American Burying Beetle

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Nicrophorus americanus - Olivier

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American Burying Beetle (ABB)
Nicrophorus americanus

Executive Summary

The American burying beetle (Nicrophorus americanus, ABB) is the largest silphid (carrion beetle) in North America, reaching 1.0 to 1.8 inches (2.5-4.5 cm) in length (Wilson 1971, Anderson 1982, Backlund and Marrone 1997). The most diagnostic feature of the ABB is the large orange-red marking on the raised portion of the pronotum (hard back plate of the front portion of the thorax of insects), a feature shared with no other members of the genus in North America (USFWS 1991). The ABB is a nocturnal species that lives only for one year. The beetles are active in the summer months and bury themselves in the soil for the duration of the winter. Immature beetles (tenerals) emerge in late summer, over-winter as adults, and comprise the breeding population the following summer (Kozol 1990a). Adults and larvae are dependent on carrion (animal carcass) for food and reproduction. They must compete for carrion with other invertebrate and vertebrate species.

Having wings, ABBs are strong fliers and have been reported moving distances ranging from 0.10 to 18.14 miles (0-29.19 kilometers) in various parts of their range (Bedick et al. 1999, Creighton and Schnell 1998, Jurzenski 2012, Jurzenski et al. 2011, Schnell et al. 1997-2006). In Oklahoma, ABBs have been recorded to move up to 10 km (6.2 miles) in 6 nights (Creighton and Schnell 1998). Carrion selection by adult ABBs for food can include an array of available carrion species and size (Trumbo 1992). ABBs also capture and consume live insects (Louis Perrotti, Roger Williams Park Zoo, Species Survival Plan administrator). Immediately upon emergence from their winter hibernation, ABBs begin searching for a mate and a proper carcass for reproduction.

Once ABB locate a suitable carcass for reproduction, inter-specific as well as intra-specific competition occurs until usually only a single dominant pair of male and female burying beetles remain (Scott and Traniello 1989). The carcass is formed into a ball and treated with the beetle's oral and anal secretions (containing antimicrobial components) (Hoback et al. 2004, Kaspari and Stevenson 2008, Rozen et al. 2008). Oviposition (laying of eggs) generally occurs within 24 hours of carcass discovery (Trumbo 1997) and is adjusted proportionately to the carcass size (Billman et al. 2014). Parental care in species of this genus is elaborate, with both parents participating in carcass burial, as well as in feeding and protecting their brood until the young disperse into the soil to pupate (Bartlett, 1988; Fetherston et al., 1990; Scott, 1990; Trumbo, 1991). The level of reproductive investment in burying beetles is influenced by both age and prior reproductive experience (Billman et al. 2014.)

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Soil conditions for suitable ABB reproductive habitat must be conducive to excavation by ABBs (Anderson 1982; Lomolino and Creighton 1996). Research indicates that brood carcasses were most likely to be buried in loose soils with high sand content and low clay content (Lomolino et al. 1995, Lomolino and Creighton 1996, Creighton et al. 1993, Smith 2007). Additionally, trapping success increased with the percentage of sand but decreased with percentage of silt and clay (lomolino et at. 1995). Level topography and a well formed detritus layer at the ground surface are typical of occupied ABB habitat (USFWS 1991).

ABBs are considered feeding habitat generalists and have been successfully live-trapped in several vegetation types including native grasslands, grazed pasture, riparian zones, coniferous forests, mature forest, deciduous forest with little undergrowth, and oak-hickory forest, as well as on a variety of soil types (Creighton et al. 1993; Lomolino and Creighton 1996; Lomolino et al. 1995; USFWS 1991, USFWS 2008b, Walker 1957). ABBs are widely believed to depend on landscape-level heterogeneity of habitat that supports the small mammals, birds and other sources of carrion necessary for their life cycle. A diverse habitat of patches of woodland, shrubland, forests and herbaceous areas are believed to be key elements for good ABB habitat (Personal communication with Daniel Howard, Assistant Professor of Biology, Augustana College, South Dakota).

Population estimates of ABB are problematic and precise estimates of absolute or even relative densities remain a challenge (USFWS 2008a). ABBs experience relatively rapid turnover rates due to factors such as natural mortality, dispersal, and burrowing underground and attending carrion/broods (Creighton and Schnell 1998). Because the ABB completes its lifecycle in one year, each year's population levels are largely dependent on the reproductive success of the previous year. Therefore, populations may be cyclic (due to weather, disease, etc.), with high numbers and abundance in one year, followed by a decline in numbers the succeeding year, or vice versa (USFWS 2008a).

Habitat fragmentation causes increased vertebrate scavenger pressure, which decreases availability of carrion of the appropriate size, and increases competition between burying beetles (Creighton et al. 2007). There is little doubt that habitat loss and alteration affect this species at local or even regional levels, and could account for the extirpation of populations once they become isolated from others (Kozol 1995, Ratcliffe 1996, Amaral et al. 1997, Bedick et al. 1999). It is unclear if an extirpated ABB population can successfully be re-established. Protection of large areas of appropriate native habitat appears to be the best known method for enhancing the conservation of the ABB. Relatively large areas of native habitat tend to support the highest known ABB populations.

The American Burying Beetle Recovery Plan (USFWS 1991) and the 5-year status review of the species (2008a) identify the following factors as potential threats to the ABB:

disease/pathogens, DDT, direct habitat loss and alteration, interspecific competition, increase in competition for prey, increase in edge habitat, decrease in abundance of prey, loss of genetic diversity in isolated populations, agricultural and grazing practices, and invasive species. None of these threats alone adequately explain why the ABB declined while congeneric species are still relatively common rangewide – there are eight sympatric congeners which are not in peril (Sikes and Raithel 2002).

