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The long-term, range-wide decline of a once common carnivore: the eastern spotted skunk (*Spilogale putorius*)

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Abstract

The eastern spotted skunk (*Spilogale putorius*) was once common throughout the midwestern and southeastern United States, with consistent annual range-wide harvests of $\gg 100\,000$ animals. In the 1940s, however, populations seemingly crashed and the species is currently listed by various state agencies as endangered, threatened, or 'of concern' across much of its range. We examined long-term harvest records from 10 states to better understand the 20th century population dynamics of eastern spotted skunks, to discern whether the putative decline was biologically real or an artifact of altered harvest pressures and to identify the timing of the decline. Analyses reveal unequivocally that the species was indeed once common in the Great Plains. Beginning in about 1940, harvests dramatically declined, although the onset of declines differed between states. By the early 1950s total harvests in all states were < 10% of pre-crash harvest. Thereafter, rates of decline slowed, but nevertheless continued, such that by the 1980s harvests were < 1% of those during pre-decline years. Analyses show that these declines are real and not an artifact of harvest effort. Although the causes of the decline remain unclear, the analyses suggest a need for immediate attention to address the long-term persistence of this species.

'On a round trip of 595 miles between Stockport and Sioux City, Iowa, during the last week of April, 1942, 19 dead spotted skunks were seen on the road for an average of about one every 26 miles. The route was retraced only 100 miles. Five of the skunks were encountered on an 11-mile stretch [. . .] in the center of the state.' (Crabb, 1948)

INTRODUCTION

As a general rule, the foremost predictor of extinction risk is the size of a taxon's geographical range. Widespread taxa tend to be at decreased risk relative to taxa with small ranges (Purvis *et al*., 2000; Jones, Purvis & Gittleman, 2003; Gittleman & Gompper, in press). An exception to this rule may exist among top predators, which exist at low population densities and range widely (Woodroffe, 2001) or among smaller, but highly carnivorous predators (e.g. river otters, *Lutra canadensis*, peregrine falcons, *Falco peregrinus*) which have been overharvested or subject to toxin-related crashes and may rapidly rebound when these proximate mechanisms of decline are addressed (Breitenmoser *et al*., 2001; U.S. Fish and Wildlife Service, 2003). But among smaller, more omnivorous predators with large geographical ranges, especially those within the mammalian order Carnivora, there have been few, if any, examples of range-wide species decline. Many of these mid-sized omnivores, such as foxes (e.g. *Vulpes vulpes*) and raccoons (*Procyon lotor*), can thrive in human-dominated environments and sustain very high harvest pressures (Sanderson, 1987; Voight, 1987). Here, however, we suggest that the eastern spotted skunk (*Spilogale putorius*) represents an example of a wide-ranging, common and omnivorous species declining throughout its range. Furthermore, the lack of widespread recognition of this decline may be, in part, a function of the very features that have been suggested to minimise the risk of extinction: a large geographical range, high population densities and an unspecialised diet.

The eastern spotted skunk is a small (*ca*. 0.5–1.5 kg) mephitid with a range that includes much of the central and the southeastern United States (Kinlaw, 1995). The natural history of *S. putorius* is poorly understood, with most information on the ecology of the species based on a study from the 1940s in Iowa (Crabb, 1948) and two 1980s studies: one examining population density on a Florida barrier island (Kinlaw, 1990) and one examining the habits of four male skunks from a Missouri Ozark population (McCullough & Fritzell, 1984). Even knowledge of basic habitat preferences is superficial; that is, whether the species is forest, prairie, or edge-associated. The paucity of ecological work on the species is perhaps due, in part, to the perceived rarity of the animal when assessed on a

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fine-grain or local scale. The work by Crabb was carried out when the species was common. Since that study, however, the species appears to have declined dramatically.

