reflects its colonial behaviour and close association with humans (Davis, Barbour & Hassell, 1968; Barbour & Davis, 1969).

HABITAT USE

For many species, bat–habitat relationships are poorly understood. Several factors complicate this relationship, including the high mobility of bats, which gives them access to a wide range of habitats (Fenton, 1997). Recent advances in radio-tracking and bat-detector technology have allowed for significant progress in our understanding of bat–habitat relationships (Fenton, 1997). The UK National Bat Habitat Survey, for example, has developed important generalizations and produced powerful predictive equations regarding habitat use by bats at local and landscape levels (Walsh & Harris, 1996a, 1996b).

Big Brown Bat habitat associations

Studies of *E. fuscus* in North America have failed to establish unique associations with specific habitats (Bell, 1980; Geggie & Fenton, 1985; Furlonger, Dewar & Fenton, 1987; Krusic & Neefus, 1996) and suggest that this bat is a habitat generalist (Furlonger *et al*., 1987; Krusic & Neefus, 1996). No clear associations are documented between city, town and rural settings (Geggie & Fenton, 1985; Furlonger *et al*., 1987) or between forest types (Bell, 1980; Krusic & Neefus, 1996). Some habitat features appear to be important to *E. fuscus* when foraging. In the White Mountains of New Hampshire, Krusic & Neefus (1996) found that the activity of *E. fuscus* was highest near standing water and roads. In Arizona, Bell (1980) observed higher activity in riparian zones. In topographically diverse regions, foraging activity by reproductive females appears to be greater at lower elevations where insect densities are higher (Cryan, Bogan & Altenbach, 2000). Foraging activity has also been shown to decrease with increasing urbanization, possibly because of lower insect abundance in these areas (Geggie & Fenton, 1985).

Habitat is probably a less important conservation component for *E. fuscus* than for other species, although current forestry practices may exert a negative impact on some tree-roosting populations (Betts, 1996; Vonhoff, 1996; Vonhoff & Barclay, 1996; Kalcounis & Brigham, 1998; Rabe *et al*., 1998). *Eptesicus fuscus* readily takes advantage of insect concentrations near lights (Geggie & Fenton, 1985; Furlonger *et al*., 1987) and readily uses human-made structures as roosts (Whitaker & Gummer, 1992, 2000; Williams & Brittingham, 1997). These two behaviours have probably lessened any potential impacts of habitat loss on *E. fuscus*. Several factors related to diet and roost selection, however, may confound the otherwise neutral (or positive; Whitaker & Gummer, 1992; Fenton, 1997) impacts that human modification of the environment has had on this species.

THE PREY BASE

Insectivorous bats are susceptible to the accumulation of toxins (e.g. pesticides) because of their high trophic rank and longevity (Clark, 1988). Knowledge of the food habitats of bats is useful for identifying potential sources of toxins (Clawson & Clark, 1989). In addition, knowledge of food habits enables the identification of agricultural pests consumed by bats (Whitaker, 1995) and publicizing this information can be a powerful conservation tool. These two issues (exposure to pesticides and consumption of insect pests) are closely linked, and both are important when considering the conservation of bats.

Food habits

A number of studies in the US and Canada have examined the food habits of *E. fuscus*; however, studies on more southern populations are generally lacking (Table 1). Black (1974) classified *E. fuscus* as a beetle-strategist (predator of Coleoptera) in New Mexico; the current literature appears to support this, with a few notable exceptions. Studies in Arizona (Warner, 1985) and Oregon (Whitaker, Maser & Keller, 1977; Whitaker, Maser & Cross, 1981) have found moths (Lepidoptera) to be major prey items, although moths are generally minor com-

Table 1. Summary of *Eptesicus fuscus* food habits in North America

Location	Method*	Dominant prey items	Second major prey items	Source
Indiana, Illinois	%v	Coleoptera: Scarabaeidae, *Diabrotica*	Hemiptera: Pentatomidae	Whitaker (1995)
Indiana	%v	Coleoptera: Carabidae, Scarabaeidae, *Diabrotica*	Hemiptera: Pentatomidae	Whitaker (1972)
Oregon	%v	Lepidoptera	Coleoptera: Scarabaeidae	Whitaker *et al*. (1977)
	%v	Coleoptera: Scarabaeidae, Carabidae	Lepidoptera	Whitaker *et al*. (1981)
	%v, %f	Trichoptera	Coleoptera: Scarabaeidae	Verts *et al*. (1999)
New Mexico	%f	Coleoptera	Not applicable	Black (1974)
Arizona	%f	Lepidoptera	Coleoptera	Warner (1985)
West Virginia	%f	Coleoptera: Scarabaeidae	Hymenoptera	Hamilton (1933)
Kansas	%v	Coleoptera: Scarabaeidae, Carabidae	Hemiptera: Pentatomidae	Phillips (1966)
Maryland	%f	Coleoptera	Hemiptera: Pentatomidae	Griffith & Gates (1985)
British Columbia	%a	Trichoptera	Diptera	Brigham (1990)
	%a	Trichoptera	Diptera, Coleoptera	Brigham & Fenton (1991)
Alberta	%v	Coleoptera	Hemiptera	Brigham & Saunders (1990)
	%v	Coleoptera	Hemiptera, Lepidoptera†, Diptera†	Hamilton & Barclay (1998)

*%v = percentage volume of prey type in faecal or stomach sample; %f = percentage frequency of occurrence of prey type; %a = percentage abundance of prey type.
†Second major prey items in the second year of the study.

ponents of the diet (Hamilton, 1933; Ross, 1967; Black, 1972, 1974; Whitaker, 1972, 1995; Griffith & Gates, 1985; Brigham & Saunders, 1990; Hamilton & Barclay, 1998). In parts of British Columbia and Oregon the dominant prey of *E. fuscus* appears to be large caddisflies (Trichoptera), whereas beetles are relatively unimportant (Brigham, 1990; Brigham & Fenton, 1991; Verts, Carraway & Whitaker, 1999). It should be noted that dietary studies are often limited temporally (e.g. Verts *et al.*'s 1999 data were restricted to July), which may bias conclusions on overall diet in an area.

The diets of most insectivorous bats probably reflect temporal, seasonal and geographical variation in insect abundance, with some degree of flexibility in prey selection (Kunz, 1974a; Anthony & Kunz, 1977; Jones, 1990; Whitaker, 1995; Whitaker, Neefus & Kunz, 1996). *Eptesicus fuscus* has large, powerful, jaws (Freeman, 1981) and preys mainly on beetles and other hard-bodied insects (e.g. Hemipterans; Table 1; S. J. Agosta & D. Morton, unpublished data from Pennsylvania and Maryland) in regions that have been studied. However, this bat can exploit a variety of other prey types and is flexible both temporally and spatially with regard to prey use (Brigham, 1991; Whitaker, 1995; Hamilton & Barclay, 1998; S. J. Agosta & D. Morton, unpublished data).

Whitaker (1995) did the most extensive study of the food habits of *E. fuscus*, examining variation among and within maternity colonies in Indiana and Illinois. Significant variation in diet existed among and within colonies, but beetles and stink bugs (Hemiptera: Pentatomidae) comprised the majority of prey. A number of food items found by Whitaker (1995) and others (Table 1) are important agricultural pests (Table 2). Estimates of the actual numbers of these pests consumed annually by one mid-western *E. fuscu*s colony are substantial (Table 2), and the potential utility of this bat as a biological control agent for harmful insects has been emphasized (Whitaker, 1993, 1995).

Pesticides

Currently, pesticides are the primary means of controlling agricultural pests, which undoubtedly places wildlife at risk of chemical exposure (Smith, 1987; McLaughlin & Mineau, 1995). Pesticides have a variety of effects on *E. fuscus* and other bat species. These include direct mortality (Clark, Laval & Krynitsky, 1980; Clark, 1981; Clark, Clawson & Stanford, 1983), altered behaviour (Clark, 1986; Clark & Rattner, 1987) and transfer of toxins to nursing

Table 2. Agricultural pests commonly preyed on by *Eptesicus fuscus*

Pest	Common name	Estimated number consumed by a mid-western colony of 150 bats/year‡	Some crops damaged§
Chyrsomelidae			
Diabrotica			
Adults	Cucumber beetles	600 000	Cucumbers, other cucurbits, corn
Larvae*	Rootworms	33,000,000	
Pentatomidae†	Stink bugs	335 000	Soybean, cotton
Scarabaeidae	Scarab beetles	194 000	Various crops, lawns and nurseries
Cicadellidae	Leafhoppers	158 000	Various crops, including potato, apple and corn

*Secondary effect of preying on adult females.
†Mainly the Green Stink Bug (*Acrosternum hilare*).
Sources: ‡Whitaker (1995); § Davidson & Lyon (1987).

young (Clark & Lamont, 1976). The adverse effects of organochlorine pesticides (e.g. DDTs) on bats have been well-documented (Jefferies, 1972; Clark, 1981, 1988). In the US, organochlorines have been banned and replaced with organophosphate and carbamate pesticides, although organochlorine residues still persist in soils and still accumulate in some bat populations (Thies, Thies & McBee, 1996).

