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B. J. Verts
Oregon State University, Corvallis, Oregon

Leslie N. Carraway
Oregon State University, Corvallis, Oregon

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DISPERSAL AND DISPERSION OF AN INTRODUCED POPULATION OF *SYLVILAGUS FLORIDANUS*

B. J. Verts[1] and Leslie N. Carraway[1]

Abstract.— Eastern cottontail rabbits, *Sylvilagus floridanus,* introduced into Linn County, Oregon, in 1941, occupied 378.1 km^2 in 1953, 637.7 km^2 in 1970, and 1501.9 km^2 in 1980. Hiatuses within the range were related to absence of adequate coverts on conifer-dominated ridge tops and in intensively cultivated areas. Flooding of riparian zones seven times during the first 12 years after introduction and three times during the 17-year interval between the first and second surveys (especially the devastating floods of December 1964 and January 1965) was believed to have retarded dispersal or periodically reduced the area occupied. Flood-control dams constructed between 1941 and 1968 on drainage systems that affect the area limited floods to two winters since 1965 and were believed responsible for cottontails extending their range within the county nearly two and one-half fold since 1970. The absence of burrow-constructing associated species was believed relatively insignificant in retarding dispersal. Removal of brushy coverts, particularly by agricultural practices, tended to increase the size of unoccupied areas within the 1970 range of the species.

Eastern cottontail rabbits (*Sylvilagus floridanus,* indigenous to most of the United States east of the Rocky Mountains (Hall and Kelson 1959) were introduced into Linn County, Oregon, near the community of Oakville in May 1941 (Graf 1955). Graf (1955) documented the unsanctioned introduction, reported on a survey of cottontail distribution in Linn County in 1953, and speculated on avenues they used for dispersal. Although the late Professor Graf did not publish his range map in the original article, he gave the map to Verts, who, with a student, repeated the survey of distribution in 1970 and published both maps with suggestions for possible mechanisms of expansion and contraction of the cottontail range during the 17 intervening years (Verts et al. 1972). We wished to reexamine the dispersion of cottontails after 10 additional years and to evaluate the vegetation at all sites at which cottontails were observed during earlier surveys to ascertain the effect of alterations on current distribution. Also, we wished to evaluate avenues for dispersal, or lack thereof, on distribution of cottontails.

Study Area

Linn County, Oregon, is roughly rectangular (59 x 114 km) and lies near the center of the Willamette Valley (44°12′–44°47′N, 121°48′–123°15′W). It is bounded by the Willamette River on the west, North Santiam River on the north, and the crest of the Cascade Range on the east; the southern border, although largely irregular, is artificial. Elevations range from about 60 m above mean sea level at the confluence of the Willamette and Santiam rivers to nearly 3200 m at the summit of Mt. Jefferson in the Cascade Range; eastward from the Willamette River, relief is

[1]Department of Fisheries and Wildlife, Oregon State University, Corvallis, Oregon 97331.

negligible to the foothills of the Cascades (about 35 km) except for a few scattered buttes near the foothills.

The portion of Linn County in the Willamette Valley is largely agricultural, with production of grass seed (mostly rye grasses, *Lolium perenne* and *L. multiflorum*), wheat, and vegetable crops predominant. Oregon white oak (*Quercus garryana*), Oregon ash (*Fraxinus latifolia*), Douglas fir (*Pseudotsuga menziesii*), and black cottonwood (*Populus trichocarpa*) are typical trees of the riparian zone along major streams. Brambles, particularly blackberries (*Rubus discolor* and *R. laciniatus*), are common along small streams, edges of woodlots, railroad rights-of-way, fencerows, and field borders. Scattered buttes and low foothills are vegetated mostly by deciduous trees, especially oaks, but ridge tops and the west slope of the Cascade Range are covered mostly by subclimax Douglas fir (Johannessen et al. 1970, Franklin and Dyrness 1969).

The climate of the Willamette Valley is moderate; at Corvallis (at the west edge of the study area) January temperatures average 3.8 C, whereas July temperatures average 18.8 C. Precipitation averages 100.8 cm annually, with 82 percent falling between November and May (U.S. Department of Commerce 1978). Temperatures decline and precipitation increases (and the proportion falling as snow increases) with increasing elevation in the Cascade Range.

Methods

Initially, to establish the current range of cottontails, we traversed all roads in western Linn County surveyed by Graf (1955) or Verts et al. (1972). We made 14 automobile trips from 1 to 18 July 1980 totaling 1390.5 km between 1900 and 2200 h Pacific Daylight Time (PDT). Roads traversed and cottontails observed during each trip were recorded on separate county road maps.

