

The rapid spread of rusty crayfish (*Orconectes rusticus*) with observations on native crayfish declines in Wisconsin (U.S.A.) over the past 130 years

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Abstract

The rusty crayfish, *Orconectes rusticus*, is one of America's best-known non-indigenous crayfishes, having been identified as extirpating native crayfishes and disrupting local aquatic ecosystems. Over the past 40–50 years, rusty crayfish have spread from its historical range in the Ohio River drainage (U.S.A.), to waters throughout much of Illinois, Michigan, Wisconsin, and Minnesota and parts of 11 other states, Ontario (Canada) and the Laurentian Great Lakes. Using a comprehensive dataset based on all known historical records and extensive present-day surveys ($n = 2,775$) this study reports on the invasion history of rusty crayfish, with observations on concomitant declines of native crayfishes in Wisconsin over the past 130 years (1870–2004). We found that rusty crayfish occurrences have increased from 7% of all crayfish records collected during the first 20 years of their invasion (1965–1984) to 36% of all records during the last 20 years, and that rusty crayfish have replaced the northern clearwater crayfish (*O. propinquus*) and virile crayfish (*O. virilis*) as the most dominant member of the contemporary crayfish fauna. In light of our results we discuss the introduction, establishment and integration phases of the rusty crayfish invasion and provide preliminary predictions of the potential distribution of rusty crayfish in Wisconsin lakes based on critical environmental requirements.

Introduction

Biological invasions are widely recognized as a significant component of human-caused environmental change and primary threat to native biodiversity (Elton 1958). The negative impacts of species invasions, together with the consequences of environmental degradation, are particularly evident in North American freshwater ecosystems (Richter et al. 1997), whose native faunas are experiencing extinction rates that exceed their terrestrial counterparts (Ricciardi and Rasmussen

1999). This ominous trend is particularly evident for freshwater fishes, mussels, and crayfishes (Master 1990).

Crayfishes are highly diverse in North America (exceeding 333 species and comprising 75% of the global fauna), though are seriously threatened by habitat alteration (Taylor et al. 1996) and non-indigenous crayfishes (Lodge et al. 2000a). Non-indigenous crayfish have been introduced throughout North America via aquaculture, aquarium and pond trades, biological supply trade, and the live bait trade (Lodge et al.

2000b), and many species have shown high rates of spread and integration into streams, rivers and lakes. In fact, competition, predation and hybridization with crayfish invaders have been identified as a primary threat for the majority (> 50%) of declining North American crayfishes (Lodge et al. 2000a; ABI 2001; Perry et al. 2001).

Rusty crayfish *Orconectes rusticus* (Girard) has proven to be a formidable invader, spreading over the last 40–50 years from its historical range in the Ohio River drainage, to waters throughout much of Illinois, Michigan, Wisconsin, and Minnesota and parts of 11 other states, Ontario and the Laurentian Great Lakes (Hobbs et al. 1989; Lodge et al. 2000a). The invasion dynamics of rusty crayfish and its ecological impacts have been most intensively studied in lakes and streams of northern Wisconsin and the Upper Peninsula of Michigan (e.g., Capelli 1982; Capelli and Magnuson 1983; Lodge et al. 1986; Olsen et al. 1991; Perry et al. 2002; Wilson 2002; Wilson and Hrabik 2006; McCarthy et al. 2006). In these invaded systems, rusty crayfish have out-competed their native congeners, leading to population declines proportional to the population growth of rusty crayfish (Lodge et al. 1986). In a recent study, Wilson et al. (2004) reported on the invasion dynamics of rusty crayfish in Trout Lake, Wisconsin, where they were first detected in 1979 (Lodge et al. 1986) and over the past 19 years have spread throughout the lake and impacted nearly all components of the littoral-zone food web. This study provided the unique opportunity to observe the invasion sequence of rusty crayfish from its initial point of introduction to the eventual occupation of the entire lake. However, while the ecology of rusty crayfish has been well studied in Trout Lake and surrounding lakes in northern Wisconsin and Michigan, in large part because of the North Temperate Lakes Long-Term Ecological Research program (NTL-LTER; Magnuson and Kratz 1999), little is known about their invasion history at broader temporal and spatial scales. Such information is needed for conservation planning and prioritization, and would provide the basis for forecasting future distributions of rusty crayfish and establishing proactive management strategies aimed at reducing further spread and ecological impacts.