Organophosphate and carbamate pesticides are expected to be less toxic than organochlorines (Smith, 1987; Clark, 1988); however, some currently used pesticides reportedly cause mortality in birds and other mammals (Grue *et al.*, 1983; Smith, 1987; Augspurger *et al.*, 1996). Pesticide exposure may be an important cause of decline for some populations of insectivorous bats (Jefferies, 1972; Reidinger, 1972), particularly species whose diet includes a substantial portion of agricultural pests. McCracken (1989) concluded that pesticides are usually not a major factor in the decline of bats, and emphasized the role of roost disturbance (see below). Despite this, little field research has been conducted on the levels of exposure or the sublethal effects of these chemicals on bats (but see Swanepoel *et al.*, 1999). In addition, few studies have attempted to link pesticide exposure to specific insect prey or specific habitats where bats are foraging (Clawson & Clark, 1989). Research is also needed to address the indirect effects of pesticide use in habitats where bats forage, particularly the potential for overall reductions of the prey base.

ROOST SELECTION

Roost selection by bats has implications for a variety of life-history traits and is vital for survival and reproduction (Kunz, 1982; Tuttle & Stevenson, 1982). Roost selection often varies seasonally and roosts serve a number of functions (reviewed by Kunz, 1982). For many temperate bats, these can be separated into winter hibernacula, maternity roosts and summer roosts (males and non-reproductive females). Selection of suitable roosts is important for growth, development and survival of young (Tuttle, 1975; Tuttle & Stevenson, 1982), protection from predators (Fenton, 1983), protection from the elements (Vaughan, 1987), and reduction of thermoregulatory costs (Kurta, 1985). In addition, many bats use specific night roosts in close proximity to foraging areas (Kunz, 1982). Night roosts may function as resting places that facilitate digestion between feeding bouts and may provide opportunities for social interactions (Kunz, 1982). Thus, it is important to understand the roosting requirements of bats to ensure adequate roost protection and availability. In general, protection of only one roost type is not adequate and temporal variation in roost selection must be accounted for when determining conservation goals (Fenton, 1997; Pierson, 1998).

Eptesicus fuscus roosts in a wide variety of structures. These include caves, tunnels and mines (Rysgaard, 1942; Twente, 1955; Beer & Richards, 1956; Mumford, 1958; Phillips, 1966; Mills, Barrett & Farrell, 1975; Gates *et al.*, 1984; Dalton, 1987; Raesly & Gates, 1987), buildings (Whelden, 1941; Davis *et al.*, 1968; Brigham & Fenton, 1986; Williams & Brittingham, 1997; Whitaker & Gummer, 2000), bat boxes (Brittingham & Williams, 2000; Tuttle & Hensley, 2000) and tree cavities (Table 4). Roosts also have been located in rock crevices (Brigham, 1988), storm sewers (Goehring, 1972) and wood piles (Mills *et al.*, 1975). Most observations of *E. fuscus* roosts have come from studies that have not focused specifically on roost selection. A few studies have examined roost selection by comparing occupied vs. unoccupied sites (Table 3 and see below; for factors influencing tree-roost selection see Betts, 1996; Vonhoff, 1996; Vonhoff & Barclay, 1996; Kalcounis & Brigham, 1998; Rabe *et al.*, 1998). Such studies are necessary to understand roost selection by bats fully, especially when the goal is to develop useful conservation strategies (Crampton & Barclay, 1998).

Buildings, caves and mines

Raesly & Gates (1987) examined winter roost selection in caves and mines by several species of bats in the north-eastern US. Factors that influenced site selection by *E. fuscus* are summarized in Table 3. Among available hibernacula, *E. fuscus* selected larger caves and mines with relatively high airflow. Within hibernacula, *E. fuscus* was a solitary hibernator (but may form small clusters; Rysgaard, 1942; Mumford, 1958; Phillips, 1966; Whitaker & Gummer, 1992) that occupied relatively cool, dry cave walls in areas with noticeable airflow. Rysgaard (1942) observed similar conditions among hibernacula in Minnesota. In buildings, selection of hibernacula may be correlated with the presence of heating that maintains temperatures above freezing (Whitaker & Gummer, 1992, 2000). Buildings otherwise suitable for maternity colonies are not always utilized as hibernacula and vice versa (Whitaker & Gummer, 1992, 2000), a fact that further complicates roost protection.

Eptesicus fuscus primarily forms maternity colonies in buildings (Davis *et al*., 1968; Barbour & Davis, 1969; Mills *et al*., 1975; Whitaker & Gummer, 1992, 2000; Williams & Brittingham, 1997) but also in tree cavities (Table 4). Williams & Brittingham (1997) examined factors influencing the selection of buildings by *E. fuscus* in Pennsylvania. Important site-selection variables are summarized in Table 3. Maternity roosts were typically present in older buildings with numerous access points (see also Schowalter & Gunson, 1979; Brigham & Fenton, 1986, 1987). Occupied buildings exhibited higher daytime temperatures and wider temperature gradients than unoccupied buildings. Roost temperature is important for growth and development (Tuttle, 1975; Tuttle & Stevenson, 1982) and it is hypothesized that bats select roosts to take advantage of factors that enhance reproductive success (Brigham & Fenton, 1986; Williams & Brittingham, 1997).

Table 3. Habitat characteristics important to roost selection by *Eptesicus fuscus*

Roost type/structure	Important habitat variables§	Location
Hibernacula/cave*	Entrance area Average passage height Maximum passage height Airflow Number of entrances Minimum ambient temperature (–)¶ Maximum ambient temperature (–) Maximum wall temperature (–) Minimum relative humidity (–) % standing water (1 km^2 radius)	Maryland, Pennsylvania, West Virginia
Maternity/building†	Number of access points Building age Attic height Roof material (tin/steel) Maximum daytime temperature Temperature gradient % surrounding agriculture	Pennsylvania
Hibernacula/building‡	Heated attic** Maintenance of temperature above freezing**	Indiana, Illinois

Sources: Raesly & Gates (1987)*; Williams & Brittingham (1997)†; Whitaker & Gummer (1992)‡.
§Variables were considered important if significantly different from unoccupied sites ($P < 0.05$).
¶(–), variable less than that of unoccupied sites.
**Did not perform statistical analyses.

Roost site selection by male and non-reproductive female *E. fuscus* is not constrained by the costs of reproduction, and they are typically not associated with maternity colonies (Mills *et al*., 1975; Hamilton & Barclay, 1994); although males may occupy separate portions of maternity roosts or gradually move into maternity roosts as the young become weaned (Davis *et al*., 1968). Selection of summer roosts by *E. fuscus* has received little attention, probably because aggregations are often small and dispersed (Barbour & Davis, 1969). It is expected that, because males and non-reproductive females are not tied to maternity roosts, they select cooler roosts that facilitate entry into torpor (Hamilton & Barclay, 1994; Grinevitch, Holroyd & Barclay, 1995). Summer roosts have been found in caves and abandoned mines (Phillips, 1966) and a variety of other structures, including buildings, shutters and wood piles (Mills *et al*., 1975). Recently, bridges have been implicated as important night roosts for both male and female *E. fuscus* in the western US (Pierson, Rainey & Miller, 1996; Adam & Hayes, 2000). In the eastern US, *E. fuscus* reportedly uses caves (Davis *et al*., 1968) and mines (Agosta, Kuhn & Morton, in press) as night roosts.