The prevailing theory regarding the ABBs' decline is habitat fragmentation (USFWS 1991) which: (1) reduced the carrion prey base of the appropriate size for ABB reproduction, and (2) increased the vertebrate scavenger competition for this prey (Kozol 1995, Ratcliffe 1996, Amaral et al. 1997, Bedick et al. 1999) due to the ABBs relatively large size and specialized breeding behavior (Creighton et al. 2007). Although much of the evidence suggesting the reduction of carrion resources as a primary mechanism of decline is circumstantial, this hypothesis fits the temporal and geographical pattern of the disappearance of ABBs, and is sufficient to explain why ABBs declined while related species did not. In a fragmented ecosystem, larger species have been shown to be negatively affected before smaller species, a phenomenon that has been well-documented with carrion and dung beetles in South America (Klein 1989).

Since the middle of the 19th century, certain animal species in the favored weight range for ABBs have either been eliminated from North America or significantly reduced over their historic range (USFWS 1991), including the passenger pigeon (*Ectopistes migratorius),* greater prairie-chicken (*Tympanchus cupido)* and wild turkey *(Meleagris gallopavo)*. Fragmentation of large contiguous habitats into smaller pieces or patches of habitat may increase species richness, but the species composition usually changes. In this way, historically large expanses of natural habitat that once supported high densities of indigenous species are now artificially fragmented, supporting fewer or lower densities of indigenous species that once supported ABB populations, and also facilitating increased competition for limited carrion resources among the "new" predator/scavenger community.

Kozol et al. (1994) examined ABB genetic variation within and between the Block Island, Rhode Island population and the eastern Oklahoma and western Arkansas population. Both populations have low levels of genetic variation, and most of the variation occurs within a single population. There were no unique diagnostic bands within either population, but they found the Oklahoma- Arkansas population to be somewhat more diverse. Reduced genetic variation is often a result of founder effect, genetic drift, and inbreeding.

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AMERICAN BURYING BEETLE (ABB) *NICORPHORUS AMERICANUS*

SPECIES ACCOUNT

Species Description

American burying beetle *Nicrophorus americanus*
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The ABB (at right) is the largest silphid (carrion beetle) in North America, reaching 1.0 to 1.8 inches in length (Wilson 1971, Anderson 1982, Backlund and Marrone 1997). Size, particularly pronotal width, is highly correlated with weight (Kozol et al. 1988). Pronotal width of ABBs ranged from 0.344 – 0.500 inches (.874 – 1.27 centimeters) in a laboratory study and 0.314 – 0.497 inches (.800 – 1.26 cm) at Block Island. The beetles are black with orange-red markings. The hardened elytra (wing coverings) are smooth, shiny black, and each elytron has two scallop shaped orange-red markings. The pronotum over the mid-section between the head and wings, is circular in shape with flattened margins and a raised central portion. The most diagnostic feature of the ABB is the large orange-red marking on the raised portion of the pronotum, a feature shared with no other members of the genus in North America (USFWS 1991). The ABB also has orange-red frons (the upper, anterior part of the head), and a single orange-red marking on the clypeus, which is the lower face located just above the mandibles. Antennae are large, with notable orange club-shaped tips.

Figure 2: Depicts the characteristics for determining male American burying beetle

Gender can be determined from markings on the clypeus **Figure 2**; males have a large, rectangular, red marking and females have a smaller, triangular, red marking. Age of adults is determined by intensity of appearance. The photo at the left demonstrates the markings of teneral ABBs (young beetles emerging after pupation, usually in summer but have been reported in the spring in Oklahoma by surveyors) are brighter and appear more uniform in color, while the exoskeleton is softer and in general more translucent. The pronotum of a mature, early summer adult tends to be darker than the

markings on its elytra, with the former appearing dark orange to red and the latter appearing orange. The senescent (mature, post-breeding) ABB has pale elytral markings and are more scarred. They often have pieces missing from the margin of the pronotum or elytra, have cracks in the exoskeleton, and/or are missing appendages such as tarsi, legs, or antennae (USFWS 2008a).

Life History

The life history of the ABB is similar to that of other burying beetles (Kozol et al. 1988; Scott and Traniello 1987; Wilson and Fudge 1984). The ABB is a nocturnal species that lives only for one year. Beetles are active in the summer months and bury themselves in the soil for the duration of the winter. Immature beetles (tenerals) usually emerge in late summer, over-winter as adults, and comprise the breeding population the following summer (Kozol 1990a). Adults and larvae are dependent on carrion for food and reproduction. They must compete for carrion with other invertebrate species, as well as vertebrate species.

Inactive Period: When the nighttime ambient air temperature is consistently below 60°F (15.5°C), ABBs bury into the soil and become inactive (USFWS 1991). In Oklahoma, this typically occurs from late September and until mid-May (USFWS 2008b), approximately 8 to 9 months. However, the length of the inactive period can fluctuate depending on temperature. Recent studies indicate that ABBs bury to depths ranging from 0 to 8 inches in Arkansas (Schnell et al. 2007). Others have found depths ranging from 0 – 27 inches (Hoback 2011). Habitat structure (i.e., woodland vs. grassland) does not appear to be an influencing factor in over-winter survival rate in Oklahoma (Holloway and Schnell 1997).

Preliminary data suggest that over-wintering results in significant mortality (Bedick et al. 1999), ranging from 25 percent to about 70 percent depending on year, location, and availability of carrion in the fall (Schnell et al. 2007; Raithel 1996-2002, unpublished data, as cited in USFWS 2008b). Over-wintering ABBs with access to a vertebrate carcass in the fall had a survival rate of 77 percent versus a 45 percent survival rate for ABBs that did not have access to a carcass (Schnell et al. 2007).

Active Period: In Oklahoma, ABBs are typically active from mid-May to mid-September. ABBs emerge from their winter inactive period when ambient nocturnal air temperatures consistently exceed 60º F and become inactive in the fall when nighttime air temperatures are below 60°F. They are most active from two to four hours after sunset, with no captures recorded immediately after dawn (Walker and Hoback 2007, Bedick et al. 1999). During the daytime, ABBs are believed to bury under the vegetation litter. ABBs begin rearing broods soon after emergence from overwintering. During late May and early June ABBs secure a mate and

carcass for reproduction. The reproductive process takes approximately 50-60 days (Kozol 1992).