The present study reports on the invasion history of rusty crayfish, with observations on concomitant declines of native crayfishes in the state of Wisconsin over the past 130 years (1870–2004). Using a comprehensive dataset based on all known historical records and extensive present-day surveys we address the following questions: (1) What are the spatial and temporal patterns of rusty crayfish invasion in Wisconsin?; (2) What fraction of the present crayfish fauna are comprised of rusty crayfish *versus* native crayfishes?; and (3) What is the potential distribution of rusty crayfish in Wisconsin lakes based on a preliminary analysis of critical environmental requirements?

Methods

We assembled a comprehensive dataset of crayfish occurrences in Wisconsin, U.S.A. (total area of state: 169,652 km²) with the primary purpose of providing a data source for improving crayfish management and conservation. Wisconsin is home to 6 native species, including *Orconectes virilis*, *O. propinquus*, *O. immunis*, *Cambarus diogenes*, *Procambarus acutus* and *P. gracilis* (Creaser 1932; Hobbs and Jass 1988), and the non-indigenous species *Orconectes rusticus*. Note that *O. propinquus* is presumed native to southern and eastern Wisconsin (Creaser 1932), and has subsequently invaded the northern parts of the state. The dataset contains 2,775 crayfish locality records collected from 1870 to 2004 throughout the entire state, including tributaries of the Upper Mississippi River Basin, Lake Superior Basin and Lake Michigan Basin.

Records include incidence, identity, and collection information for the complete holdings of major regional museum collections, numerous smaller holdings, records from peer-reviewed and gray literature sources, university theses and dissertations, and recent field surveys by the authors. Major data sources included: Hobbs and Jass (1988), Creaser (1932), Capelli (1975), Magnuson et al. (1975), Lang (1977), Sheffy (1978), Lorman (1980), Capelli and Magnuson (1983), Lodge and Hill (1994), National Park Service (unpublished data), Jass (2001), and Wisconsin

Department of Natural Resources (DNR) (data provided by David Lodge and colleagues, the North-Temperate Lakes-Long Term Ecological Research Program (NTL-LTER), unpublished crayfish DNR survey data, personal communication with DNR staff). Notably, 126 records of rusty crayfish from the DNR were obtained from an invasive species survey that included only rusty crayfish records.

Present-day records were the result of extensive field sampling in 2004 across the entire state of Wisconsin by the authors McCarthy and Fetzer ($n=143$ stream segments and lakes), and the Wisconsin DNR ($n=108$ stream segments and lakes). Sampling locations were primarily in the vicinity of boat launches or road crossings for accessibility reasons, which will tend to minimize the probability of false absences for rusty crayfish because these are principle areas of human introductions, but at the same time, could underestimate the occurrences of native species. The authors used modified minnow traps (entrance holes ca. 5 cm diameter) baited with beef liver or sardines that were set in a variety of bottom types in lakes, streams and rivers. At these sites, 5–10 traps were set at a depth range of 0.25–1.0 m in streams and 1.0–2.0 m in lakes for 20–24 h. Streams were sampled using a combination of trapping, dip netting and hand collection techniques, and lakes were sampled using two transects of 5 minnow traps each. Temperature ($^{\circ}\text{C}$), dissolved oxygen (mg/l) and conductivity ($\mu\text{s}/\text{cm}$) measurements were taken using YSI instrumentation, local habitat characteristics were recorded for each site, and water samples were taken to measure total nitrogen, total phosphorous and major cation concentrations. DNR collected crayfish using a combination of minnow trapping and hand collection (38% of sampling sites), mini-fyke nets (7%), and electro-shocking (55%). Crayfish collected from both surveys were preserved in the field using 95% ethanol and later identified by the authors at the University of Wisconsin-Madison Center for Limnology.

All crayfish records were geo-referenced in a Geographic Information System (ArcGIS, Environmental Systems Research Institute, v. 8.3). Sporadic occurrence records preclude us from examining yearly changes in rusty crayfish distributions over time, but based on the timing of

major collection events we were able to explore the invasion sequence by partitioning the dataset into 3 time periods: (1) pre-invasion years (1870–1964), (2) early post-invasion years (1965–1984: 20 years), and (3) extant years (1985–2004: 20 years).