In the early 20th century the eastern spotted skunk was a common and important furbearer wherever it occurred and especially in the Great Plains, where annual multi-state harvests of $\gg 100\,000$ animals were typical. Based on data from Missouri (Sampson, 1980) for instance, the value of the 1945 and 1955 spotted skunk harvests ranked 5th and 4th, respectively, among carnivore species. Currently, however, the spotted skunk is listed as endangered, threatened, or 'of concern' in virtually every state in the Midwestern portion of its range (DeSanty, 2001) and in multiple states in the eastern portion of its range (based on a September 2004 examination of websites run by state agencies responsible for wildlife management and conservation), including Indiana, Pennsylvania, Kentucky, Virginia, South Carolina and Louisiana. While several studies (Choate, Fleharty & Little, 1974; Sampson, 1980; Wires & Baker, 1994; Landholdt & Genoways, 2000) have noted the decline of spotted skunk populations within individual states and some of these have alluded to the range-wide decline of the species, thorough assessments of the latter has not been carried out. Indeed, Kinlaw (1995) suggested that the species is 'still abundant' in Florida and Choate *et al.* (1974) suggested that spotted skunk numbers in the early 20th century were abnormally high, that skunks had expanded into areas where they were not normally found and that population levels were simply returning to levels existing before the 'unnatural' population increase commenced. Perhaps because of this diversity of opinion and the lack of range-wide examination, the species has received relatively little attention at a national level and attempts to identify causes of the putative declines are generally site-specific and not rigorously assessed (see below). In this paper we collect and analyse multi-state data sets on the harvest of eastern spotted skunks as an indirect mechanism to better understand the dynamics of eastern spotted skunk populations. More specifically, we identify the timing of putative population declines and assess whether these declines are real or based on decreased trapping efforts. We follow these analyses by discussing possible causes of population change.

MATERIALS AND METHODS

Long-term annual data on spotted skunk harvests were obtained from the following 10 states: Iowa (Iowa Department of Natural Resources, 2002), Missouri (Bennitt & Nagel, 1937; Sampson, 1980; unpublished data), Nebraska (Krause, 1980; Novak *et al*., 1987), Tennessee (Tennessee Wildlife Resource Agency, 1997), Kansas, Oklahoma, Minnesota, Arkansas, Georgia and Mississippi (Deems & Pursley, 1978; Novak *et al*., 1987; Caire *et al*., 1989). Data sets from some states were less complete than others due to missing data during some years or data on spotted skunk harvests that were combined with striped skunk (*Mephites mephitis*) harvest data. We recognise that a significant portion (e.g. 8–10%: Erickson, 1982) of furs may have been harvested outside the state in which they were eventually sold, but feel that the multi-state, long-term perspective taken here should minimise the impact of this pelt trade on the general trend lines.

For states with more complete and long-term data sets (Missouri, Nebraska and Iowa), data were also obtained on annual pelt prices, while for Missouri, the number of licensed trappers/year and the length of the trapping season was also available. To partially correct for biases in harvest effort, we calculated the number of trappers on the landscape/year (= number of trapper-days) and divided this by the length of the trapping season to calculate the harvest/trapper/day. A consumer price index (U.S. Dept. of Labor, Bureau of Labor Statistics, available from http://www.bls.gov/) was used to adjust the price of pelts for inflation to a 2003 baseline; all pelt price analyses used only the inflation-adjusted values.

On the coarsest level, annual harvest levels per state were graphed, with more detailed analyses carried out for Missouri, Nebraska and Iowa, in which linear regression was used to assess the role of capture effort on spotted skunk harvest. We looked for relationships between pelt price and annual harvest, subdividing the data sets into pre-decline periods (Iowa only), decline periods and post-decline periods (1955–present). Pre-decline and decline periods differed between states and overlapped slightly within each state; pre-decline periods were designated as all years up to and including the peak year prior to the start of continuous harvest declines in the 1940s. The peak year was also included as the first year of the decline periods, which were designated on the basis of the start of a 5 year continuously decreasing harvest phase and continued through 1955. For Missouri we also examined the relationship between number of trappers and annual harvest, length of trapping season and annual harvest and number of trapper days (number of trappers $\times$ length of season) and annual harvest. Because much spotted skunk harvest may be derived from incidental harvest that occurred while trappers were targeting other furbearer species (e.g. fox, raccoon), multiple regression was used (Missouri only) to compare the relative importance of pelt price and number of trapper-days for spotted skunk harvests (Lewis & Zielinski, 1996). We assumed quasi-independence between pelt price and number of trapper-days, based on low correlation coefficients (see below) and so did not include an interaction term in the regression.