Weather conditions, such as rain and strong winds, result in reduced ABB activity (Bedick et al. 1999). However, on Block Island, Rhode Island, burying beetles were successfully trapped repeatedly on both rainy and windy nights, provided the temperature was above 59º F (15º C, Kozol et al. 1988). Capture rates for ABBs are highest from mid-June to early-July and again in mid-August (Kozol et al. 1988, Bedick et al. 2004, USFWS 1991) across the more northern latitudes within the range of the species, however survey data shows captures per unit effort in Oklahoma for ABB is highest in July (unpublished Service data).

Movement

Figure 3. An ABB takes flight. ABB has been recorded moving 29.19 kilometers in one night (Jurzenski 2012). Photo credit: Aaron Goodwin.

ABBs are nocturnal and have shown limited capabilities to fly during heavy rains, and high winds. Although data is lacking, ABBs have been reported moving distances ranging from 0.10 to 18.14 miles (1 to 29.19 km) in various parts of their range (Bedick et al. 1999, Creighton and Schnell 1998, Jurzenski 2012, Jurzenski et al. 2011, Schnell et al. 1997-2006). The Service has

re-evaluated the published literature, both new and old, to describe ABB movement, and to among other things, develop live-trapping guidance. Survey data for ABBs in Oklahoma has documented both positive and negative ABB survey results in the same calendar year and even the same ABB active season within the same general location. The number of traps and the relative distance between them may influence the capture of *N. americanus* (Bedick 2004). Placing traps in proximity to other traps may decrease individual trap success rates as multiple traps compete for the same localized population (Bedick et al. 2004). American burying beetles can be attracted to carrion from distances ranging from 0.16-6.2 miles (0.25–10.0 km) over a six night period with an average of 0.76 miles per night (1.23 km per night – Creighton and Schnell 1998), and Peyton (1996) recovered a specimen from as far away as 7 miles (11.2 km.) Bedick et al. (2004) reported five recaptures from distances of 2-4 miles (3–6 km) and an average nightly movement of 0.62 mile (1 km) within the large proportion (85%) of recaptures, moving distances of 0.31 mile (0.5 km) per night.

Creighton *et al.* (1992) reported that individual ABBs moved over 4 miles (6.4 km) in only a few days. Creighton and Schnell (1998) reported an average nightly movement of 0.76 mile (1.23 km), and maximum distances of 4 miles (6.5 km) in 5 nights (0.8 mile per night – 1.28 km per night) and 6.2 miles (10 km) in 6 nights (1.03 miles per night – 1.66 km per night), a minimum distance of 0.15 mile (0.24 km) in one night, and a mean nightly movement of 1.67 miles (2.70 km). Mark and recapture data at Camp Gruber and Fort Chaffee did not find any ABBs that moved between these installations, a distance of about 54 miles (87 km – Schnell and Hiott, 1997-2003). But in Nebraska, one ABB was recently reported to move, wind-aided, approximately 18.14 miles (29.19 km) in one night (Jurzenski et al. 2011) establishing the longest record of a 1-night movement by an ABB, demonstrating an increase to the previously poorly understood potential dispersal distance. Bedick et al. (1999) chose to use 1 km (0.6 miles) for the radius of attractiveness for traps since this corresponded to a reasonable distance in which ABB are known to respond to traps. Taking all this information into account, the effective radius for a survey transect was determined to remain at 0.5 mile (0.8 km).

Feeding

When not involved with brood rearing, carrion selection by adult ABBs for food can include an array of available carrion species and sizes (Trumbo 1992), as well as capturing and consuming live insects. Burying beetles are capable of finding a carcass between one and 48 hours after death at a distance up to 2 miles (3.22 km) but finding them after a day or two is more customary (Ratcliffe 1996). Success in finding carrion depends upon many factors including availability of optimal habitats for small vertebrates (Lomolino and Creighton 1996), density of competing invertebrate and vertebrate scavengers, individual searching ability, reproductive condition, and temperature (Ratcliffe 1996, Wilson and Knollenberg 1984). Kozol et al. (1988) found no significant difference in the ABB's preference for avian verses mammalian carcasses.

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Habitat

Feeding Habitat: ABBs are considered feeding habitat generalists and have been successfully live-trapped in several vegetation types including native grasslands, grazed pasture, riparian zones, coniferous forests, mature forest, deciduous forest with little undergrowth, and oak-hickory forest, as well as on a variety of various soil types (Creighton et al. 1993; Lomolino and Creighton 1996; Lomolino et al. 1995; USFWS 1991, USFWS 2008b, Walker 1957). Ecosystems supporting ABB populations are diverse and include primary forest, scrub forest, forest edge, grassland prairie, riparian areas, mountain slopes, and maritime scrub communities (Ratcliffe 1996; USFWS 1991). The ABB readily moves between different habitats (Creighton and Schnell 1998, Lomolino et al. 1995) (USFWS 2008b).

Using baited pitfall traps, Holloway and Schnell (1997), found significant correlation between the number of ABBs captured and the biomass of mammals (0-200 g), and combined mammals and birds at Fort Chaffee, Arkansas. ABBs are widely believed to depend on landscape-level heterogeneity of habitat that supports the small mammals, birds and other sources of carrion necessary for their life cycle. A diverse habitat of patches of woodland, shrubland, forests and herbaceous areas are believed to be key elements for good ABB habitat. It is the interspersion of the vegetative cover types that creates discontinuity of habitat needed for these carrion species.

Soil conditions for ABB habitat must be conducive to excavation by ABBs (Anderson 1982; Lomolino and Creighton 1996). Soils in the vicinity of captures are all well drained and include sandy loam and silt loam, with a clay component noted at most sites. Level topography and a well formed detritus layer at the ground surface are common (USFWS 1991). At Fort Chaffee, ABBs were captured in areas where the soils contained less than 40 percent sand, greater than 50 percent silt, and greater than 20 percent clay (Schnell and Hiott 2005). In 1996, more than 300 ABBs were captured in Nebraska habitats consisting of grassland prairie, forest edge, and scrubland (Ratcliffe 1996).