To determine the location and extent of vegetative changes affecting current dispersion of cottontails, we classified all sites at which cottontails were observed during 1953 and 1970 surveys as occupiable or unoccupiable coverts on the basis of the physiognomy of vegetative communities where we saw cottontails in 1980. Because established populations of cottontails in Oregon seem to require an interspersion of grassy and brushy vegetation, similar to that described for the species in its native range (Schwartz and Schwartz 1959, Atzenhofer and Leedy 1947), we defined an unoccupiable site as one without brushy vegetation within 200 m. This analysis required six trips (20–27 July 1980 between 0430 h and 0745 h PDT) totaling 621.1 km; we recorded roads traversed and cottontails observed as before.

On the basis of the physiognomy of vegetative communities at sites occupied by cottontails, we extended our survey to similar roadside communities from the eastern limit of the 1970 cottontail range to the foothills of the Cascades. From 28 July to 3 August 1980, we made seven trips totaling 1035.6 km between 0445 and 0815 h PDT. We limited our survey at the foothills because we saw no cottontails in coniferous forests and such areas did not support the requisite grassy and brushy vegetation.

We considered the range occupied by cottontails as that area east of the Willamette River that extended 0.8 km beyond the furthermost points at which cottontails were seen, the same criterion used by Verts et al. (1972). Areas of ranges were estimated by use of a compensating polar planimeter.

Results

In 1980, 96 eastern cottontail rabbits were seen in an area of about 1501.9 km^2; thus, the range of the cottontail in Linn County increased nearly two and one-half fold from the estimated 637.7 km^2 in 1970, which, in turn, was about 40.7 percent larger than the 378.1 km^2 estimated for 1953 (Fig. 1). However, cottontails were not observed in all areas searched; relatively large areas in the vicinity of Scio, Sweet Home, and Harrisburg seemingly did not contain rabbits (Fig. 1). Also, within the region seemingly invaded within the last decade, distribution was not uniform, and, within the 1970 range, unoccupied areas that were occupied formerly (Verts et al. 1972) continued to increase in size. Nevertheless, approximately three times as many cottontails were observed per 100 km traveled within the 1970 range as in the area

searched in 1970 but in which no cottontails were seen (Table 1).

We judged that only 61 of 111 sites at which cottontails were observed in 1953 by Graf (Verts et al. 1972) supported coverts occupiable by cottontails, whereas 40 of 48 sites at which cottontails were seen in 1970 were judged to continue to support occupiable vegetative communities (Fig. 2). Current differences in numbers of occupiable

TABLE 1. Distances traveled, cottontails seen, and cottontails seen per 100 km traveled within and outside the 1970 cottontail range in Linn County, Oregon, 1 July–3 August 1980.

Area	Distance traveled		Cottontails seen		Cottontails/100 km	
	Morning	Evening	Morning	Evening	Morning	Evening
Within 1970 range	460.9	820.9	41	18	8.9	2.2
Outside 1970 range	1195.8	569.6	33	4	2.8	0.7