RESULTS

Spotted skunk harvests were high until the 1940s when the populations crashed sharply, a pattern seen in multiple states and best seen in the relatively complete data sets of Missouri, Iowa and Nebraska (Fig. 1). Until the 1940s spotted skunk harvests in the Midwest were $>100\,000$/year and perhaps far higher given that data sets for most states are incomplete. Peak harvest of individual states include 117 309 in Kansas (1930: Choate *et al*., 1974) and 89 000 in Iowa (1933). While these

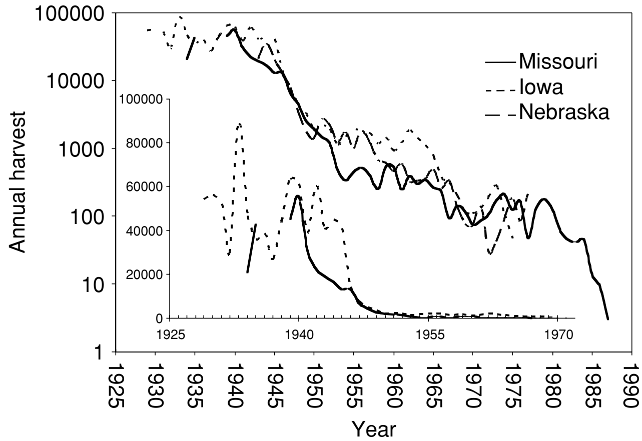

Fig. 1. Annual harvest of eastern spotted skunk (*Spilogale putorius*) in the Midwestern United States (Iowa, Nebraska, Missouri). Primary figure shows data (1925–1990) on a log-scale. Inset figure shows unlogged data (1925–1970) for Iowa and Missouri only.

represent extremes, high harvests were sustained in many Midwestern states during this period (Figs 1 & 2).

In the 1940s, annual harvests declined steeply (Fig. 1). The timing of the decline varied between states. Missouri spotted skunk harvests declined steadily during 1940–1945, from 55 000 to 13 000 animals. Oklahoma and Arkansas harvests also declined, starting in the early 1940s (Fig. 2). During this period, however, Iowa and Nebraska harvests remained relatively high. Iowa harvests, for example, varied between 38 000 and 63 000 over this period. Nebraska declines commenced by 1945 and Iowa declines commenced by 1946. In Iowa, 1946, 1947, 1948, 1949 and 1950 harvests were 34, 19, 11, 8 and 5% of the 1945 harvest of 40 661 individuals, respectively, with a mean annual decline of 56.5% (range: 27–76%). By 1950, the combined harvest for Missouri, Iowa and Nebraska was *ca*. 5200 individuals, or 5.5% of the 1941 harvest. From the early 1950s through the 1980s, harvests continued to decline, although at a slower rate, such that