Reproduction Habitat: While studies indicate that the ABB is a habitat generalist in terms of feeding, it is likely more restricted when selecting burial sites for breeding. It is widely understood that ABB needs to bury a carcass in the soil for reproduction, and soils that are too hard or too compact may limit the ability of ABB to create a suitable brood chamber. Likewise, soils that are too loose, such as those with too much sand, will not support the walls of the chamber and therefore also are not suitable for brood chambers. Moreover, ABBs are subject to drowning, so soils that are saturated are unsuitable for reproduction. Therefore, certain soil conditions such as very xeric (dry), or loose soils , sandy soils,and saturated, are generally accepted to be unsuitable for carcass burial and thus are unlikely reproductive habitats.

Anderson (1982) postulated that paired ABBs placed on carcasses would be more reproductively successful in forested habitats due to the rich, loose soils conducive to digging. Lomolino and Creighton (1996) found reproductive success was higher in forest verses grassland habitat, because more carcasses were buried in the forested habitat than the grassland. Carcasses may be more difficult to secure in grassland due to the near absence of a litter layer and may be more difficult to bury due to the tendency of grassland soils to be more compact than those in forests. However, of the carcasses buried in the two different habitats, brood size did not seem to be influenced by habitat characteristics. In Oklahoma, ABBs are thought to select undisturbed, mature oak-hickory forests with substantial litter layers and deep, loose soils as well as grasslands or bottomland forests where the substrate is conducive for carcass burial (Lomolino and Creighton 1996; Creighton et al. 1993). Holloway and Schnell (1997) found significant correlations between the numbers of ABBs caught in traps and the biomass of mammals and birds, irrespective of the predominant vegetation (USFWS 2008b) suggesting that the habitat *per se* is not the key environmental driver for occupation of an area by ABB, but rather the density of their reproductive resources (small mammals and birds) found within those habitats.

Reproduction

Reproductive activity usually begins in mid-May to June once temperatures become suitable and is thought to be complete by mid-August to September while temperatures are suitable (see Life History section). Immediately upon emergence from their winter hibernation, ABBs begin searching for a mate and proper sized carcass for reproduction. Burying beetles are capable of finding a carcass between one and 48 hours after death at a distance up to 2 miles (3.22 km – Ratcliffe 1996), but finding them after a day or two is more customary (Conley 1982, Ratcliffe 1996). Success in finding carrion depends upon many factors including availability of optimal habitats for small vertebrates (Lomolino and Creighton 1996), density of competing invertebrate and vertebrate scavengers, individual searching ability, reproductive condition, and temperature (Ratcliffe 1996, Wilson and Knollenberg 1984). ABB has shown no preference for avian verses mammalian carcasses (Kozol et al. 1988). Once a carcass has been found, inter-specific as well as intra-specific competition occurs until usually only a single dominant male and female burying beetle remain (Scott and Traniello 1989). The ABB typically out-competes other burying beetles as a result of its larger size (Kozol et al. 1988). Once the ABB battle for the rights to the carcass, the victorious couple will bury the carrion and construct a brood chamber around the carcass.

Parental care in this genus is elaborate and unique because both parents participate in the rearing of young (Bartlett 1987, Fetherston et al. 1990, Scott 1990, and Trumbo 1990), with care by at least one parent, usually the female, being critical for larval survival (Ratcliffe 1996). In Nebraska, Bedick et al. (1999) found that ABBs reproduce only once per year. However, in a

laboratory setting, Lomolino and Creighton (1993) found that five of eight ABB pairs succeeded in producing a second brood. Further, research into reproduction in burying beetles revealed that the level of reproductive investment in burying beetles is influenced by both age and prior reproductive experience. Females reproducing on low-quality carcasses allocated more to future reproduction by producing smaller offspring and gaining more mass than females on high-quality carcasses (Billman et al 2014).

Male and female ABBs typically cooperatively bury a carcass, but individuals of either sex are capable of burying a carcass alone (Kozol et al. 1988). Once underground, both parents strip the carcass of fur or feathers, roll the carcass into a ball and treat it with anal and oral secretions that retard the growth of mold and bacteria. The female ABB lays eggs in the soil near the carcass. Brood sizes of ABBs can sometimes exceed 25 larvae, but 12-18 is more typical (Kozol 1990b).

One or both of the parents may remain with the pupae for several days and at least one parent, usually the female, may remain with the pupae until they pupate (Kozol 1995). The reproductive process from carcass burial to eclosure (emergence from pupae) is about 48 to 65 days (Bedick et al. 1999, Kozol 1995, Ratcliffe 1996). Females are reproductively capable immediately upon eclosure. Young beetles emerging in summer over-winter as adults, and comprise the breeding population the following summer (Kozol 1990a).

While the ABB has life history requirements similar to other carrion beetles, it is the largest *Nicrophorus* in North America and requires a larger carrion item to reach its maximum reproductive potential (i.e., to raise a maximum number of offspring) than the other burying beetles (USFWS 1991, Kozol et al. 1988, Trumbo 1992, Billman et al 2014). Preferred carrion sources for reproduction are dead birds and mammals weighing from 1.7-10.5 ounces (48.19 – 297.67 g), with an optimum weight of 3.5-7.0 ounces (99.22 – 198.45 g, USFWS 1991).

Status and Distribution

Status: The ABB was proposed for federal-listing in October 1988 (53 FR 39617) and designated as an endangered species on July 13, 1989 (54 FR 29652), and retains this status. Critical habitat has not been designated for the ABB. The Final Recovery Plan was signed on September 27, 1991. At that time (1991), only two, disjunct, natural populations occurred at the extremities of the species historical range of 35 states, i.e., four counties in Oklahoma and one small island off the coast of Rhode Island (USFWS 2008a). Due to the severity of the species decline, and uncertainty about the causes for that decline, recovery actions were focused on near-term improvement on the status of the species, rather than addressing a more broad range of actions and criteria to bring about full recovery. Therefore, criteria were developed

for downlisting, but not for recovery (USFWS 1991, 2008a). Recovery objectives from the 1991 recovery plan and the criteria for achieving them are provided below.