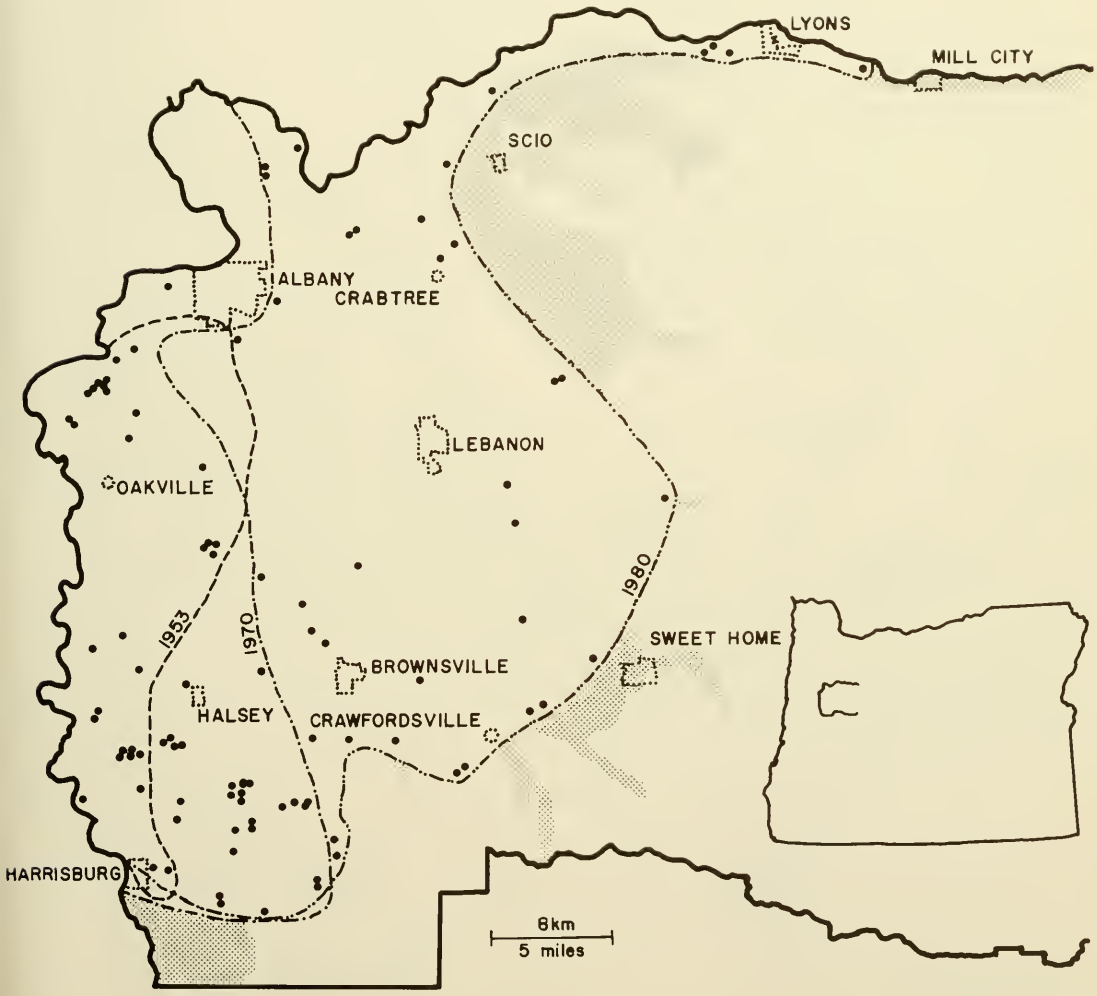

Fig. 1. Distribution of 96 eastern cottontail rabbits observed during roadside surveys conducted 1 July–3 August 1980 and ranges of cottontails in western Linn County, Oregon, in 1953, 1970, and 1980. Roads within stippled areas were searched but no cottontails were observed. Inset depicts location of study area in Oregon. Ranges of cottontails in 1953 and 1970 after Verts et al. (1972).

and unoccupiable sites between the two earlier surveys were significantly different (X^2 = 11.624, df = 1, $P < 0.01$).

Most cottontails observed in the area seemingly invaded since 1970 occurred in close proximity to water courses (Fig. 3); large hiatuses in the newly occupied range occurred primarily in areas without drainage by permanent streams.

DISCUSSION

Changes in the Range

In the 12 years between introduction and the first survey in 1953, cottontails extended their range about 25 km southward but only about 6 km eastward (Graf 1955). The continuity of suitable coverts along north-south

Fig. 2. Sites at which eastern cottontail rabbits were observed in western Linn County, Oregon, in 1953 (circles) and 1970 (squares) (after Verts et al. 1972). Open symbols indicate sites at which no brushy vegetation occurred within 200 m in 1980, thus were judged to be unoccupiable by cottontails.

railroad rights-of-way and the paucity of similar continuous suitable cover eastward from the point of release were offered as possible explanations for directional differences in range expansion (Graf 1955). Destruction of coverts as a result of agricultural practices and winter flooding of riparian zones were offered as explanations for cottontails failing to extend their range to areas beyond the limits of the 1970 range during the 17 years between the first and second surveys (Verts et al. 1972). Because the rate of occupation of new range during the first 29 years after introduction was comparatively modest, the relatively rapid two and one-half fold expansion in range during the last decade requires explanation.