Tree cavities

Although often referred to as a cave bat, *E. fuscus* also utilizes tree cavities in some regions (Table 4). Tree-roosting *E. fuscus*, primarily maternity colonies, occur mainly in the western US and Canada (Table 4). However, the current distribution of tree-roosting populations may reflect a bias in study objectives and methods (e.g. radio-tracking individuals). Brigham (1991) studied eight *E. fuscus* maternity colonies in British Columbia that primarily occupied tree cavities. This suggests that the availability of tree cavities is important to some populations. In parts of Saskatchewan, *E. fuscus* is a secondary cavity rooster, occupying Trembling Aspens (*Populus tremuloides*) excavated by Sapsuckers (*Sphyrapicus varius*) (Kalcounis & Brigham, 1998). They concluded that aspen cavities may be a limiting resource for *E. fuscus* in Saskatchewan.

Historically, *E. fuscus* probably formed maternity colonies exclusively in tree cavities (Whitaker & Gummer, 1992; Williams & Brittingham, 1997). More recently, the incidence of tree-roosting behaviour may be interpreted either as a preference for natural roosts where they are available or the use of natural roosts where buildings are not abundant (Brigham, 1991). Human development may actually have decreased the relative importance of natural roosts in regions where buildings are abundant and offer relatively large, permanent, structures. Higher fidelity by *E. fuscus* to buildings than to tree cavities (Brigham, 1991) suggests that buildings offer some advantages. Buildings may often be more abundant than tree cavi-

Table 4. Tree–roost associations of *Eptesicus fuscus* in North America

Location	Tree species	Roost type	Source
British Columbia	*Pinus ponderosa*	Maternity	Brigham (1991), Vonhoff (1996)
	Thuja plicata	Maternity	Vonhoff & Barclay (1996)
	Populus tremuloides	Maternity	Vonhoff (1996)
	Psuedotsuga menziesii	Maternity	Vonhoff (1996)
Saskatchewan	*Populus tremuloides*	Maternity	Kalcounis & Brigham (1998)
Arizona	*Pinus ponderosa*	Maternity	Rabe *et al*. (1998)
Oregon	*Pinus ponderosa*, *Populus trichocarpa*	Maternity	Betts (1996)
California	*Sequoia sempervirans*	Hibernacula	Rainey *et al*. (1992)
Maryland	*Quercus* spp.	Maternity	Christian (1956)
Michigan	*Fagus grandifolia*	Maternity	Kurta (1980)

ties near preferred habitat features (e.g. lights, water and roads) and may offer more stable microclimates.

More work is needed on tree-roost selection by *E. fuscus* to warrant a discussion on the importance of these roosts relative to building roosts (Brigham, 1991); however, previous authors discuss some important management implications (Vonhoff & Barclay, 1996; Kalcounis & Brigham, 1998). *Eptesicus fuscus* has been found roosting in trees in Michigan (Kurta, 1980) and Maryland (Christian, 1956), suggesting that this behaviour is more prevalent in the eastern US than the current literature indicates. Radio-tracking studies of *E. fuscus* in the eastern US are needed. The remainder of this discussion focuses on building-, cave- and mine-roosting populations, while acknowledging that natural tree cavities are an important component of the roosting ecology of *E. fuscus*.

Human impacts to roosts

Bats roosting in buildings, caves and mines are particularly vulnerable to human disturbance and exclusion. Human disturbance to roosts, including the activities of researchers, can have deleterious effects on resident bat populations (Mohr, 1972; Reidinger, 1972; Tuttle & Stevenson, 1982; McCracken, 1989). For example, Tuttle (1975) reported that disturbances to Gray Bat (*Myotis grisescens*) maternity colonies can result in heavy mortality of the young, who may be abandoned by fleeing females. Reidinger (1972) attributed declines in several Arizona bat populations partly to human disturbances at roosts. Recently, Thomas (1995) has shown that increased flight activity by hibernating bats occurs subsequent to human presence, which may cause premature depletion of fat reserves and increased winter mortality. This potentially important source of mortality requires more study, particularly because researchers often conduct population censuses when bats are highly aggregated in hibernacula.

Although many natural caves and mines are now protected (e.g. gated and fenced), unauthorized visitation still occurs and the effects of these disturbances have not been properly assessed in most situations. Culver *et al.* (2000) have even suggested that current methods of cave gating, while providing protection for bats, may have negative impacts on other cave fauna. Many obligate cave fauna in the US are considered vulnerable or threatened (e.g. > 95% of the terrestrial and aquatic species). Evidence that current methods of cave gating negatively impact these species may create a need for new solutions that provide protection for a broader array of cave fauna, not only bats (Culver *et al.*, 2000). Bats roosting in caves and mines are also vulnerable to environmental disturbance (e.g. floods and structural collapse). With some foresight, structural collapse and floods may be avoided, although providing protection for all roosts is probably not feasible. Caves and mines supporting large populations or high species diversity should be assessed at a state-wide level and given special concern (Gates *et al.*, 1984; Dalton, 1987; Arita, 1996).

Bats that roost in buildings are often perceived as a nuisance and are vulnerable to exclusion and eradication attempts (Brigham & Fenton, 1986, 1987; Neilson & Fenton, 1994; Williams & Brittingham, 1997; Brittingham & Williams, 2000). Little information exists on the effects of the displacement of bats from buildings on their reproductive and survival success. Radio-tracking has shown that *E. fuscus* excluded from buildings readily moves to nearby buildings, but that reproductive output may be reduced (Brigham & Fenton, 1986, 1987). Goehring (1972) observed an increase in a population of *E. fuscus* roosting in a sewer that coincided with the removal of old buildings in the area. Neilson & Fenton (1994) banded 547 Little Brown Myotis (*M. lucifugus*) prior to exclusion from buildings. Only five individuals were found to relocate to nearby buildings, suggesting a significant decline in the local population. Assuming that attempts at exclusion from buildings are similar to disturbances at caves and mines, the effects of these practices on bats may be expected to include reduced survival and reproduction. Proximate causes of these effects may include occupation of buildings with less desirable microclimates and greater distances to water and foraging areas.

SYNTHESIS

Conservation implications

As theory in conservation science shifts from a single species or closed system approach to an ecosystems approach (Minta, Kareiva & Curlee, 1999), the importance of abundant species becomes clearer. Insectivorous bats, as a group, are primary insect consumers. In this context, abundant species (e.g. *E. fuscus*, *M. lucifugus* and *Tadarida brasiliensis* in North America) probably play critical ecosystem roles (Pierson, 1998). Therefore, while in practice conservation efforts may continue to focus on rare and endangered species, relatively abundant species should be considered important for bat conservation as a whole. Continuing research to identify sources of population declines and important life-history requirements of abundant bats, so defining their conservation needs, should be useful in directing research for other species. In addition, preserving the continued abundance of abundant bats, in an otherwise declining group of mammals, is consistent with an ecosystems approach to conservation.

What lessons concerning bat conservation can we learn from the well-studied Big Brown Bat? First, this species illustrates the difficulty of applying dietary information from one area to unstudied areas. This may be particularly important when trying to monitor the prey base for potential sources of toxins or when trying to determine the extent of predation on agricultural pests. For example, the vast majority of food habits studies suggest that beetles, particularly scarab beetles (Scarabaeidae), are the major prey of *E. fuscus* throughout its range (Table 1). However, in certain areas beetles appear to be relatively unimportant, whereas large caddisflies are (Table 1). Vaughan (1997) reviewed the diets of British bats and observed that many species exhibit geographical variation in diet, but she concluded that the source of this variability was unclear. For *E. fuscus*, it is possible that either a temporal (e.g. seasonal and yearly) or spatial component is the key factor in the disparity between dietary studies. It may be significant, however, that studies where caddisflies were the dominant prey are restricted to the north-western portion of its range (Table 1). Are *E. fuscus* populations that feed primarily on caddisflies less susceptible to pesticide exposure than, for example, the mid-western colony cited in Table 2?

Secondly, a review of roost use and selection by *E. fuscus* illustrates the difficulty of providing adequate roost protection for bats. A threatened population may require simultaneous protection of a maternity roost, a variety of summer day roosts, a variety of summer night roosts, and a number of hibernacula that may or may not be different from the maternity roost. In Indiana, Whitaker & Gummer (2000) estimated that a single maternity colony of 150 *E. fuscus* will disperse into about 85 building hibernacula. Protecting roosts is further complicated by the fact that maternity roosts and hibernacula are often located in buildings that are privately owned, and the remaining roost types are difficult to locate. For *E. fuscus* and other species associated with humans, local and regional initiative is needed to encourage the public to report bat roosts routinely to state agencies or local researchers. This can best be done with continued emphasis in the media on the importance of bats and their dependence on anthropogenic structures.