Results

Rusty crayfish are now broadly distributed across the state of Wisconsin. They have been recorded 386 times from streams, rivers or lakes, and comprise 17% of all crayfish records collected since its first sighting in 1965 (Figure 1a). Extant distribution of rusty crayfish includes 36 of 42 sub-watersheds (86% of watersheds), where the highest frequency of occurrence (controlling for the total number of records) is in Wisconsin's Northern Highlands Lake-District (Figure 1b). The proportion of records containing rusty crayfish has increased five-fold in recent years from 7% of sites between 1965 and 1984 (130 out of 1,776 records) to 36% of sites (130 out of 366 records, excluding the 126 sites from the invasive species survey mentioned previously) during the last 20 years (Figure 2). Interestingly, rusty crayfish appear to have invaded lakes (49% of the records) at higher frequencies than expectations based on sampling effort (19% of all records since 1965).

The nature of our dataset (i.e., species collected sporadically over space and time) precludes us from being able to make robust statements regarding distributional declines in native crayfishes over time. However, substantial changes in relative proportion of native crayfish records suggest that there have been a major shift in species dominance, most notably for *O. virilis*. Before rusty crayfish invasion (pre-1965), *O. virilis* comprised 62% of the records, whereas 20 years after the invasion (1965–1984) and during the past 20 years (1985–2004) they represented 54% and 34% of the records, respectively (Figure 2). These findings agree with Lodge et al. (2000a) who reported that of the 107 lakes and 50 stream reaches surveyed in northern Wisconsin and the Upper Peninsula of Michigan where *O. virilis* was the only common crayfish in the first decades of this century (Creaser 1932) – *O. virilis* now occurs

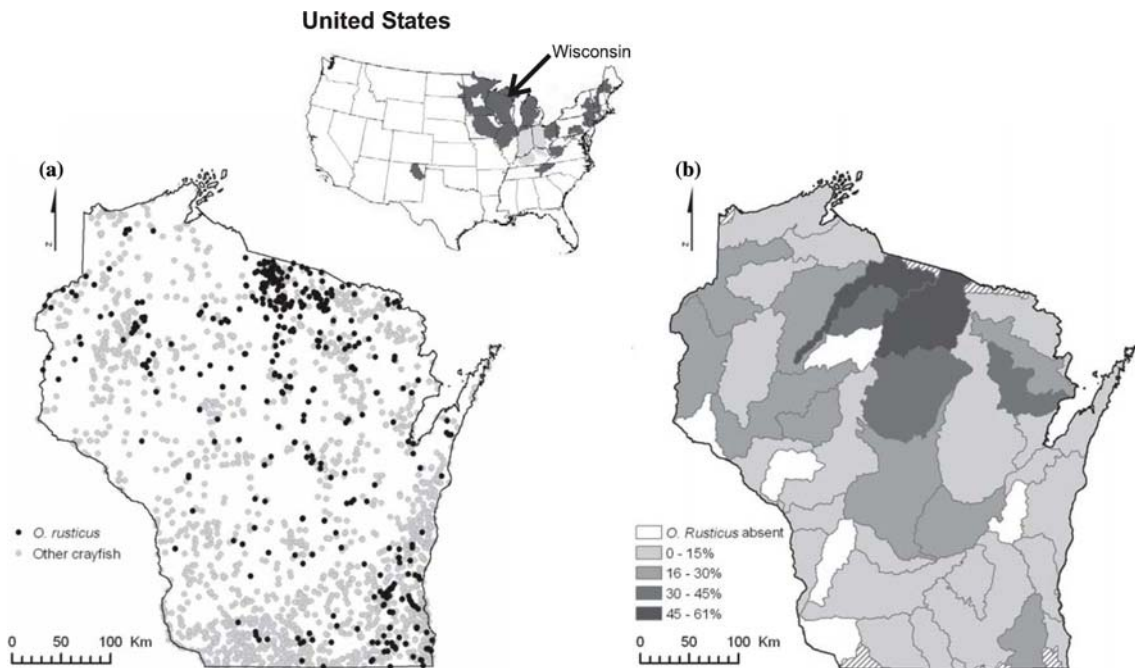


Figure 1. (a) Occurrence records of rusty crayfish (black circles) and all other native crayfish species (grey circles) in Wisconsin collected between 1870 and 2004 ($n=2,775$). (b) Frequency of rusty crayfish collections (expressed as a percentage of the total number of crayfish records) by sub-watersheds (8-digit hydrologic units: <http://water.usgs.gov/>). Top inset illustrates the native (light grey) and non-native (dark grey) distributions of rusty crayfish in the United States, and the state of Wisconsin is indicated by the arrow (source: <http://nas.er.usgs.gov/>).