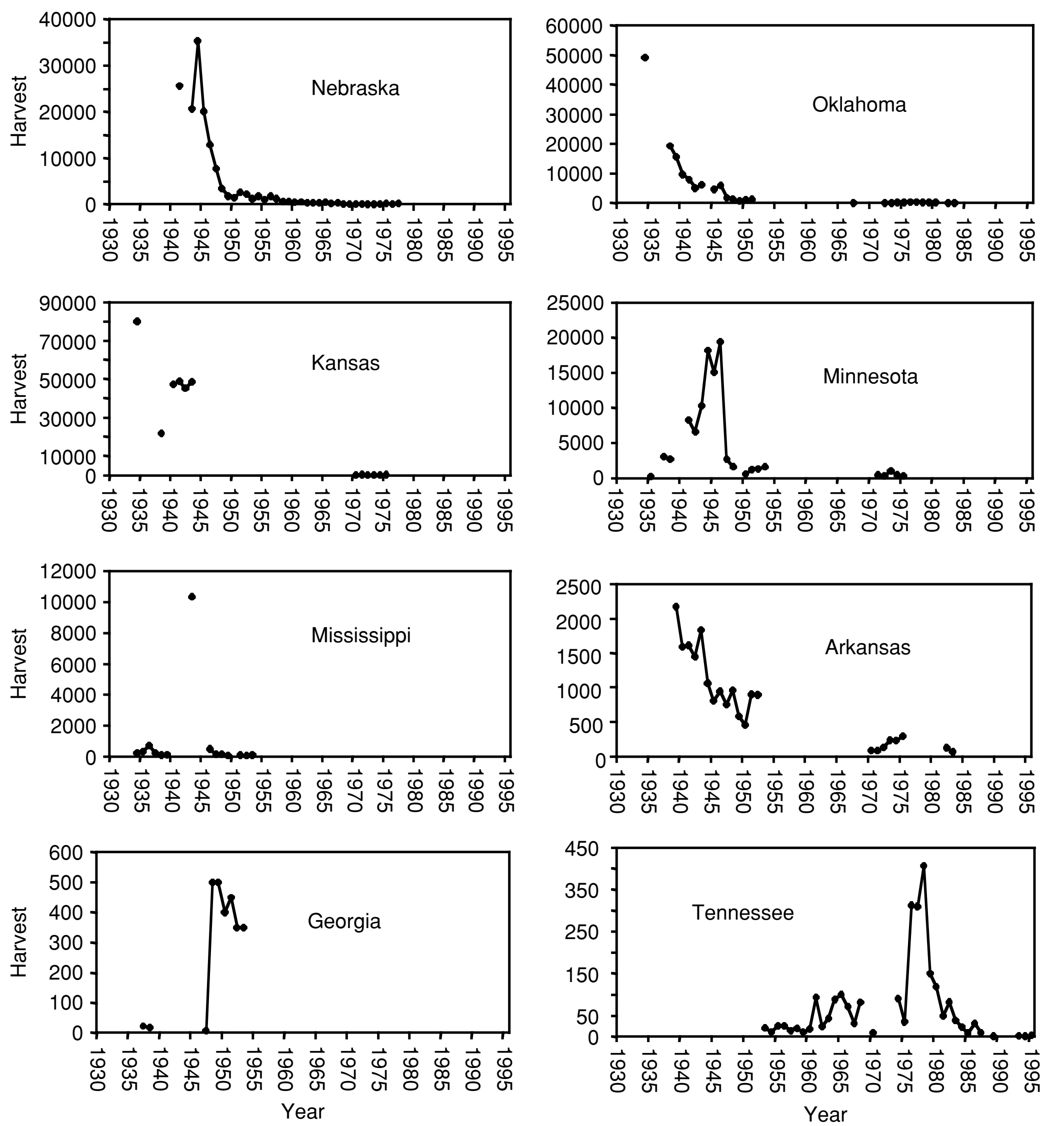

Fig. 2. Annual harvest (1930–1995) of eastern spotted skunk for eight states from the Midwestern and Southeastern United States. Lines connect harvest data from consecutive years.

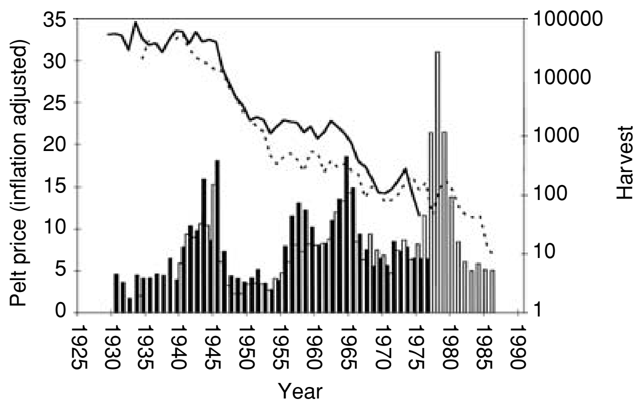

Fig. 3. Yearly log-scaled harvest and inflation-adjusted (to 2003) pelt prices for eastern spotted skunk in Missouri (broken line, open bars, respectively) and Iowa (continuous line, filled bars, respectively).

by the 1970s, combined annual harvest for the three states was less than 1000 animals or < 1% of historic harvest levels.