A further consideration is regional differences in the relative importance of roost types. Currently it appears that distinct regional differences exist in the selection of maternity roosts by *E. fuscus* (see above); however, more work is needed to determine the relative importance of roost types in these regions (Brigham, 1991). If regional differences in roost selection do exist, caution must be taken when trying to apply information from one area to another. An important issue that needs to be addressed in the future is the degree to which populations and individuals exhibit plasticity in roost selection. Brigham (1991) compared two *E. fuscus* populations in British Columbia and Ontario and observed differences in roost structure and roost fidelity, indicating flexibility among populations. Unfortunately, long-term data are lacking on the reproductive and survival success of individual bats forced to exploit alternative roost types after former roost types or conditions become unavailable.

Future research

Several areas of research regarding the conservation and protection of *E. fuscus* populations in North America can be identified from this discussion. These should apply to other relatively abundant bat species and/or species with similar food or roost habits. In addition, the information gained from this research should allow for useful generalizations regarding bat conservation.

Effects of roost disturbance

More research is needed on the levels and effects of disturbance at *E. fuscus* roosts, particularly buildings that house maternity colonies. It is likely that many roosts have not been accounted for (Mills *et al.*, 1975; Whitaker & Gummer, 2000) and that most disturbances have gone unnoticed. In addition, public concern about rabies continues to pose threats to bats roosting in anthropogenic structures, and attempts at exclusion are likely to continue. Often, buildings (and caves and mines) may act as ecological traps (*sensu* Hassinger, 1994; Pulliam, 1996), whereby they offer suitable roost characteristics but ultimately lead to population declines because of human activities (Hassinger, 1994). This issue should be addressed, particularly in the context of source–sink dynamics (Pulliam, 1996).

More work is also needed to determine the effects of exclusion in order to develop methods that minimize human–bat conflict (Brigham & Fenton, 1987) and maximize reproductive and survival success. One option is to encourage bats to occupy alternative roosts, such as bat boxes (Williams & Brittingham, 1997; Brittingham & Williams, 2000; Tuttle & Hensley, 2000). Success in encouraging evicted maternity colonies to occupy bat boxes has been variable (Neilson & Fenton, 1994). In Pennsylvania, Brittingham & Williams (2000) have demonstrated that *E. fuscus* and *M. lucifugus* maternity colonies excluded from buildings will move successfully to bat boxes, provided the boxes are in close proximity to previous roosts and offer suitable microclimates.

Biological control

More research is needed to address the role of *E. fuscus* and other bats as biological agents for controlling harmful insects (for a review of biological control see Waage & Mills, 1992). Efforts to quantify (rather than speculate about) the potential economic benefits of bats to the agricultural industry may lead to reductions in the use of pesticides and an increase in the acceptance of bats. Demonstrating and quantifying the credibility of bats as an alternative to some pesticides will take creative manipulative experiments, such as those applied to insectivorous birds (Holmes, Schultz & Nothnagle, 1979; Atlegrim, 1989). However, the benefits to be gained from such studies should be considered. The success of projects such as Bat Conservation International's North American Bat House Research Project (Tuttle & Hensley, 2000) are encouraging, and suggest that large populations of bats (notably *E. fuscus* and *M. lucifugus*) are readily established in a variety of settings. Similar success has been reported with Brown Long-eared Bats (*Plecotus auritus*) in Europe (Boyd & Stebbings, 1989; Benzal, 1991).

Pesticides
More research is needed on the presence and levels of pesticides in bats, the presence and levels of pesticides in prey, and the effects of these pesticides on the reproduction and survival of both bats and their prey. The toxicity of different pesticides to wildlife is varied (Clark, 1981; Smith, 1987). This dictates a need for food habits studies that examine sources and types of pesticide exposure to bats. Once the important prey items are identified, efforts should be made to examine pesticide levels in insects sampled in potential foraging areas (Clawson & Clark, 1989). In addition, knowledge of the relationship between pesticide residues in bats captured at roosts and the proximity of roosts to known areas of pesticide use would be useful (Reidinger, 1972). Geographic information systems (GIS) have been used increasingly as a conservation tool and could be used to develop spatial models relating pesticide use in the surrounding landscape to risk of exposure to bats. For *E. fuscus* and other species that commonly form maternity colonies in anthropogenic structures, the well-documented detrimental effects of chemically treated wood on European bats (Racey & Swift, 1986; Mitchell-Jones *et al.*, 1989) should be a cause for concern and immediate research.

Autecological studies
Although well-studied compared with other species, more research is needed on the general ecology of *E. fuscus* throughout much of its extensive range. In addition, little attention has been given to the possibility of ecological variation between subspecies. From a conservation standpoint, more information is needed on diet and roost selection, particularly outside the US and Canada. Information on summer roost selection by male and non-reproductive female bats is practically non-existent, and factors influencing selection of night roosts are just beginning to be understood (Adam & Hayes, 2000). More information is especially needed on the relationship between prey selection and specific habitats where bats forage (J.O. Whitaker, personal communication), and on the foraging habitat preferences of bats at a landscape level (cf. Walsh & Harris, 1996a, 1996b).

Long-term population monitoring
Long-term monitoring of *E. fuscus* populations needs to be initiated or continued. Because this species is widespread, it can be found in areas impacted to varying degrees by humans. This presents the opportunity to assess the effects of various types of land use and disturbance on reproduction and survival by comparing long-term population trends. Care should be taken to design robust monitoring programmes, in which representative *E. fuscus* populations associated with different types of land use and degrees of disturbance are monitored at suitable spatial and temporal scales. Such monitoring programmes are essential to extrapolate population trends to larger scales and to make meaningful comparisons of population trends across different habitats (Gibbs, 2000). Comparing population trends under a variety of conditions (e.g. high vs. low pesticide-use areas) may help to determine what factors are limiting to *E. fuscus* populations; the factors limiting bat populations have been a long-standing question among bat biologists (Fenton, 1997).

Demographic data suitable for risk assessment
Long-term *E. fuscus* monitoring programmes should include the collection of demographic data suitable for models of risk assessment. Population viability analysis (PVA), for example,

has been used increasingly as a conservation tool to model the persistence (probability of extinction) of populations over specified periods of time, and to investigate the sensitivity of populations to changes in parameters that affect population persistence (Boyce, 1992; White, 2000). Demographic models of population persistence are often applied to small populations with some form of conservation status (e.g. endangered species). Demographic modelling may also be useful with species such as *E. fuscus* to make relative comparisons between the trajectories of populations associated with different types of land use and levels of disturbance.

A major problem with demographic modelling is obtaining empirical data to drive the models (i.e. the parameters of the model are often based on limited data or guess-work), resulting in many applications that are of little practical use for conservation and management (Beissinger & Westphal, 1998; White, 2000). Essential data needed to conduct demographic risk assessment, in which conservation and management decisions can be based, include at a minimum estimates of age-specific survivorship and fecundity. For these models to perform realistically, some estimate of spatial, temporal and individual variation in these parameters must also be available (White, 2000). Collecting data suitable for models of risk assessment thus requires long-term demographic studies at suitable spatial scales. However, conducting these studies on endangered, rare or small populations is often impossible. In such cases, White (2000) recommended using surrogate data from closely related species or species in similar ecological guilds. Although this recommendation referred to the use of long-term data sets available from game species, it can be extended to include data collected from readily studied, relatively abundant, species such as *E. fuscus*.

Currently, data suitable for demographic analysis do not exist for most bat species. One problem is that the structure and dynamics of bat populations are not well-understood (Fenton, 1997), although recent studies have elucidated the population structure of some species (Burland *et al.*, 1999; Entwistle, Racey & Speakman, 2000). Entwistle *et al.* (2000), for example, found that colonies of *P. auritus* occupying bat boxes exhibited minimal immigration and emigration and high roost fidelity, which is consistent with a metapopulation model (Hanski & Gilpin, 1997). While good data on *E. fuscus* colony size (Whitaker & Gummer, 2000) and roost fidelity (Brigham, 1991) exist for some regions, little or no data exist on immigration and emigration. Estimates of *E. fuscus* survival rates (Beer, 1955; Goehring, 1972; Mills *et al.*, 1975; Hitchcock, Keen & Kurta, 1984) and mean litter sizes (Kunz, 1974b) are available, although most studies do not include data on spatial or temporal variation in these parameters (but see Hitchcock *et al.*, 1984). The available data also come from various locations at various points in time, which would reduce the reliability of demographic models applied to real populations.