in only 44% and 38% of the lakes and streams, respectively. The remaining native species that were less frequently collected in historical surveys showed similar proportional declines in their relative occurrences; with the exception of *O. propinquus*.

Based on simple patterns of watershed co-occurrence, rusty crayfish showed significant spatial overlap with all native species in the following decreasing order: *Orconectes virilis* (36 of 42 watersheds, 86%); *O. propinquus* (36 of 42 watersheds, 86%); *Cambarus diogenes* (27 of 30 watersheds, 90%); *Procambarus acutus* (15 of 16 watersheds, 94%); *O. immunis* (11 of 12 watersheds, 92%); and *P. gracilis* (3 of 3 watersheds, 100%). This result indicates that the potential for the negative interactions and possible hybridization with native crayfish species is high (Perry et al. 2002). Moreover, because of the large spatial scale of this study, our analysis likely under-estimates the overall geographic distribution of both rusty crayfish and native species.

Discussion

Rusty crayfish has successfully invaded the entire state of Wisconsin and now constitutes a significant component of the crayfish fauna. Long-term occurrence records from 1870 to 2004 show that (1) rusty crayfish occurrences have increased from 7% of all crayfish records collected during the first 20 years of their invasion (1965–1984) to 36% of all records during the last 20 years, and (2) rusty crayfish have replaced the northern clearwater crayfish (*O. propinquus*) and virile crayfish (*O. virilis*) as the most dominant member of the contemporary crayfish fauna. A rich body of literature from research conducted in northern Wisconsin and Michigan provide strong insight into the introduction, establishment and integration phases of the rusty crayfish invasion, and below we briefly discuss each of these in turn.

Vectors of rusty crayfish introduction include bait bucket discharge from recreational anglers (Ludwig and Leitch 1996) and intentional releases by lake-users for nuisance weed control

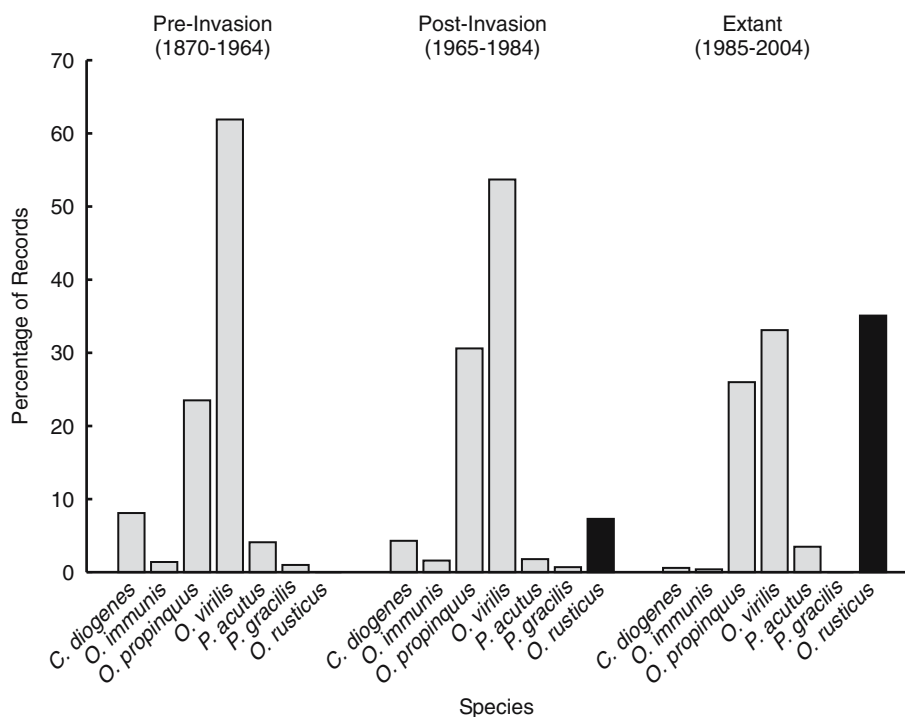


Figure 2. Percentage of rusty crayfish records (black bar) and native crayfishes records (grey bars) of Wisconsin for three time periods: (1) pre-invasion years (1870–1964), (2) post-invasion years (1965–1984: 20 years), and (3) extant years (1985–2004: 20 years).