Data sets on spotted skunk harvests for other states (Fig. 2) are less complete and therefore more difficult to assess. This is especially true for southeastern states (Tennessee, Georgia, Mississippi, Arkansas), whose historic harvest numbers are unavailable and are lower than the Great Plains states (Kansas, Minnesota, Oklahoma). Nevertheless, for several of these states (Arkansas, Oklahoma, Kansas) a long-term decline is observed. Minnesota harvests were relatively low (< 3100) in the late 1930s to early 1940s, increased sharply in the mid–late 1940s (6500–19 400) and then declined by 1950, thereafter remaining relatively low. Mississippi shows a similar harvest pattern; annual harvests of < 750 throughout the century, excepting 1944 when the harvest spiked to > 10 000. Georgia and Tennessee had relatively low harvest levels (< 700/year) with three to ≫ sixfold increases in the late 1940s (Georgia) and the late 1970s (Tennessee).

Long-term data on pelt prices were available for Iowa (1930 onwards), Missouri (1940 onwards) and Nebraska (1951 onwards). Although there was considerable long-term variability in pelt prices, the general pattern was one of increasing pelt price in the late 1930s–mid 1940s (peak inflation-adjusted Missouri and Iowa prices were $15.33 and $18.09, respectively, in 1945), followed by a sharp decline in pelt prices in the late 1940s–early 1950s (Fig. 3). Thereafter prices gradually increased again, with peaks occurring in the mid 1960s (e.g. inflation adjusted prices for Nebraska 1964 = $11.28; Iowa 1964 = $18.58; Missouri 1965 = $14.31), followed by generally decreasing prices through the 1980s. An exception to this later decline in prices occurred in 1977–79, especially in Missouri when inflation-adjusted prices reached $31.02. Pelt prices were highly correlated ($r = 0.62 - 0.81$) among states.

Peak pelt prices in the early–mid 1940s did not co-occur with peaks in state harvests. In Missouri, prices increased steadily through 1945 while harvest declined over this period. Immediately following this period, both pelt prices and harvest levels in Missouri declined steeply. In Nebraska, peak harvest occurred in 1944, but a doubling of pelt price in 1945 was not associated with an increased harvest. In Iowa, early 1940s increases in pelt prices were associated with generally increased harvests. High 1945 prices did not, however, result in a simultaneous peak in harvest relative to prior years.

By 1947–8 pelt prices had declined to pre-1940s levels (Fig. 3). During this period, spotted skunk harvests also declined. In the late 1950s prices again increased and remained high through the mid 1960s. During this period the harvest rates continued to decline, although less rapidly than during the late 1940s–1950s (Fig. 3). Several states had increased harvests in the late 1970s (e.g. Tennessee; Fig. 2). These harvests occurred when pelt prices in other states increased sharply (e.g. Missouri; Fig. 3). It should be noted, however, that harvest levels in these states were relatively low (< 700 per state). A relatively small increase in capture effort could drive these increases, which may therefore give little insight into population dynamics. States with higher historic harvests showed no increase in harvest during this period.

Regression analyses of the relationship between harvest and pelt price were carried out for Iowa (pre-decline, decline and post-decline phases), Missouri (decline and post-decline phases) and Nebraska (post-decline phase only). In Iowa prior to the observed population decline (1930–1945), there was no significant relationship between price and harvest ($P = 0.722$). During decline phases, however, a strong positive relationship occurred in Iowa (1945–1955; $P < 0.001$) which explained 88% of the variance in spotted skunk harvest. Missouri's decline-phase (1940–1955) relationship is weaker ($P = 0.08$), primarily because of the inclusion of 1 year of high harvest at a mid-range pelt price (1940); excluding this value, the harvest–pelt price relationship was highly significant ($P = 0.002$; $r = 0.74$). During the post-decline period there was no significant relationship between pelt prices and harvest for Missouri (1955–1989; $P = 0.901$) or Nebraska (1955–1976; $P = 0.226$). Iowa's harvest (1955–1975), however, remained correlated with pelt price during the post-decline phase ($P = 0.006$; $r = 0.58$).