Long-term *E. fuscus* monitoring programmes are therefore needed to (i) detect changes in abundance; (ii) relate population trends to various types of land-use; and (iii) collect demographic data suitable for modelling population persistence, both for *E. fuscus* and as surrogate data for other bat species. Parallel research is also needed to determine the structure and dynamics of *E. fuscus* populations at various scales. Currently, *E. fuscus* population structure is being investigated at a regional scale (A. Turmelle *et al.*, unpublished data), which should give valuable insights into the proper scale and design of monitoring programmes.

Expanding Big Brown Bat populations?

Finally, research is needed to address the possibility of expanding *E. fuscus* populations. Historically, the abundance of *E. fuscus* in the northern portion of its range may have been limited by the availability of suitable winter hibernacula (e.g. hibernacula that maintain temperatures above freezing). Whitaker & Gummer (2000) suggested that *E. fuscus* populations are increasing in the northern portion of its range because of the availability of buildings with heated attics. One consequence of expanding *E. fuscus* populations may be competition with other bat species, particularly *M. lucifugus*, which often forms summer colonies in buildings (Whitaker & Gummer, 2000).

Competition for resources has been difficult to demonstrate with bats, primarily because experimental manipulations are extremely difficult (Findley, 1993). Researchers have documented evidence of competition between sibling bat species (Arlettaz, Perrin & Hausser, 1997) and of past competitive interactions that may have shaped some New World bat assemblages (Stevens & Willig, 1999). Recently, Arlettaz, Godat & Meyer (2000) found evidence of competition for food between *P. pipistrellus* and the Lesser Horseshoe Bat (*Rhinolophus hipposideros*) in Switzerland. They suggested that competition with expanding *P. pipistrellus* populations may contribute to dramatic declines of *R. hipposideros* in western Europe.

Comparative studies indicate little dietary overlap between *E. fuscus* and *M. lucifugus* (Whitaker, 1972; Whitaker *et al*., 1977, 1981; Griffith & Gates, 1985). If expanding *E. fuscus* populations are causing increased competitive interactions with *M. lucifugus*, competition for roosts, not food, seems likely. *Eptesicus fuscus* is twice the size of *M. lucifugus* (14–30 g and 5–14 g, respectively; Nowak, 1999) and direct (interference) competition within roosts would probably favour the larger species. Mills *et al*. (1975) observed the movement of *E. fuscus* into the attic of a church that was occupied by 600 *M. lucifugus*. After a year, the *E. fuscus* colony increased from 20 to 50 individuals while the *M. lucifugus* colony decreased by 75%. Roost sites previously occupied by *M. lucifugus*, but later occupied by *E. fuscus*, have also been reported (Cope, Whitaker & Gummer, 1991).

CONCLUSIONS

Eptesicus fuscus is unique in many North American bat assemblages in that it is often the most abundant species adapted to a hard-bodied diet (Freeman, 1981). As a result, it contributes the greatest level of consumption of certain insects, several of which are important agricultural pests. In addition, the ability of *E. fuscus* to take advantage of human-made structures as roosts and exploit a variety of foraging habitats has probably lessened any potential impact of habitat loss, and increased its abundance from historical levels (Whitaker & Gummer, 1992), as has the presence of human-induced prey concentrations (e.g. lights; Fenton, 1997). This may further the potential of this bat to be utilized as a biological agent for controlling economically important insect pests. However, this may be confounded by the fact that bats living in anthropogenic landscapes are subjected to a variety of pressures that may limit populations.

Currently, two issues complicate our ability to understand the conservation needs of bats. First, we have yet to define, unequivocally, the structure and dynamics of bat populations (i.e., what constitutes a population of bats), although important advances have been made by use of molecular genetics (Burland *et al*., 1999). Secondly, although we have a general idea of the factors negatively affecting bats (e.g. roost disturbance, pesticide exposure, habitat loss, etc.), the natural history of many species is poorly understood. Without specific information on habitat use, roost selection and diet, and how these vary over space and time, it is difficult to draw conclusions regarding species-specific conservation needs. Fortunately, studies of widely distributed and relatively common species can provide, and have provided (e.g. UK National Bat Habitat Survey; Racey, 1998), valuable information that can be built into broad conservation and management plans.

In light of these issues, the importance of abundant bats should be continually emphasized. In our race to conserve rare and endangered species, we must also conserve the abundance of species such as *E. fuscus*. Their ecosystem role may vastly exceed the role of inherently rare or currently endangered species. In addition, widespread, abundant bats such as *E. fuscus* provide a wealth of research opportunities from which we may be able to draw some general conclusions about bat conservation as a whole.

ACKNOWLEDGEMENTS

I thank Kellie M. Kuhn for useful comments on earlier versions of this manuscript, and Dr Michael A. Steele and Dr Durland Shumway for their reviews of a later version of the manuscript. Dr Robert Hilderbrand offered useful suggestions regarding the discussion of demographic modelling. Critical reviews and comments by Dr D.W. Yalden and two anonymous referees were vital to the improvement of the final manuscript. I would also like to thank Dr John O. Whitaker for his help with my research on *E. fuscus* food habits and Amy Turmelle and colleagues for allowing me to cite their current work on *E. fuscus* population structure. I am also grateful to Cal M. Butchkoski for giving K.M. Kuhn and myself the opportunity to witness the success of Pennsylvania's bat box programme, and to Dan Feller and Dr Richard L. Raesly for helping me locate bats in western Maryland. Finally, I am grateful to Dr David Morton for encouraging my research on bats.

REFERENCES

Adam, M.D. & Hayes, J.P. (2000) Use of bridges as night roosts by bats in the Oregon Coast Range. *Journal of Mammalogy*, **81**, 402–407.

Agosta, S.J., Kuhn, K.M. & Morton, D. (in press) Bat night roost at an abandoned mine in western Maryland. *Canadian Field-Naturalist*.

Anthony, E.L.P. & Kunz, T.H. (1977) Feeding strategies of the little brown bat, *Myotis lucifugus*, in southern New Hampshire. *Ecology*, **58**, 775–786.

Arita, H.T. (1996) The conservation of cave-roosting bats in Yucatan, Mexico. *Biological Conservation*, **76**, 177–185.

Arita, H.T. & Ortega, J. (1998) The middle American bat fauna: conservation in the Neotropical-Nearctic border. In: *Bat Biology and Conservation* (Ed. by T. H. Kunz & P. A. Racey), pp. 295–308. Smithsonian Institution Press, Washington, DC.

Arlettaz, R.A., Godat, S. & Meyer, H. (2000) Competition for food by expanding pipistrelle bat populations (*Pipistrellus pipistrellus*) might contribute to the decline of lesser horseshoe bats (*Rhinolophus hipposideros*). *Biological Conservation*, **93**, 55–60.

Arlettaz, R.A., Perrin, N. & Hausser, J. (1997) Trophic resource partitioning and competition between two sibling bat species *Myotis myotis* and *Myotis blythii*. *Journal of Animal Ecology*, **66**, 897–911.

Atlegrim, O. (1989) Exclusion of birds from bilberry stands: impact on insect larval density and damage to the bilberry. *Oecologia*, **79**, 136–139.

Augspurger, T., Smith, M.R., Meteyer, C.U. & Converse, K.A. (1996) Mortality of passerines adjacent to a North Carolina corn field treated with granular carbofuran. *Journal of Wildlife Diseases*, **32**, 113–116.

Barbour, R.W. & Davis, W.H. (1969) *Bats of America*. University of Kentucky Press, Lexington, KY.

Beer, J.R. (1955) Survival and movements of banded big brown bats. *Journal of Mammalogy*, **36**, 242–248.

Beer, J.R. & Richards, A.G. (1956) Hibernation of the big brown bat. *Journal of Mammalogy*, **37**, 31–41.

Beissinger, S.R. & Westphal, M.I. (1998) On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management*, **62**, 821–841.

Bell, G.P. (1980) Habitat use and response to patches of prey by desert insectivorous bats. *Canadian Journal of Zoology*, **58**, 1876–1883.

Benzal, J. (1991) Population dynamics of the brown long-eared bat (*Plecotus auritus*) occupying bird boxes in a pine forest plantation in central Spain. *Netherlands Journal of Zoology*, **41**, 241–249.