(Magnuson et al. 1975) and commercial crayfish retailers (Gunderson 1999). Support for these mechanisms comes from Capelli and Magnuson (1983) who found that human activity and lack of geographic isolation were the best predictors of rusty crayfish occurrence in lakes of northern Wisconsin. Natural inter-lake dispersal of rusty crayfish is also possible and may represent an important vector of introduction (Olsen et al. 1991; Bryon and Wilson 2001). In 1982, Wisconsin prohibited the use of crayfish as live bait and the introduction of live crayfish in inland waters¹; however, the impact of this law on slowing rusty crayfish invasion is difficult to assess.

Once introduced, successful establishment of rusty crayfish depends on the environmental and biological suitability of the receiving waters. In addition to the availability of firm substrates (Kershner and Lodge 1995) and shelter for egg- or young-carrying females and molting individuals, the persistence of rusty crayfish appears to be dependent on two key physiochemical factors – dissolved calcium and pH. Correlative studies

have identified two critical thresholds where rusty crayfish are absent from lakes with pH values lower than 5.5 (Berrill et al. 1985) and dissolved calcium concentrations less than 2.5 mg/l (Capelli and Magnuson 1983). A preliminary analysis plotting pH and Ca^{2+} values for 527 lakes in Wisconsin², demonstrates that 463 or 88% of lakes exceed these critical thresholds, and therefore can be considered potentially suitable for rusty crayfish persistence (Figure 3). Similarly, Vander Zanden et al. (2004a) found that 70% of North American Shield lakes (626 out of 895 lakes) are environmentally-suitable based on the same thresholds. With more than 15,000 lakes and 32,000 miles of perennially flowing waters embedded in the Wisconsin landscape, we present these results to illustrate the need to develop models that forecast the potential distribution of rusty crayfish at broad spatial scales. This general approach to forecasting future invaders based on potential occurrences and food web impacts was recently demonstrated by Vander Zanden et al. (2004b). Similar analysis for rusty crayfish and