For Missouri, we examined the relationship between pelt price and the number of trappers, the length of the trapping season and the number of trapper-days (number trappers × length of season). In the late 1930s through to 1940, there was a large increase in the statewide harvest/day (Fig. 4). In 1941 these measures of harvest per unit effort declined greatly and this decline continued throughout the decade, such that by 1945, when pelt prices peaked, harvest rates/day were less than the 1935 levels when adjusted pelt prices were *ca.* 80% lower. By 1950, harvest/day was < 15% of the 1935 values. Measures of pre-decline harvest/trapper/day were 0.017 (1934) and 0.29 (1942). Peak 1950s measures of this parameter are 15–27% of these pre-decline values and average 1950s values (1953–1953) are 11% and 19.5% of the 1934 and 1942 values, respectively. There was no significant relationship between spotted skunk pelt price and number of trapper-days ($P = 0.449$; $r = 0.13$), but across all years

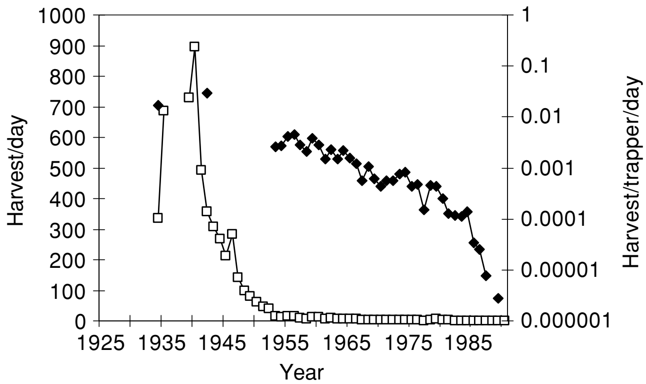

Fig. 4. Long-term harvest of eastern spotted skunk in Missouri corrected for length of trapping season (harvest/day, open squares) and corrected for the length of trapping season and number of licensed trappers (harvest/trapper/day, filled diamonds).

for which data were available, multiple regression analyses revealed that Missouri harvest was strongly predicted by pelt price and number of trapper days ($n = 35$ years with data; $F = 36.794$; $P < 0.001$; adj $r^2 = 0.678$), with harvest being more strongly predicted by number of trapper-days ($t = 8.474$; $P < 0.001$) than by pelt price ($t = -0.200$; $P = 0.842$). This general relationship also held when only the post-decline years (1955 onward) were examined.

DISCUSSION

These analyses of long-term datasets reveal three important patterns. First, spotted skunk harvests were once far greater than they are now and the patterns of these declines, coupled with declines in harvest per unit of capture effort, indicate a population decline. Throughout the Midwest, annual harvest numbers were measured in the tens of thousands until the 1940s when the species declined, at first precipitously and then at a slower rate, but nevertheless steadily. Thus, the regional observations of this pattern (Choate *et al.*, 1974; Wires & Baker, 1994; Landholdt & Genoways, 2000) can be seen across the range of the species, including some areas outside the Midwest. Prior to the closure of trapping seasons for spotted skunks throughout most of the Midwest, annual harvests were only a small fraction of historic harvests. Second, the sharp harvest declines were observed range-wide throughout the 1940s but the onset of the decline differed between states. Population crashes occurred first in Oklahoma and Missouri in the late 1930s and early 1940s. Nebraska declines commenced in the mid-1940s, while Iowa harvests remained sizable (> 50 000/year) until a precipitous decline in 1946. The onset of the Kansas decline is unknown but, like Iowa, the state had high annual harvests throughout the first half of the 1940s. Third, the decline is biologically real and not an artifact of a decline in the number of trappers or a decline in the demand (as measured by pelt price) for spotted skunks. Even when pelt prices increased steadily in the 1950s and 1960s and spiked upwards to an inflation-adjusted price of $31 in Missouri in 1978, the harvest failed to respond except for increases of several hundred animals harvested in the southern and eastern states.

Although numerous factors have been tied to the increased likelihood of extinction (McKinney, 1997), no studies have closely assessed the causes of spotted skunk population decline. Several authors have, however, qualitatively discussed the issue in a regional perspective, suggesting habitat change and the advent of pesticide use as primary mechanisms of the decline (Choate *et al.*, 1974; Krause, 1980; McCullough, 1983; DeSanty, 2001; Schwartz & Schwartz, 2001). These suggestions are related to the modernisation in agriculture that commenced in the 1940s. The decline of the family farm, the advent of clean farming (maximal use of available land for crops, with edges cleared of plants to keep undesirable species from invading fields), the start of intensive synthetic pesticide use, improved grain management practices and the end of large haystack construction may have limited den site and food availability and, perhaps, directly or indirectly influenced mortality and reproduction.