Betts, B.J. (1996) Roosting behaviour of silver-haired bats (*Lasionycteris noctivagans*) and big brown bats (*Eptesicus fuscus*) in northeast Oregon. In: *Bats and Forests Symposium*, *October 19–21*, *1995*, *Victoria*, *British Columbia* (Ed. by R. M. R. Barclay & R. M. Brigham), pp. 55–61. Working paper 23/1996. Research Branch, Ministry of Forests, Victoria, Canada.

Black, H.L. (1972) Differential exploitation of moths by the bats *Eptesicus fuscus* and *Lasiurus cinereus*. *Journal of Mammalogy*, **53**, 598–601.

Black, H.L. (1974) A north temperate bat community: structure and prey populations. *Journal of Mammalogy*, **55**, 138–157.

Boyce, M.S. (1992) Population viability analysis. *Annual Review of Ecology and Systematics*, **23**, 481–506.

Boyd, I.L. & Stebbings, R.E. (1989) Population changes of brown long-eared bats (*Plecotus auritus*) in bat boxes at Thetford forest. *Journal of Animal Ecology*, **26**, 101–112.

Brigham, R.M. (1988) *The influence of wing morphology, prey detection system and availability of prey on the foraging strategies of aerial insectivores.* PhD Thesis. York University, North York, Ontario, Canada.

Brigham, R.M. (1990) Prey selection by big brown bats (*Eptesicus fuscus*) and common nighthawks (*Chordeiles minor*). *American Midland Naturalist*, **124**, 73–80.

Brigham, R.M. (1991) Flexibility in foraging and roosting behaviour by the big brown bat (*Eptesicus fuscus*). *Canadian Journal of Zoology*, **69**, 117–121.

Brigham, R.M. & Fenton, M.B. (1986) The influence of roost closure on the roosting and foraging behaviour of *Eptesicus fuscus* (Chiroptera: Vespertilionidae). *Canadian Journal of Zoology*, **64**, 1128–1133.

Brigham, R.M. & Fenton, M.B. (1987) The effect of roost sealing as a method to control maternity colonies of big brown bats. *Canadian Journal of Public Health*, **78**, 47–50.

Brigham, R.M. & Fenton, M.B. (1991) Convergence in foraging strategies by two morphologically and phylogenetically distinct nocturnal aerial insectivores. *Journal of Zoology*, *London*, **223**, 475–489.

Brigham, R.M. & Saunders, M.B. (1990) The diet of big brown bats (*Eptesicus fuscus*) in relation to insect availability in southern Alberta, Canada. *Northwest Science*, **64**, 7–10.

Brittingham, M.C. & Williams, L.M. (2000) Bat boxes as alternative roosts for displaced bat maternity colonies. *Wildlife Society Bulletin*, **28**, 197–207.

Burland, T.M., Barratt, E.M., Beaumont, M.A. & Racey, P.A. (1999) Population genetic structure and gene flow in a gleaning bat, *Plecotus auritus*. *Proceedings of the Royal Society of London*, *B*, *Biological Sciences*, **266**, 975–980.

Burnett, C.D. (1983) Geographic and climatic correlates of morphological variation in *Eptesicus fuscus*. *Journal of Mammalogy*, **64**, 437–444.

Christian, J.J. (1956) The natural history of a summer aggregation of the big brown bat, *Eptesicus fuscus fuscus. American Midland Naturalist*, **55**, 66–95.

Clark, D.R. Jr (1981) Bats and environmental contaminants: a review. *United States Department of the Interior*, *Fish and Wildlife Service*, *Special Scientific Report-Wildlife*, **235**, 1–27.

Clark, D.R. Jr (1986) Toxicity of methyl parathion to bats: mortality and coordination loss. *Environmental Toxicology and Chemistry*, **5**, 191–195.

Clark, D.R. Jr (1988) How sensitive are bats to insecticides? *Wildlife Society Bulletin*, **16**, 399–403.

Clark, D.R. Jr & Lamont, T.G. (1976) Organochlorine residues in females and nursing young of the big brown bat (*Eptesicus fuscus*). *Bulletin of Environmental Contamination and Toxicology*, **15**, 1–8.

Clark, D.R. Jr, Clawson, R.L. & Stafford, C.J. (1983) Gray bats killed by dieldrin at two additional Missouri caves: aquatic macroinvertebrates found dead. *Bulletin of Environmental Contamination and Toxicology*, **30**, 214–218.

Clark, D.R. Jr, Laval, R.K. & Krynitsky, A.J. (1980) Dieldrin and heptachlor residues in dead gray bats, Franklin County, Missouri: 1976 versus 1977. *Pesticides Monitoring Journal*, **13**, 137–140.

Clark, D.R. Jr & Rattner, B.A. (1987) Orthene® toxicity to little brown bats (*Myotis lucifugus*): acetylcholinesterase inhibition, coordination loss, and mortality. *Environmental Toxicology and Chemistry*, **6**, 705–708.

Clawson, R.L. & Clark, D.R. Jr (1989) Pesticide contamination of endangered gray bats and their food base in Boone County, Missouri, 1982. *Bulletin of Environmental Contamination and Toxicology*, **42**, 431–437.

Constantine, D.G. (1970) Bats in relation to the health, welfare, and economy of man. In: *Biology of Bats*, Vol. II (Ed. by W. A. Wimsatt), pp. 319–449. Academic Press, New York, NY.

Cope, J.B., Whitaker, J.O. Jr & Gummer, S.L. (1991) Duration of bat colonies in Indiana. *Proceedings of the Indiana Academy of Science*, **99**, 199–201.

Crampton, L.H. & Barclay, R.M.R. (1998) Selection of roosting and foraging habitat by bats in different-aged aspen mixed wood stands. *Conservation Biology*, **12**, 1347–1358.

Cryan, P.M., Bogan, M.A. & Altenbach, J.S. (2000) Effect of elevation on distribution of female bats in the Black Hills, South Dakota. *Journal of Mammalogy*, **81**, 719–725.

Culver, D.C., Master, L.L., Christman, M.C. & Hobbs, H.H. III (2000) Obligate cave fauna of the 48 contiguous United States. *Conservation Biology*, **14**, 386–401.

Dalton, V.M. (1987) Distribution, abundance, and status of bats hibernating in caves in Virginia. *Virginia Journal of Science*, **38**, 369–379.

Davidson, R.H. & Lyon, W.F. (1987) *Insect Pests of Farm, Garden, and Orchard*, 8th edn. John Wiley and Sons, New York, NY.

Davis, W.H., Barbour, R.W. & Hassell, M.D. (1968) Colonial behavior of *Eptesicus fuscus. Journal of Mammalogy*, **49**, 44–50.

Entwistle, A.C., Racey, P.A. & Speakman, J.R. (2000) Social and population structure of a gleaning bat, *Plecotus auritus*. *Journal of Zoology, London*, **252**, 11–17.

Fenton, M.B. (1983) Roosts used by the African bat, *Scotophilus leucogaster* (Chiroptera: Vespertilionidae). *Biotropica*, **15**, 129–132.

Fenton, M.B. (1997) Science and the conservation of bats. *Journal of Mammalogy*, **78**, 1–14.

Fenton, M.B. & Rautenbach, I.L. (1998) Impacts of ignorance and human and elephant populations on the conservation of bats in African woodlands. In: *Bat Biology and Conservation* (Ed. by T. H. Kunz & P. A. Racey), pp. 261–270. Smithsonian Institution Press, Washington, DC.

Fenton, M.B., Acharya, L., Audet, D., Hickey, M.B.C., Merriman, C., Obrist, M.K., Syme, D.M. & Adkins, B. (1992) Phyllostomid bats (Chiroptera: Phyllostomidae) as indicators of habitat disruption in the Neotropics. *Biotropica*, **24**, 440–446.

Findley, J.S. (1993) *Bats: A Community Perspective*. Cambridge University Press, Cambridge, UK.

Freeman, P.W. (1981) Correspondence of food habits and morphology in insectivorous bats. *Journal of Mammalogy*, **62**, 166–173.

Furlonger, C.L., Dewar, H.J. & Fenton, M.B. (1987) Habitat use by foraging insectivorous bats. *Canadian Journal of Zoology*, **65**, 284–288.

Gates, J.E., Feldhamer, G.A., Griffith, L.A. & Raesly, R.L. (1984) Status of cave-dwelling bats in Maryland: importance of marginal habitats. *Wildlife Society Bulletin*, **12**, 162–169.