(1) Reduce the immediacy of the threat of extinction…,

- Protect and maintain the two extant populations (i.e., in 1991),
- Re-establish (or locate and protect) at least two additional self-sustaining wild populations of 500 or more animals each, one in the eastern and one in the western part of the species historic range

(2) Improve status of ABB so that it can be reclassified from endangered to threatened.

- Re-establish three populations of the species (or discover additional populations) within each of four broad geographical areas of its historical range: the Northeast, the Southeast, the Midwest and the Great Lakes States…;
- Each population should contain a minimum of 500 adults as estimated by capture rates per trap night and black lighting effort; and
- Each population is to be demonstrably self-sustaining for at least five consecutive years (or is sustainable with established long-term management programs).

Figure 3: The three broad geographic areas described in the 1991 ABB Recovery Plan

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Since the Recovery Plan was developed in 1991, numerous other populations have been discovered, and the recovery objective of reducing the immediate threat of extinction through discovery or establishment of new populations has been met (USFWS 2008a). Currently, at least four EPA Level III eco-regions support ABB populations estimated at greater than 1,000 ABBs (USFWS 2008a). Based on extinction modeling, Amaral et al. (2005) surmised that populations of greater than 1,000 ABBs have the potential to remain demographically viable over the long term in the absence of severe catastrophic events or reductions in carrying capacity through reduced carcass availability, habitat loss or fragmentation. However, the 2008 five year review (USFWS 2008a) found that, based on the information available, the ABB remains endangered throughout its current range due to lack of populations in the Southeast and Great Lakes States and remaining threats to existing populations (USFWS 2008a).

Distribution: Historically, the geographic range of the ABB included over 150 counties in 35 states, covering most of temperate eastern North America and the southern borders of three eastern Canadian provinces (USFWS 1991; Peck and Kaulbars 1987). However, documentation of records is not uniform throughout the broad historical range. More records exist from the Midwest into Canada and in the northeastern United States than from the southern Atlantic and Gulf of Mexico region (USFWS 1991). During the 20th century, the ABB disappeared from over 90 percent of its historical range (Ratcliffe 1995). The last ABB specimens along the mainland of the Atlantic seaboard, from New England to Florida, were collected in the 1940s (USFWS 1991). At the time of listing, known populations were limited to one on Block Island, Rhode Island; and one in Latimer County, Oklahoma. After the species was listed in 1989, survey efforts increased and the ABB was discovered in more locations, particularly in South Dakota, Nebraska and Oklahoma.

Currently, the ABB is known to occur in eight states: on Block Island off the coast of Rhode Island, Nantucket Island off the coast of Massachusetts, eastern Oklahoma, western Arkansas (Carlton and Rothwein 1998), Loess Hills in south-central Nebraska and Sandhills in north-central Nebraska (Ratcliffe 1996, Bedick et al. 1999), Chautauqua Hills region of southeastern Kansas (Sikes and Raithel 2002), south-central South Dakota (Backlund and Marrone 1995, Ratcliffe 1996), northeast Texas (Godwin 2003), and Missouri (personal communication with Bob Mertz, St. Louis Zoo, May 30, 2013). The ABBs in Missouri are part of a nonessential experimental population (under section 10(j) of the ESA) that was reintroduced in 2012. Most populations are located on private land. Populations known to exist on public land include: Ouachita National Forest, Arkansas / Oklahoma; Ozark-St. Francis National Forests, Arkansas; Camp Gruber, Oklahoma; Fort Chaffee, Arkansas; Lake Eufaula, Oklahoma; Sequoyah National Wildlife Refuge, Oklahoma; Block Island National Wildlife Refuge, Rhode Island; Valentine National Wildlife Refuge, Nebraska; and Camp Maxey, Texas.

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Confirmed Oklahoma ABB sightings since 1992 include the following counties: Atoka, Bryan, Cherokee, Choctaw, Coal, Craig, Creek, Haskell, Hughes, Johnston, Latimer, Le Flore, Marshall, Mayes, McCurtain, McIntosh, Muskogee, Okfuskee, Okmulgee, Osage, Pittsburg, Pontotoc, Pushmataha, Rogers, Seminole, Sequoyah, Tulsa, and Wagoner, and Washington (29 counties). Additional counties with ABB habitat and potential occurrence due the proximity to the above counties include: Adair, Carter, Delaware, Garvin, Kay, Lincoln, Love, McClain, Murray, Nowata, Ottawa, Pawnee, Payne, and Pottawatomie.

Numerous ABB surveys have been conducted throughout eastern Oklahoma. The majority of these surveys are undertaken to determine whether ABBs were located in areas anticipated to have soil disturbance actions associated with development projects. Most survey data are collected sporadically and without systematic or complete coverage across Oklahoma. Presently, eastern Oklahoma contains a large concentration of ABBs within their historical range. The population of ABBs at Camp Gruber has shown persistence since 1991 when annual surveys on the installation were initiated. While the numbers and high density areas of ABBs have changed annually or biennially, indicating ABBs are typically a cyclic species (Schnell and Hiott, 2003), they appear to be a self-sustaining population or metapopulation. In 2007, a total of 676 ABBs were captured in 1,305 trap nights at Camp Gruber. In 2009, a total of 423 ABBs were captured at the 59 stationary locations at Camp Gruber.

In 2010, reports from researchers at The Nature Conservancy's Tallgrass Prairie Preserve in Osage County indicated a healthy population of approximately 1,400 ABBs (C Hall, Augustana College, pers.comm. 2011). Camp Gruber and the Tallgrass Prairie Preserve represent high densities of ABBs localized into smaller areas. In Texas, the ABB has been found on Camp Maxey, Lamar County from 2004 - 2008, and a single ABB was documented at the Nature Conservancy's Lennox Woods, Red River County in 2004. No ABBs have been documented at Camp Maxey from 2009 - 2012, despite intensive surveying.