We cannot discount entirely the possibility that cottontails actually occupied much larger ranges in 1953 and 1970 than described (Verts et al. 1972), and that the rapid increase in range expansion in the last decade was an artifact of survey methods used earlier. However, the three-fold greater numbers of cottontails seen during the 1980 survey in the area occupied by cottontails before 1970 than in the area seemingly invaded during the last decade (Table 1) and the large

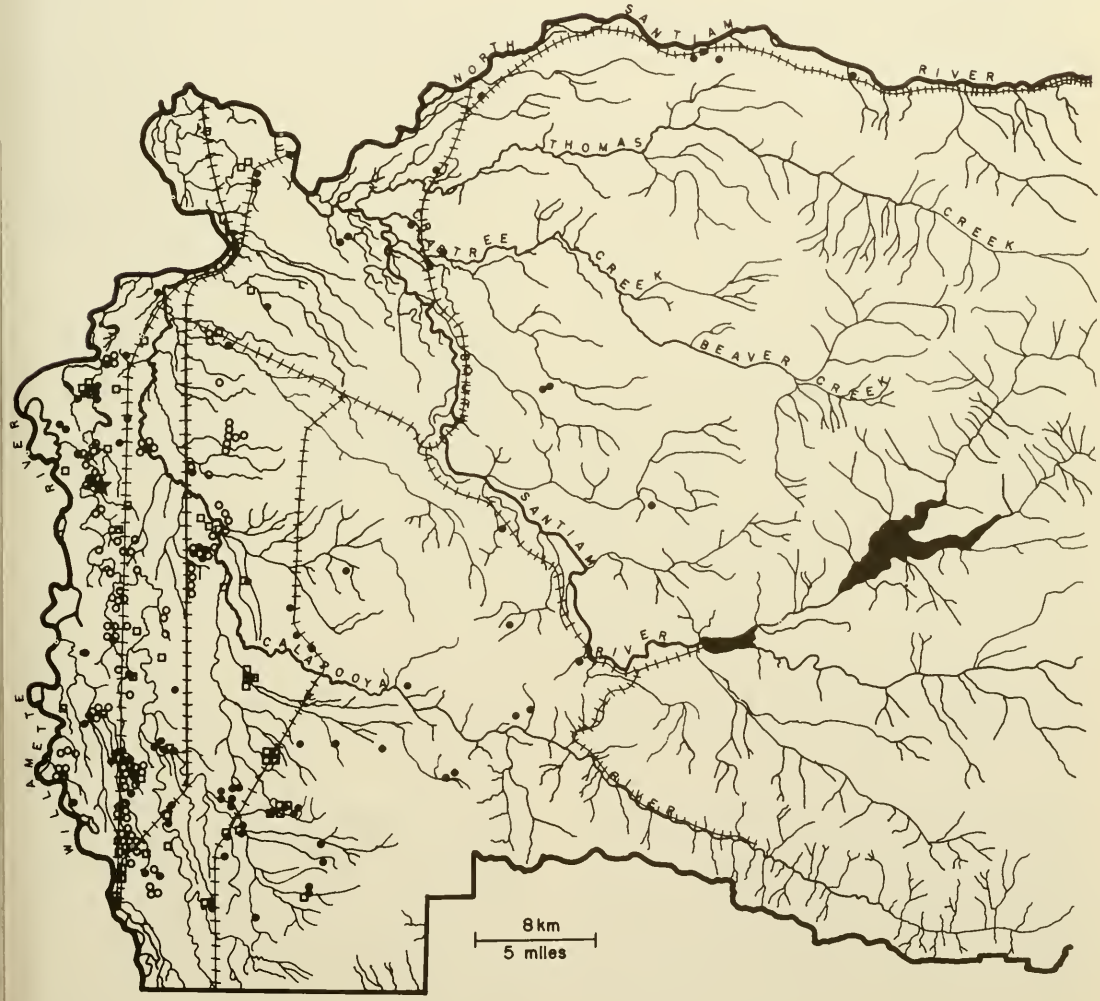

Fig. 3. Distribution of eastern cottontail rabbits observed during roadside surveys conducted in western Linn County, Oregon, in 1953 (open circles), 1970 (open squares), and 1980 (solid circles) in relation to water courses and railroad rights-of-way. Data for 1953 and 1970 from Verts et al. (1972).

hiatuses in distribution within the range occupied since 1970 (Fig. 1) indicate that invasion east of the 1970 range was likely of relatively recent occurrence.

The proximity of sightings of cottontails to streams in areas recently occupied (Fig. 3) indicates that coverts in riparian zones likely were important avenues for cottontail dispersal. Also, in newly invaded range, the relative infrequency that cottontails were seen in areas remote from permanent streams suggests that upland coverts were occupied more slowly than riparian zones. Therefore, we suspect that winter flooding of riparian areas had a significant deleterious impact on cottontail dispersal, and that the frequency and magnitude of floods was responsible for differences in observed rates that new range was invaded.