Geggie, J.F. & Fenton, M.B. (1985) A comparison of foraging by *Eptesicus fuscus* (Chiroptera: Vespertilionidae) in urban and rural environments. *Canadian Journal of Zoology*, **63**, 263–266.

Gibbs, J.P. (2000) Monitoring populations. In: *Research Techniques in Animal Ecology: Controversies and Consequences* (Ed. by L. Boitani & T. K. Fuller), pp. 213–252. Columbia University Press, New York, NY.

Goehring, H.H. (1972) Twenty-year study of *Eptesicus fuscus* in Minnesota. *Journal of Mammalogy*, **53**, 201–207.

Griffith, L.A. & Gates, J.E. (1985) Food habits of cave-dwelling bats in the central Appalachians. *Journal of Mammalogy*, **66**, 451–460.

Grinevitch, L., Holroyd, S.L. & Barclay, R.M.R. (1995) Sex differences in the use of daily torpor and foraging time by big brown bats (*Eptesicus fuscus*) during the reproductive season. *Journal of Zoology, London*, **235**, 301–309.

Grinnell, H.W. (1918) A synopsis of the bats of California. *University of California Publications in Zoology*, **17**, 223–404.

Grue, C.E., Fleming, W.J., Busby, D.G. & Hill, E.F. (1983) Assessing hazards of organophosphate pesticides to wildlife. *Transactions of the North American Wildlife Resource Conference*, **48**, 200–220.

Hamilton, I.M. & Barclay, R.M.R. (1994) Patterns of daily torpor and day-roost selection by male and female big brown bats (*Eptesicus fuscus*). *Canadian Journal of Zoology*, **72**, 744–749.

Hamilton, I.M. & Barclay, R.M.R. (1998) Diets of juvenile, yearling, and adult big brown bats (*Eptesicus fuscus*) in southwestern Alberta. *Journal of Mammalogy*, **79**, 764–771.

Hamilton, W.J. Jr (1933) The insect food of the big brown bat. *Journal of Mammalogy*, **14**, 155–156.

Hanski, I. & Gilpin, M.E. (1997) *Metapopulation Biology, Ecology, Genetics and Evolution*. Academic Press, New York, NY.

Hassinger, J.D. (1994) Ecological traps: a growing management challenge with a price tag. In: *First Annual Conference of the Wildlife Society*, Albuquerque, New Mexico. *Symposium Session 4.*

Hitchcock, H.B., Keen, R. & Kurta, A. (1984) Survival rates of *Myotis leibii* and *Eptesicus fuscus* in southeastern Ontario. *Journal of Mammalogy*, **65**, 126–130.

Holmes, R.T., Schultz, J.C. & Nothnagle, P. (1979) Bird predation on forest insects: an exclosure experiment. *Science*, **206**, 462–463.

Jefferies, D.J. (1972) Organochlorine insecticide residues in British bats and their significance. *Journal of Zoology, London*, **166**, 245–263.

Jones, G. (1990) Prey selection by the greater horseshoe bat (*Rhinolophus ferrumequinum*): optimal foraging by echolocation? *Journal of Animal Ecology*, **59**, 587–602.

Kalcounis, M.C. & Brigham, R.M. (1998) Secondary use of aspen cavities by tree-roosting big brown bats. *Journal of Wildlife Management*, **62**, 603–611.

Krusic, R.A. & Neefus, C.D. (1996) Habitat associations of bat species in the White Mountain National Forest. In: *Bats and Forests Symposium, October 19–21, 1995, Victoria, British Columbia* (Ed. by R. M. R. Barclay

& R. M. Brigham), pp. 185–198. Working paper 23/1996. Research Branch, Ministry of Forests, Victoria, Canada.

Kunz, T.H. (1974a) Feeding ecology of a temperate insectivorous bat (*Myotis velifer*). *Ecology*, **55**, 693–711.

Kunz, T.H. (1974b) Reproduction, growth, and mortality of the Vespertilionid bat, *Eptesicus fuscus*, in Kansas. *Journal of Mammalogy*, **55**, 1–13.

Kunz, T.H. (1982) Roosting ecology. In: *Ecology of Bats* (Ed. by T. H. Kunz), pp. 1–55. Plenum Press, New York, NY.

Kurta, A. (1980) *The bats of southern lower Michigan*. MSc Thesis. Michigan State University, East Lansing, MI.

Kurta, A. (1985) External insulation available to a non-nesting mammal, the little brown bat (*Myotis lucifugus*). *Comparative Biochemistry and Physiology A*, **82**, 413–420.

Kurta, A. & Baker, R.H. (1990) *Eptesicus fuscus*. *Mammalian Species*, **356**, 1–10.

McCracken, G.F. (1989) Cave conservation: special problems of bats. *Bulletin of the National Speleological Society*, **51**, 49–51.

McLaughlin, A. & Mineau, P. (1995) The impact of agricultural practices on biodiversity. *Agriculture Ecosystems and Environment*, **55**, 201–212.

Marinho-Filo, J. & Sazima, I. (1998) Brazilian bats and conservation biology: a first survey. In: *Bat Biology and Conservation* (Ed. by T. H. Kunz & P. A. Racey), pp. 282–294. Smithsonian Institution Press, Washington, DC.

Medellin, R.A., Equihua, M. & Amin, M.A. (2000) Bat diversity and abundance as indicators of disturbance in Neotropical rainforests. *Conservation Biology*, **14**, 1666–1675.

Mills, R.S., Barrett, G.W. & Farrell, M.P. (1975) Population dynamics of the big brown bat (*Eptesicus fuscus*) in southwestern Ohio. *Journal of Mammalogy*, **56**, 591–604.

Minta, S.C., Kareiva, P.M. & Curlee, A.P. (1999) Carnivore research and conservation: learning from history and theory. In: *Carnivores in Ecosystems: The Yellowstone Experience* (Ed. by T. W. Clark, A. P. Curlee, S. C. Minta & P. M. Kareiva), pp. 323–404. Yale University Press, New Haven, CT.

Mitchell-Jones, A.J., Cooke, A.S., Boyd, I.L. & Stebbings, R.E. (1989) Bats and remedial timber treatment chemicals: a review. *Mammal Review*, **19**, 93–110.

Mohr, C.E. (1972) The status of threatened species of cave-dwelling bats. *Bulletin of the National Speleological Society*, **34**, 33–47.

Mumford, R.E. (1958) Population turnover in wintering bats in Indiana. *Journal of Mammalogy*, **39**, 253–261.

Neilson, A.L. & Fenton, M.B. (1994) Responses of little brown myotis to exclusion and to bat houses. *Wildlife Society Bulletin*, **22**, 8–14.

Nowak, R.M. (1999) *Walker's Mammals of the World*, Vol. I, 6th edn. John Hopkins University Press, Baltimore, MD.

O'Donnell, C.F.J. (2000) Conservation status and causes of decline of the threatened New Zealand long-tailed bat *Chalinolobus tuberculatus* (Chiroptera: Vespertilionidae). *Mammal Review*, **30**, 89–106.

Phillips, G.L. (1966) Ecology of the big brown bat (Chiroptera: Vespertilionidae) in northeastern Kansas. *American Midland Naturalist*, **75**, 168–198.

Pierson, E.D. (1998) Tall trees, deep holes, and scarred landscapes: conservation biology of North American bats. In: *Bat Biology and Conservation* (Ed. by T. H. Kunz & P. A. Racey), pp. 309–325. Smithsonian Institution Press, Washington, DC.

Pierson, E.D., Rainey, W.E. & Miller, R.M. (1996) Night roost sampling: a window on the forest bat community in northern California. In: *Bats and Forests Symposium*, *October 19–21*, *1995*, *Victoria*, *British Columbia* (Ed. by R. M. R. Barclay & R. M. Brigham), pp. 151–163. Working paper 23/1996. Research Branch, Ministry of Forests, Victoria, Canada.

Poulson, T.L. (1972) Bat guano ecosystems. *Bulletin of the National Speleological Society*, **34**, 55–59.

Pulliam, H.R. (1996) Sources and sinks: empirical evidence and population consequences. In: *Population Dynamics in Ecological Space and Time* (Ed. by O. E. Rhodes Jr, R. K. Chesser & M. H. Smith), pp. 45–69. University of Chicago Press, Chicago, IL.

Rabe, M.J., Morrell, T.E., Green, H., deVos, J.C. Jr & Miller, C.R. (1998) Characteristics of ponderosa pine snag roosts used by reproductive bats in northern Arizona. *Journal of Wildlife Management*, **62**, 612–621.