The sentinel population of ABBs on Block Island off the coast of Rhode Island is stable, as is the population of ABBs in southern Tripp County, South Dakota. The moderately large Nebraska Loess Hills population was thought to be declining in 2006 and 2007, but that short-term decline was likely caused by the effects of drought on carrion availability (W. Hoback, University of Nebraska, pers. comm., March 24, 2011) and the population there has increased in recent years with relief from the drought. Based on trapping efforts over the last 2 years in the Nebraska Sandhills, many more ABBs occur in that population than previously recognized. In 2010, more than 1,000 ABBs were trapped on and near Project lands in Nebraska with relatively limited trapping. Population levels in Oklahoma and Arkansas fluctuate every other year or so, but downward or upward trends in the long term are difficult to ascertain. Fort Chaffee in western Arkansas and Camp Gruber in eastern Oklahoma along with populations in Nebraska, all have robust populations that are believed to be resilient to the effects of stochastic weather

events (USFWS 2008a). Little information is available on trends in the small populations of ABB in Kansas and there is some evidence that the small population of ABBs known to occur in northern Lamar County, Texas, may be declining (USFWS 2008a) because surveys performed on Camp Maxey in Lamar County, Texas have not captured ABB since 2008.

Reasons for decline: The ABB's uneven distribution and density, and their vulnerability to extinction are likely due to the species having specialized resource requirements with carrion being a finite resource widely scattered in space and time (Karr 1982, Pimm et al. 1988, Peck and Kaulbars 1987). Data available for the ABB on Block Island, Rhode Island supports the contention that the primary mechanism for the species rangewide declines "lies in its dependence on carrion of a larger size class relative to that used by all other North American burying beetles, and that the optimum-sized carrion resource base has been reduced throughout the species range" (USFWS 1991Since the middle of the 19th century, certain animal species in the favored weight range for ABBs have either been eliminated from North America or significantly reduced over their historic range (USFWS 1991), including the passenger pigeon (*Ectopistes migratorius),* greater prairie-chicken (*Tympanchus cupido)* and wild turkey *(Meleagris gallopavo)*.

The passenger pigeon was estimated at one time to have been the most common bird in the world, numbering 3 to 5 billion (Ellsworth and McComb 2003). There were once as many passenger pigeons within the approximate historic range of the ABB as there are numbers of birds of all species overwintering in the United States today. Wild turkeys, for example, occurred throughout the range of the ABB, and until recently, were extirpated from much of their former range. Black-tailed prairie dogs (*Cynomys ludovicianus)* which occur in the northern portion of the ABB's range have drastically declined (Miller et al. 1990) and previously dense populations of these black-tailed prairie dogs may also have supported ABBs (USFWS 2008a). During the westward expansion of settlement in North America, the removal of top-level carnivores such as the grey wolf (*Canis lupis)* and eastern cougar (*Puma concolor)* occurred simultaneously with land use changes that fragmented native forests and grasslands and created more edge habitats (such as the edge between forest and grassland, or grassland and cropland). These two processes, (extirpation and fragmentation) resulted in meso-carnivores (mid-sized) becoming more abundant. Meso- carnivores prey on small mammals and birds and directly compete with carrion beetles for carrion.

Fragmentation of large contiguous habitats into smaller pieces or patches of habitat may increase species richness, but the species composition usually changes. Fragmentation of forests and grasslands cause a decrease of indigenous species and an increase in meso-carnivores that thrive in areas disturbed by humans such as: American crow (*Corvus brachyrhynchos)*, raccoon (*Procyon lotor)*, red fox (*Vulpus fulva)*, opossum (*Didelphis virginiana)*, striped skunk (*Mephitis mephitis)*, coyotes (*Canis latrans),* feral cats (*Felis*

domesticus), and other opportunistic predators (Wilcove et al. 1986). Historically large expanses of natural habitat that once supported high densities of indigenous species are now artificially fragmented, supporting fewer or lower densities of indigenous species that once supported ABB populations, and also facilitates increased competition for limited carrion resources among the "new" predator/scavenger community. A number of these species, especially the raccoon and striped skunk, have undergone dramatic population increases over the last century (Garrott et al. 1993), and the coyote and opossum have expanded their range. These scavengers may extend hundreds of feet from edges into forest in eastern North America. Matthews (1995) experimentally placed 64 carcasses in various habitats in Oklahoma where ABBs and the roundneck sexton beetle (*N. orbicollis*, another type of burying beetle) had been previously documented, then tracked the organisms that scavenged them. Of the carcasses, 83 percent were claimed by ants, flies, and vertebrate scavengers; about 11 percent were claimed by the roundneck sexton beetle, and only one was claimed by ABBs.

ABBs are the largest species of burying beetle in the New World (Western Hemisphere) and require carcasses of 3.5 to 7.0 ounces (100 to 200 g, Kozol et al. 1988) to maximize its fecundity, whereas all other burying beetles can breed abundantly on much smaller carcasses, with the smaller species using carcasses of 0.11 to 0.18 ounces (3.12 to 5.10 g, Trumbo 1992). However, Lou Perrotti, the Species Survival Plan Coordinator at the Roger Williams Park Zoo, Rhode Island, has been raising ABBs for over 20 years, and has stated that for ABB the optimal size of vertebrate carcass weighs "about 180 grams;" further stating: "anything less than this and the beetles just don't use it." (Personal communication, June 2014.)

Population Estimate: While ABB are relatively easy to capture, population estimates of ABB are problematic. The standard mark and re-capture technique used to estimate population size assumes that marked and unmarked individuals are equally likely to be captured, and that a substantial number of the animals would be recaptured from one trapping period to the next. However, due to ability of the ABBs to range widely and their reproductive strategy that includes retreating underground for several weeks, these assumptions may not apply. This may be less of a problem for the insular population on Block Island, Rhode Island where, because of the relatively small size of the island (2,614 ha), a significant proportion of the population can be monitored. Elsewhere, however, precise estimates of absolute or even relative densities remain a challenge (USFWS 2008a).