Since introduction of cottontails, winter flooding was reduced significantly by 10 flood-control dams constructed between 1941 and 1968 (International Commission on Large Dams 1973) on streams or tributaries to streams that drain the study area (Fig. 4). In the 12-year interval between introduction of cottontails and the first survey of distribution in 1953, flooding of riparian zones occurred seven times, possibly explaining the relatively limited dispersal of cottontails during that period (Graf 1955). Although riparian zones were flooded only three times during the 17-year period between the first and second surveys, the floods of December 1964 and January 1965 were of such magnitude that populations not occupying coverts remote from streams likely were eliminated or severely reduced in numbers. Thus, the 1970 survey (Verts et al. 1972) possibly was conducted after a major reduction in the cottontail range and before cottontails redispersed from coverts unaffected by the 1964–65 floods. Since 1970, however, flooding of riparian zones occurred only twice; no flooding occurred since January 1974 (Fig. 4). Although dispersal of cottontails likely was retarded and the range possibly reduced by floods during the early part of the decade between the second and third surveys, we believe that the 6 years since the last flood were adequate for cottontails to extend their range two and one-half fold (Fig. 1). High ground, not subject to flooding, and the nearly continuous suitable cover provided along the railroad right-of-way adjacent to the North Santiam River (Fig. 3) may explain the extent of cottontail dispersal along the north boundary of our study area (Fig. 1).

Unoccupied Areas within the Range

Treatment of cottontail dispersion on the study area must include explanation of several relatively large areas seemingly unoccupied in 1980 that were occupied during earlier surveys (Fig. 1). The increase in size of the unoccupied area south of Albany since 1970 (Fig. 1) and the appearance of unoccupied areas south of Oakville and north of Harrisburg (Fig. 1) likely were related to loss of brushy coverts (Fig. 2). We found one or more coverts occupied by cottontails in 1953 or 1970 replaced by industrial complexes, warehouses, or condominiums. However, modification of most sites judged no longer occupiable by cottontails (Fig. 2) was related to agricultural practices, particularly removal of brushy fencerows.

Within the newly occupied range, cottontails were not found on ridge tops or in agricultural areas between major stream systems. We suspect that coniferous forests that exclude understories of brushy and grassy species make many ridge tops unsuitable for occupancy by cottontails. Disjunct brushy coverts in agricultural areas, although sufficiently large and of adequate quality to support cottontails, may not be occupied because intervening crops do not serve as suitable cover at seasons that juveniles disperse. These coverts may become occupied by cottontails in the future.

Also, a large area in the vicinity of Scio, searched, but seemingly not occupied by cottontails (Fig. 1), may be invaded in the future. We are unable to offer a plausible explanation for the absence of cottontails in the area, because Thomas Creek and Crabtree Creek (Fig. 3) should provide avenues for dispersal, and brushy fencerows interconnecting with riparian zones to support cottontails were relatively abundant. A small unoccupied area near Sweet Home (Fig. 1) seemed to support vegetative communities adequate for cottontails, but coverts suitable for cottontails were absent in much of the