The timing and rate of spotted skunk declines do not, however, unequivocally support pesticide use and habitat change as the primary mechanisms driving the initial decline in spotted skunk numbers. Industrial farming and associated improvements in grain and haystack management are unlikely to have occurred so rapidly (3–5 years) as to drive the observed precipitous declines and the timing of the declines in some states predates the widespread use of synthetic pesticide. The first broadly used organochlorine insecticide was Dichloro-diphenyl-trichlorethane (DDT), which was used for disease vector control beginning in 1939, but whose widespread use in agriculture commenced after 1945. The use of other synthetic organochlorine and organophosphate pesticides, including aldrin, chlordane and their degradation products such as dieldrin, commenced in the 1950s. As such, the use of these compounds fails to explain sharp declines in skunk numbers in the early 1940s (Missouri, Oklahoma). The use of DDT may, however, have contributed to the population declines of the late 1940s as exemplified by the Iowa harvest trends. It is also plausible that large-scale changes in agricultural practices may have contributed to the slower, but steady, decline in spotted skunk harvests beginning about 1950.

While the positive relationship between pelt prices and harvest levels seen during the decline phases of several states (Missouri, Iowa) suggests that these species were targeted when pelt prices increased, multiple regression analyses suggest that the number of trapper-days, a measure of the length of the trapping season and the number of trappers, was a better predictor of harvest than was pelt price. We interpret this to mean that while spotted skunks may have been targeted by trappers when pelt prices were particularly high, in most cases these animals are captured incidentally to attempts to trap other, more valuable, species. It should also be noted that correlations between pelt price, trapper numbers and harvest are not, by themselves, sufficient to fully implicate over-harvesting as a mechanism of decline. Data interpretation is made more difficult by the relatively low spotted skunk pelt prices of the late 1940s–early 1950s, during which time harvest numbers were also low, and by possibly altered trapping pressures during World War II. Thus, perceived declines may be confounded by reduced harvest effort. Nevertheless, it should be emphasised that, independent of the extent to which spotted skunk capture and harvest was deliberate or incidental, the harvest per unit effort declined strongly throughout the 1940s and 1950s.

Disease outbreak is an additional possible explanation for the eastern spotted skunk decline that deserves attention, since pathogens and, especially, generalist viruses such as distemper and rabies have been implicated in the decline of other carnivore taxa (Funk *et al*., 2001). However, the observed rapid declines in spotted skunks, with no apparent population increase following the decline, do not support a rabies or distemper-related population crash. Epidemics of these viruses generally have predictable periodicities and spatial dynamics (Roscoe, 1993; Childs *et al*., 2001), neither of which is apparent in the spotted skunk data. However, other viruses, especially parvoviruses, have emerged and spread very rapidly with long-term and persistent effects on population viability. Rapid global emergence of a mink enteritis virus, for example, was first documented from mink farms in the 1940s (Pearson & Gorham, 1987) and spill-over into spotted skunks could plausibly have contributed to declines. Closely related canine parvoviruses infected canid species worldwide in less than 4 years and impacts of that novel infection were observed in the population dynamics of particular canids species (Parrish *et al*., 1988; Funk *et al*., 2001). We are not, however, aware of any evidence of a skunk parvovirus and so the support for a disease-related decline due to a parvovirus or other pathogens is, at best, conjectural.

Given the furbearer status of the eastern spotted skunk, the widespread nature of the decline, the qualitative or quantitative recognition of the decline in most Midwestern states resulting in some level of regional conservation concern (DeSanty, 2001), why has the species not received increased attention on a range-wide scale? In a recent review of the current status of spotted skunks in 10 Midwestern states, DeSanty (2001) found that few had monitoring programes and none had current or proposed management programmes. This may be, in part, due to the observation (Choate *et al*., 1974) that in some regions past high densities were associated with recent or ephemeral range expansions. On a range-wide scale, however, the lack of widespread recognition of this decline and the associated lack of mitigation efforts may also be, in part, a function of features that generally are viewed as inhibiting extinction processes – a large geographical range, high perceived (past or localised) population densities and unspecialised resource requirements. Lack of recognition of range-wide declines, despite observations of local population declines, may be underscored by a belief that the species remains relatively stable or common elsewhere, despite limited supporting evidence.

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