Because the ABB completes its lifecycle in one year, each year's population levels are largely dependent on the reproductive success of the previous year. This fluctuation is thought to be a function of the boom and bust nature of the carrion resources on which they depend. Therefore, populations may be cyclic (due to weather, disease, etc.), with high numbers and abundance in one year, followed by a decline in numbers the succeeding year. These short-term stochastic events should not have long-term effects in robust populations (USFWS 2008a).

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Schnell et al. (1997-2003, 1997-2005) reported that areas of high concentration appeared to shift annually throughout Fort Chaffee, Arkansas and Camp Gruber, Oklahoma, even though land use within each area stayed relatively stable (USFWS 2008b). Losses associated with one-time or short-duration pulse are less likely to affect population survival than longer-duration adverse effects.

False negative results are possible outcomes of ABB surveys. Standard transects on Camp Gruber that resulted in ABB captures in one year failed to capture ABBs in another year. Additionally, surveys conducted in a given area have resulted in ABB captures during one survey effort, but surveys conducted in the same area within the same active season have resulted in negative ABB captures. This indicates a relatively rapid turnover rate in the trappable ABB population due to factors such as natural mortality, dispersal, and burrowing underground and attending carrion/broods (Creighton and Schnell 1998).

Conservation

It is unclear if an extirpated ABB population can successfully be re-established. Individuals released at a site may disperse from the area, making it difficult to establish a self-sustaining population. A long-term reintroduction effort on Nantucket Island, Massachusetts, is still being evaluated and has not yet reached either the population size or persistence target. However, in 2011, more ABBs were caught than in any previous year and in fewer trap-nights than any year since 2006 (LoPresti et al. 2011). In Ohio, a multi-year reintroduction effort has been implemented. However, to date no ABBs have been captured in post-release years. A reintroduction effort started in Missouri in the summer of 2012 has shown successful reproduction of ABBs *in situ*, though it is unknown if the population will remain viable.

Protection of large areas of appropriate native habitat appears to be the best known method for enhancing the conservation of the ABB. Relatively large areas of native habitat tend to support the highest known ABB populations. Large blocks of military lands such as Ft. Chaffee in Arkansas, Camp Gruber and the McAlester Army Ammunition Plant in Oklahoma and other large areas of intact native habitat such as the Tall Grass Prairie Preserve support relatively large and secure ABB populations. Creating or protecting more secure and actively managed lands in areas known to support ABBs should make populations more viable and contribute towards recovery. Additional lands were added and managed at the TNC Tall Grass Prairie Preserve through ABB mitigation funds and multiple ABB mitigation banks have been established in Oklahoma that should contribute to the recovery of the species.

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Threats

The American Burying Beetle Recovery Plan (USFWS 1991) and the 5-year Status Review of the species (2008a) identify the following factors as potential threats to ABB: direct habitat loss and alteration, interspecific competition, increase in competition for prey, increase in edge habitat, decrease in abundance of prey, loss of genetic diversity in isolated populations, disease/pathogens, DDT, agricultural and grazing practices, and invasive species. While none of these theories alone adequately explain why the ABB declined while congeneric species are still relatively common rangewide [there are eight sympatric congeners which are not in peril (Sikes and Raithel 2002)], and much of the evidence suggesting the reduction of carrion resources as a primary mechanism of decline is circumstantial, this hypothesis fits the temporal and geographical pattern of the disappearance of ABBs, and is sufficient to explain why ABBs declined while related species did not.

Direct Habitat Loss and Alteration

In a fragmented ecosystem, larger species have been shown to be negatively affected before smaller species, a phenomenon that has been well-documented with carrion and dung beetles in South America (Klein 1989). Due to the ABBs relatively large size and specialized breeding behavior (Creighton et al. 2007,) the prevailing theory regarding the ABBs' decline is habitat fragmentation (USFWS 1991) which reduced the carrion prey base of the appropriate size for ABB reproduction, and increased the vertebrate scavenger competition for this prey (Kozol 1995, Ratcliffe 1996, Amaral et al. 1997, Bedick et al. 1999). There is little doubt that habitat loss and alteration affect this species at local or even regional levels, and could account for the extirpation of populations once they become isolated from others (Kozol 1995, Ratcliffe 1996, Amaral et al. 1997, Bedick et al. 1999).

Projects that cause ABB habitat fragmentation are common. For example, between October 1, 2012, and September 30, 2013, the Service's Oklahoma Ecological Services Field Office reviewed 777 proposed projects in Oklahoma that may have impacted the ABB. Projects evaluated included pipelines, roads, quarries, communication towers, residential housing development, bridges, mining, petroleum production, commercial development, recreational development, transmission lines, and water and wastewater treatment facilities. Impacts from these activities varied in size and duration, with projects such as quarries being hundreds of acres and having permanent impacts, to water treatment facilities of a few acres with both permanent and temporary impacts.

Land conversion to agriculture and development, logging, fire suppression, and intensive domestic livestock grazing are the primary causes of habitat loss and fragmentation within eastern Oklahoma today. For example, large areas of native grasslands have been converted to

introduced grasses such as fescue and bermuda varieties to improve pastures for intensive cattle grazing operations. Since European settlement, fires have been largely suppressed within eastern Oklahoma, leading to changes in community types and species composition. Riparian areas and bottomland habitats have been severely degraded not only as a result of conversion to agriculture and logging, but also because of inundation by numerous reservoirs (Ruth 2006). The anthropogenic breakdown of barriers to dispersal also has permitted the invasion of non-indigenous species (Northern Prairie Wildlife Research Center 2006) such as johnsongrass (*Sorghum halepense)*, Russian olive (*Elaeagnus augustifolia)*, saltcedar (*Tamarix ramosissima)*, and *Sericea lespedeza*.