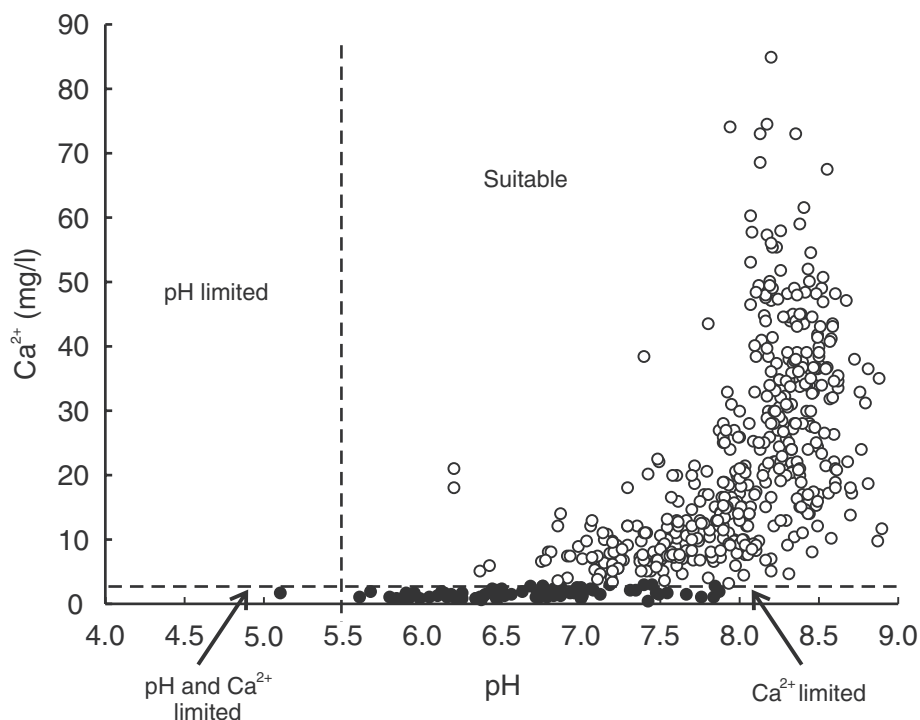


Figure 3. Preliminary analysis of physiochemical thresholds potentially limiting the establishment of rusty crayfish in Wisconsin lakes. The vertical line delineates the pH threshold of 5.5 and the horizontal line delineates the Ca^{2+} threshold of 2.5 mg/l, above which rusty crayfish are predicted to occur (empty circles) and below which are predicted to be unsuitable for establishment (filled circles).

other invaders in the upper Midwest are currently in progress, specifically where ecological niche modeling based on multi-scaled descriptors of the environment are being used to predict rusty crayfish distributions and design conservation plans for native crayfishes throughout Wisconsin.

Once established, the highly aggressive and omnivorous feeding behavior of rusty crayfish has resulted in numerous ecological impacts manifested across entire lake food webs. In this region, rusty crayfish invasions have been associated with negative effects on benthic algae (Charlebois and Lamberti 1996), macrophytes (Lodge and Lorman 1987), aquatic invertebrates and snails (Olsen et al. 1991) and fish (Wilson et al. 2004), in addition to displacing and hybridizing with native species, especially *O. propinquus* and *O. virilis* (e.g., Lorman 1980; Capelli 1982; Lodge et al. 1986; Olsen et al. 1991; Hill and Lodge 1999; Perry et al. 2001). In a long-term study of Trout Lake, Wisconsin, Wilson et al. (2004) found that rusty crayfish reduced mean lake-wide

abundance of Odonata, Amphipoda and Trichoptera, decreased snail densities and reduced submerged macrophyte species richness at some locations, and all but eliminated resident *O. propinquus* and *O. virilis* populations. Taken together, crayfish play a pivotal role in aquatic systems (Momot 1995), and consequently the invasion of rusty crayfish have often been accompanied with negative impacts on littoral-zone food webs (Lodge et al. 1994).

Perhaps the best proactive method for controlling the introduction of rusty crayfish is through the education of anglers, bait dealers and the lay public regarding the ecological threats posed by rusty crayfish (Gunderson 1999). Distributional maps of rusty crayfish (such as the one presented here) would provide a means of identifying those lakes and watersheds where introductions have been the most frequent and where educational efforts should be targeted. In contrast, more reactive approaches may include chemical control (although selective chemical agents targeting just

rusty crayfish and not native species do not exist: Bills and Marking 1988), enhancing fishery management practices to promote “healthy” bass and sunfish populations to control crayfish population levels via predation (Momot 1984), and developing a viable commercial harvest of rusty crayfish from natural lakes that would serve to discourage intentional introductions by trappers (although only a few commercial trappers remain active: Arora and Wik 1988). In fact, some lake owners associations have voluntarily promoted catch and release fisheries of smallmouth bass with the hope of naturally-controlling rusty crayfish densities.

In conclusion, our study shows that rusty crayfish have rapidly invaded streams, rivers and lakes throughout the entire state of Wisconsin over the past 40 years. A striking result is that rusty crayfish has replaced *O. propinquus* and *O. virilis* as the most dominant member of the contemporary crayfish fauna. This pattern of rapid expansion across the Wisconsin landscape stands in contrast with the relatively slow spread of rusty crayfish within Trout Lake reported by Wilson et al. (2004), where it took nearly 20 years for rusty crayfish to occupy the available littoral zone habitat of this northern Wisconsin lake. This apparent mismatch of invader spread at different scales highlights our limited understanding of the dynamics of exotic invader spread on landscapes, and is an area of ongoing research. We are currently using expert-based modeling using crayfish occurrence data to provide site-specific probabilities of rusty crayfish arrival, establishment and integration into native ecosystems of Wisconsin, with the ultimate goal of incorporating this information into statewide efforts to manage invasive species spread.

Acknowledgments

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Notes

1. Wisconsin Administrative Code, DNR Chapter NR 19.27(4), 2002.
2. U.S. Environmental Protection Agency STORET database, <http://www.epa.gov/storet/>.

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