Racey, P.A. (1998) Ecology of European bats in relation to their conservation. In: *Bat Biology and Conservation* (Ed. by T. H. Kunz & P. A. Racey), pp. 249–260. Smithsonian Institution Press, Washington, DC.

Racey, P.A. & Swift, S.M. (1986) The residual effects of remedial timber treatments on bats. *Biological Conservation*, **35**, 205–214.

Raesly, R.L. & Gates, J.E. (1987) Winter habitat selection by north temperate cave bats. *American Midland Naturalist*, **118**, 15–31.

Rainey, W.E. (1998) Conservation of bats on remote Indo-Pacific islands. In: *Bat Biology and Conservation* (Ed. by T. H. Kunz & P. A. Racey), pp. 326–341. Smithsonian Institution Press, Washington, DC.

Rainey, W.E., Pierson, E.D., Colberg, M. & Barclay, J.H. (1992) Bats in hollow redwoods: seasonal use and role in nutrient transfer into old growth communities. *Bat Research News*, **33**, 71.

Reidinger, R.F. Jr (1972) *Factors influencing Arizona bat populations*. PhD Thesis. Arizona State University, Tucson, AZ.

Richards, G.C. & Hall, L.S. (1998) Conservation biology of Australian bats: are recent advances solving our problems? In: *Bat Biology and Conservation* (Ed. by T. H. Kunz & P. A. Racey), pp. 271–281. Smithsonian Institution Press, Washington, DC.

Ross, A. (1967) Ecological aspects of the food habits of insectivorous bats. *Proceedings of the Western Foundation of Vertebrate Zoology*, **1**, 204–263.

Rysgaard, G.N. (1942) A study of the cave bats of Minnesota with especial reference to the large brown bat, *Eptesicus fuscus fuscus* (Beauvois). *American Midland Naturalist*, **28**, 245–267.

Schowalter, D.B. & Gunson, J.R. (1979) Reproductive biology of the big brown bat (*Eptesicus fuscus*) in Alberta. *Canadian Field-Naturalist*, **93**, 48–54.

Smith, G.J. (1987) *Pesticide Use and Toxicology in Relation to Wildlife: Organophosphorous and Carbamate Compounds*. Publication 170. US Fish and Wildlife Service Resources.

Stevens, R.D. & Willig, M.R. (1999) Size assortment in New World bat communities. *Journal of Mammalogy*, **80**, 644–658.

Swanepoel, R.E., Racey, P.A., Shore, R.F. & Speakman, J.R. (1999) Energetic effects of sublethal exposure to lindane on pipistrelle bats (*Pipistrellus pipistrellus*). *Environmental Pollution*, **104**, 169–177.

Thies, M.L., Thies, K. & McBee, K. (1996) Organochlorine pesticide accumulation and genotoxicity in Mexican free-tailed bats from Oklahoma and New Mexico. *Archives of Environmental Contamination and Toxicology*, **30**, 178–187.

Thomas, D.W. (1995) Hibernating bats are sensitive to nontactile human disturbance. *Journal of Mammalogy*, **76**, 940–946.

Tuttle, M.D. (1975) Population ecology of the gray bat (*Myotis grisescens*): factors influencing early growth and development. *Occasional Papers of the Museum of Natural History*, *University of Kansas*, **36**, 1–24.

Tuttle, M.D. & Hensley, L. (2000) *The Bat House Builder's Handbook*. University of Texas Press, Austin, TX.

Tuttle, M.D. & Stevenson, D. (1982) Growth and survival of bats. In: *Ecology of Bats* (Ed. by T. H. Kunz), pp. 105–150. Plenum Press, New York, NY.

Twente, J.W. Jr (1955) Aspects of a population study of cavern-dwelling bats. *Journal of Mammalogy*, **36**, 379–390.

Utzurrum, R.C.B. (1998) Geographic patterns, ecological gradients, and the maintenance of tropical fruit bat diversity: the Philippine model. In: *Bat Biology and Conservation* (Ed. by T. H. Kunz & P. A. Racey), pp. 342–353. Smithsonian Institution Press, Washington, DC.

Vaughan, N. (1997) The diets of British bats (Chiroptera). *Mammal Review*, **27**, 77–94.

Vaughan, T.A. (1987) Behavioral thermoregulation in the African yellow-winged bat. *Journal of Mammalogy*, **68**, 376–378.

Verts, B.J., Carraway, L.N. & Whitaker, J.O. Jr (1999) Temporal variation in prey consumed by big brown bats (*Eptesicus fuscus*) in a maternity colony. *Northwest Science*, **73**, 114–120.

Vonhoff, M.J. (1996) Roost-site preferences of big brown bats (*Eptesicus fuscus*) and silver-haired bats (*Lasionycteris noctivagans*) in the Pend d'Oreille Valley in southern British Columbia. In: *Bats and Forests Symposium*, *October 19–21*, *1995*, *Victoria*, *British Columbia* (Ed. by R.M.R. Barclay & R.M. Brigham), pp. 62–80. Working paper 23/1996. Research Branch, Ministry of Forests, Victoria, Canada.

Vonhoff, M.J. & Barclay, R.M.R. (1996) Roost-site selection and roosting ecology of forest-dwelling bats in southern British Columbia. *Canadian Journal of Zoology*, **74**, 1797–1805.

Waage, J.K. & Mills, N.J. (1992) Biological control. In: *Natural Enemies: The Population Biology of Predators*, *Parasites and Diseases* (Ed. by M. J. Crawley), pp. 412–430. Blackwell Scientific Publications, Oxford, UK.

Walsh, A.L. & Harris, S. (1996a) Foraging habitat preferences of vespertilionid bats in Britain. *Journal of Applied Ecology*, **33**, 508–518.

Walsh, A.L. & Harris, S. (1996b) Factors determining the abundance of vespertilionid bats in Britain: geographic, land class, and local habitat relationships. *Journal of Applied Ecology*, **33**, 519–529.

Warner, R.M. (1985) Interspecific and temporal dietary variation in an Arizona bat community. *Journal of Mammalogy*, **66**, 45–51.

Whelden, R.M. (1941) Hibernation of *Eptesicus fuscus* in a New Hampshire building. *Journal of Mammalogy*, **22**, 203.

Whitaker, J.O. Jr (1972) Food habits of bats from Indiana. *Canadian Journal of Zoology*, **50**, 877–883.

Whitaker, J.O. Jr (1993) Bats, beetles and bugs: more big brown bats mean less agricultural pests. *Bats*, **11**, 23.

Whitaker, J.O. Jr (1995) Food of the big brown bat *Eptesicus fuscus* from maternity colonies in Indiana and Illinois. *American Midland Naturalist*, **134**, 346–360.

Whitaker, J.O. Jr & Gummer, S.L. (1992) Hibernation of the big brown bat, *Eptesicus fuscus*, in buildings. *Journal of Mammalogy*, **73**, 312–316.
Whitaker, J.O. Jr & Gummer, S.L. (2000) Population structure and dynamics of big brown bats (*Eptesicus fuscus*) hibernating in buildings in Indiana. *American Midland Naturalist*, **143**, 389–396.
Whitaker, J.O. Jr, Maser, C. & Cross, S.P. (1981) Food habits of eastern Oregon bats based on stomach and scat analysis. *Northwest Science*, **55**, 281–292.
Whitaker, J.O. Jr, Maser, C. & Keller, L.E. (1977) Food habits of bats of western Oregon. *Northwest Science*, **51**, 46–55.
Whitaker, J.O. Jr, Neefus, C. & Kunz, T.H. (1996) Dietary variation in the Mexican free-tailed bat (*Tadarida brasiliensis mexicana*). *Journal of Mammalogy*, **77**, 716–724.
White, G.C. (2000) Population viability analysis: data requirements and essential analysis. In: *Research Techniques in Animal Ecology: Controversies and Consequences* (Ed. by L. B. Boitani & T. K. Fuller), pp. 288–331. Columbia University Press, New York, NY.
Williams, L.M. & Brittingham, M.C. (1997) Selection of maternity roosts by big brown bats. *Journal of Wildlife Management*, **61**, 359–368.
Zielinski, W.J. & Gellman, S.T. (1999) Bat use of remnant old-growth redwood stands. *Conservation Biology*, **13**, 160–167.

Submitted 6 December 2000; returned for revision 15 May 2001; revision accepted 12 October 2001