Interspecific competition

For most guilds (a group of organisms that exhibit similar habitat requirements and that respond in a similar way to changes in their environment), larger species tend to feed on larger prey, occupy a greater diversity of habitats, dominate in interference competition, and maintain larger home ranges, but may suffer from exploitative competition from smaller species (Ashmole 1968, Gittleman 1985, Hespenheide 1971, Rosenzweig 1968, Schoener and Gorman 1968, Werner 1974, Wilson 1975, and Zaret 1980). Larger prey is less abundant than smaller prey (Peters 1983, Brown and Maurer 1987, Damuth 1991, and Lawton 1990) and larger guild members require larger home ranges. In contrast to other guild members, the ABB must range over a larger area and a greater diversity of habitats to find suitable carcasses. In addition, larger carcasses are harder to bury than smaller ones (Creighton et al. 2007). While large size alone does not necessarily confer endangerment, rarity and extinctions tend to be higher for the larger species within trophic levels or guilds (Diamond 1984; Martin and Klein 1984; Vrba 1984; Owen-Smith 1988; and Stevens 1992). Although less than 2 grams in weight, the ABB is nevertheless the largest member of a guild that specializes on vertebrate carcasses, a rare and unpredictable resource.

Size appears to be the most important determinant of success in competition for securing carrion; the largest individuals displace smaller burying beetles (Kozol et al. 1988). ABBs have been recorded as commandeering a carcass that has been buried by another burying beetle species. However, factors other than size (e.g., temperature or activity patterns) might also affect the outcome of competition (Wilson and Fudge 1984). Trumbo (1992) showed that the potential for competition for carrion from other burying beetles species (i.e., congeners) increased with carcass size, and Scott et al. (1987) found the same results with carrion-feeding flies. Habitat fragmentation caused increased vertebrate scavenger pressure, which decreased availability of carrion of the appropriate size, and increased competition between burying beetles (Creighton et al. 2007). As ABB populations decline, the competition between ABBs and sympatric congeners for sub-optimally sized carcasses would be expected to increase.

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The ABBs most similar congener is *N. orbicollis*. The figure at **right** shows a photograph taken for comparison between *N. orbicollis,* and *N. americanus*. Based on historical geographic range, presumably the ecological tolerances (e.g., diel periodicity, breeding season), and phylogenetic information indicates these species may be each other's closest surviving relatives (Szalanski et al. 2000). Being so similar, they likely are each other's greatest congeneric competitors (Sikes and Raithel 2002), and interspecific competition may affect populations at the local level. Typically, surveys for ABBs result in 10 or more times more *N. orbicollis* than ABBs (Lomolino and Creighton 1996, Amaral et al. 1997, Carlton and Rothwein 1998). Kozol (1989) demonstrated that *N. orbicollis* was about eight times more abundant than ABBs on Block Island, Rhode Island while Walker (1957) collected 19 times more *N. orbicollis* (175) than ABBs (9) in the single trapping array where the latter species was encountered in Tennessee. While the ABB is more successful than *N. orbicollis* in utilizing carcasses greater than 100 g, these data suggest that *N. orbicollis* may be a formidable competitor for the ABB (Sikes and Raithel 2002) and may have actually increased (have been released from competition) in those areas where ABBs disappeared (USFWS 1991). In addition, *N. marginatus* may also be a formidable competitor to ABBs. *N. marginatus* is on average slightly larger and utilizes larger carcasses than *N. orbicollis* and in Nebraska and South Dakota is typically more abundant (Backlund and Marrone 1997, Bedick et al. 1999). Another threat to ABB reproductive success is brood parasitism after the oviposition by other burying beetle species near an ABB buried carcass (Müller et al. 1998, Trumbo 1994). Trumbo (1992) found that mixed species burying beetle broods were more common on larger carcasses.

The imported fire ant (*Solenopsis invicta)* has become a formidable competitor for carrion and a potential source of mortality for burying beetles when they co-occur at a food source (Warriner 2004, Godwin and Minich 2005). Scott et al. (1987) concluded that the inability of *N. carolinus* to successfully bury carrion provided experimentally in Florida was due to interference by imported fire ants. Only 5 of 48 carcasses were successfully exploited by *N. carolinus*, despite pitfall trapping that demonstrated that *N. carolinus* was locally abundant. Collins and Scheffrahn (2005) noted that fire ants may reduce ground-nesting populations of rodents and birds, and in some instances, may completely eliminate ground-nesting species from a given area. Fire ant infestations are not evenly distributed; rather, they tend to be more numerous in open, disturbed habitats (Carlton in lit. 1996). Of the states containing populations of ABB, fire ants now infest all or parts of Arkansas**,** Oklahoma, and Texas (USDA 2003).

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Loss of Genetic Diversity in Isolated Populations

Kozol et al. (1993) examined ABB genetic variation within and between the Block Island, Rhode Island population and the eastern Oklahoma and western Arkansas population. Both populations have low levels of genetic variation, and most of the variation occurs within a single population. There were no unique diagnostic bands within either population, but they found the Oklahoma- Arkansas population to be somewhat more diverse. Reduced genetic variation is often a result of founder effect, genetic drift, and inbreeding. Kozol et al. (1993) suggest that multiple bottleneck events, small population size, and high levels of inbreeding may be factors contributing to the pattern of genetic variation in ABBs.

Szalanski et al. (2000) expanded on Kozol et al.'s 1993 study and examined ABBs from five populations: Block Island in Rhode Island, Arkansas, South Dakota, Oklahoma, and Nebraska. The authors found little evidence that the five populations have maintained unique genetic variation and no evidence to suggest that these five populations should be treated as separate, genetically independent conservation segments.

Changing Climate at the Periphery of the Range

While data is lacking for direct evidence that implicates a changing climate may jeopardize the continued existence of some populations/metapopulations of ABB, there is much anecdotal information that seems to indicate this may be the case in the southern and western terminus of its range. Research is ongoing into this area and will be addressed when more data becomes available.

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Nicrophorus americanus

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