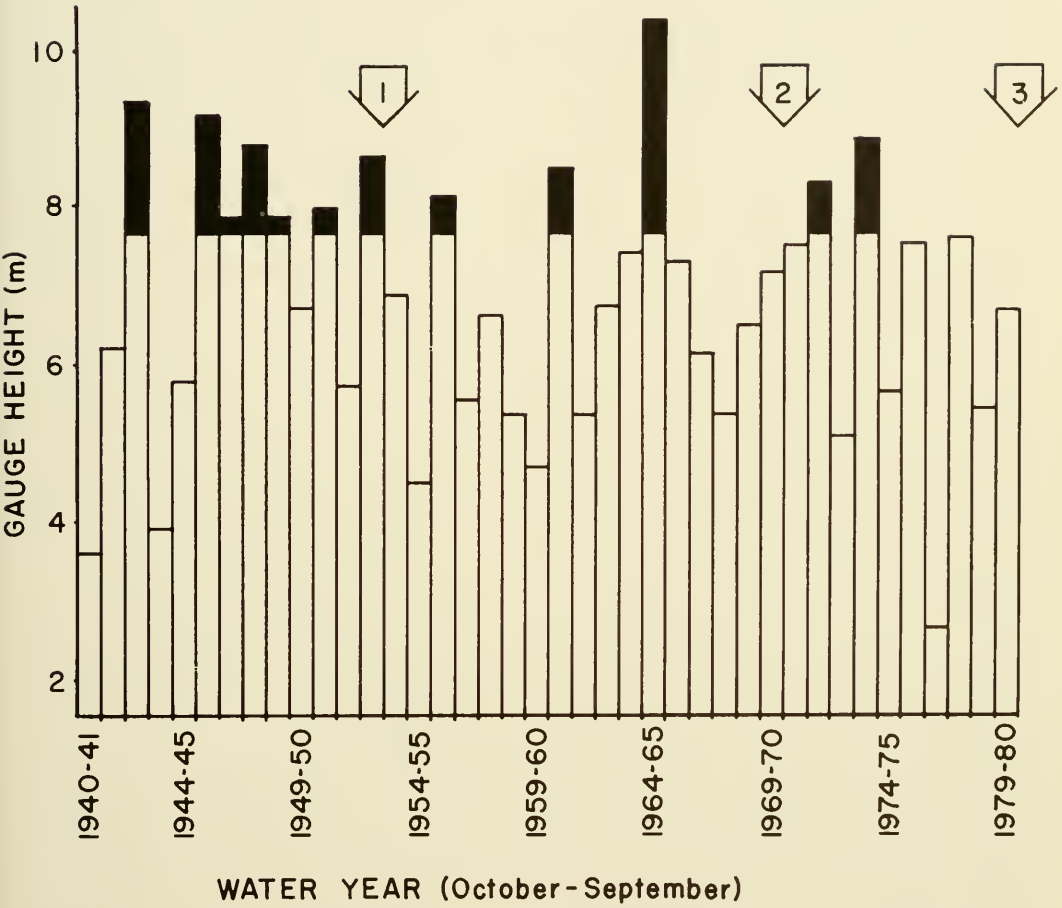

Fig. 4. Maximum gauge height for the Willamette River at Albany, Oregon, each water year, 1940–41 to 1979–80. Datum of gauge is 52.48 m above mean sea level. Solid portions of bars indicate height above flood stage (7.62 m) established by the U.S. Weather Bureau. Arrows indicate years that the three surveys of cottontail distribution were conducted. Hydrologic data are from Hulsing and Kallio (1964), U.S. Department of the Interior (1958–1978), and L. Hubbard, U.S. Geological Survey (pers. comm.).

unoccupied area south of Harrisburg, except for the narrow riparian zone along the Willamette River (Fig. 1).

Comparative Rates of Dispersal

The rate of dispersal of cottontails on our Linn County study area was infinitesimally slow in comparison with the more than 113 km per year that introduced European rabbits (*Oryctolagus cuniculus*) averaged in New South Wales, Australia (Keast 1966). The disparity was especially great in view of differences in productivity reported for introduced populations of the two species; female European rabbits in Australia produced about 26 young in four or five litters during the annual breeding season (Myers and Poole 1962), whereas female cottontails in Oregon produced about 39 young in eight litters

(Trethewey and Verts 1971). Also, juvenile female cottontails older than 3.5 months commonly bred and some produced at least two litters during the breeding season in which they were born (Trethewey and Verts 1971), but confined populations of European rabbits were not reported to produce offspring in the season of their birth (Myers and Poole 1962), and, among wild populations, 95 percent of the productivity was by females more than six months old (Dunsmore 1971). In addition to having lower natality than cottontails, dispersing European rabbits in Australia were subjected to intensive control measures (Troughton 1943), whereas cottontails in Oregon have not become pests (Verts and Carraway 1980) and hunting of introduced cottontails has not become a popular sport (M. Henjum, pers. comm.).

Myers and Parker (1965) suggested that unoccupied burrow systems of the boodie (*Bettongia lesueuri*) preconditioned the habitat for warren-dwelling European rabbits and contributed to their rapid dispersal. Grizzell (1955), Linduska (1947), Hamilton (1934) and others documented the use of woodchuck (*Marmota monax*) burrows by cottontails and believed that burrows were important to survival of cottontails in the northern portion of their native range. The absence of a burrow-constructing ecological equivalent to *Bettongia* or *Marmota* west of the Cascade Range in Oregon possibly contributed to the slow rate of cottontail dispersal. However, use of burrows by cottontails in their native range usually was limited to inclement weather (Linduska 1947) more severe than occurs commonly in the Willamette Valley, Oregon.

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