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Descendants of eastern cottontails from Ohio (Sylvilagus floridanus) introduced in Benton County, Oregon and cottontails from Ohio were sampled and analyzed morphometrically and colorimetrically. In general, Oregon cottontails were smaller and lighter in color than Ohio rabbits. Introgression and interspecific competition with the smaller and darker colored native brush rabbit (S. bachmani) were considered unlikely explanations for observed small size and light color in introduced cottontails. Seasonal differences in rainfall between Ohio and Oregon were suggested as a possible selective force because of the apparent effect of rainfall on population dynamics of Nuttall's cottontails

(*S. nuttallii*). Random processes (genetic drift and an unrepresentative founding population) could not be rejected as possible causes for both small body size and light pelage color. A combination of selective and random processes seems the likely explanation for observed morphological differences.

Morphological Changes in Introduced Eastern Cottontails in Oregon

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MORPHOLOGICAL CHANGES IN INTRODUCED EASTERN COTTONTAILS IN OREGON

INTRODUCTION

In 1939, about 100 offspring born in captivity in Oregon to six pairs of eastern cottontails, Sylvilagus floridanus, purchased near Kent, Ohio, were released near Corvallis, Benton County, Oregon (Graf, 1955). Graf (1955) believed the Willamette River acted as a barrier to dispersal and prevented mixing of this population with one established 2 years later in Linn County with cottontails brought from Illinois. Systematic surveys in 1953 (Graf, 1955), 1970 (Verts et al., 1972), and 1980 (Verts and Carraway, in press) indicated that the Linn County population was established and had spread to habitats unoccupied previously. Casual observations of eastern cottontails in Benton County indicated that they were established at the time of the first Linn County survey (Graf, 1955), and Trethewey and Verts (1971) found sufficient rabbits near the point of introduction to sample nearly 500 specimens from a 708-ha study area. The Benton County population also was reported at least as productive as populations in the native range of the species (Trethewey and Verts, 1971).

To become established as self-sustaining populations, introduced mammals must overcome or avoid pressures of new competitors (De Vos et al., 1956), new predators (Hershkovitz, 1968), new backgrounds for concealment (Sumner and Swarth, 1924; Dice and Blossom, 1937; Ingles, 1950), new climates (Hershkovitz, 1968; Baker et al., 1978), and new diseases (De Vos et al., 1956). Other mammals, introduced elsewhere, presumably better adapted to their new environments through changes in behavior (Davis, 1950; Lindemann, 1956) or through morphological changes (Turček, 1949; De Vos et al., 1956; Foster, 1964; Hershkovitz, 1968; Berry et al., 1978).

Eastern cottontails were subjected to new environmental pressures in Oregon. For example, Chapman and Verts (1969) reported agonistic interactions between cottontails and native brush rabbits (S. bachmani), and McCoy and Steenbergen (1969) and Trethewey and Verts (1971) found massive staphylococcal infections, unknown in the native range, to affect large proportions of samples of eastern cottontails in Oregon. Also, seasonal weather patterns (U. S. Department of Commerce, 1959, 1960) differ markedly between Oregon and the vicinity of the source of the introduced stock in Ohio (Fig. 1).

Many organisms that inhabit warm humid climates are

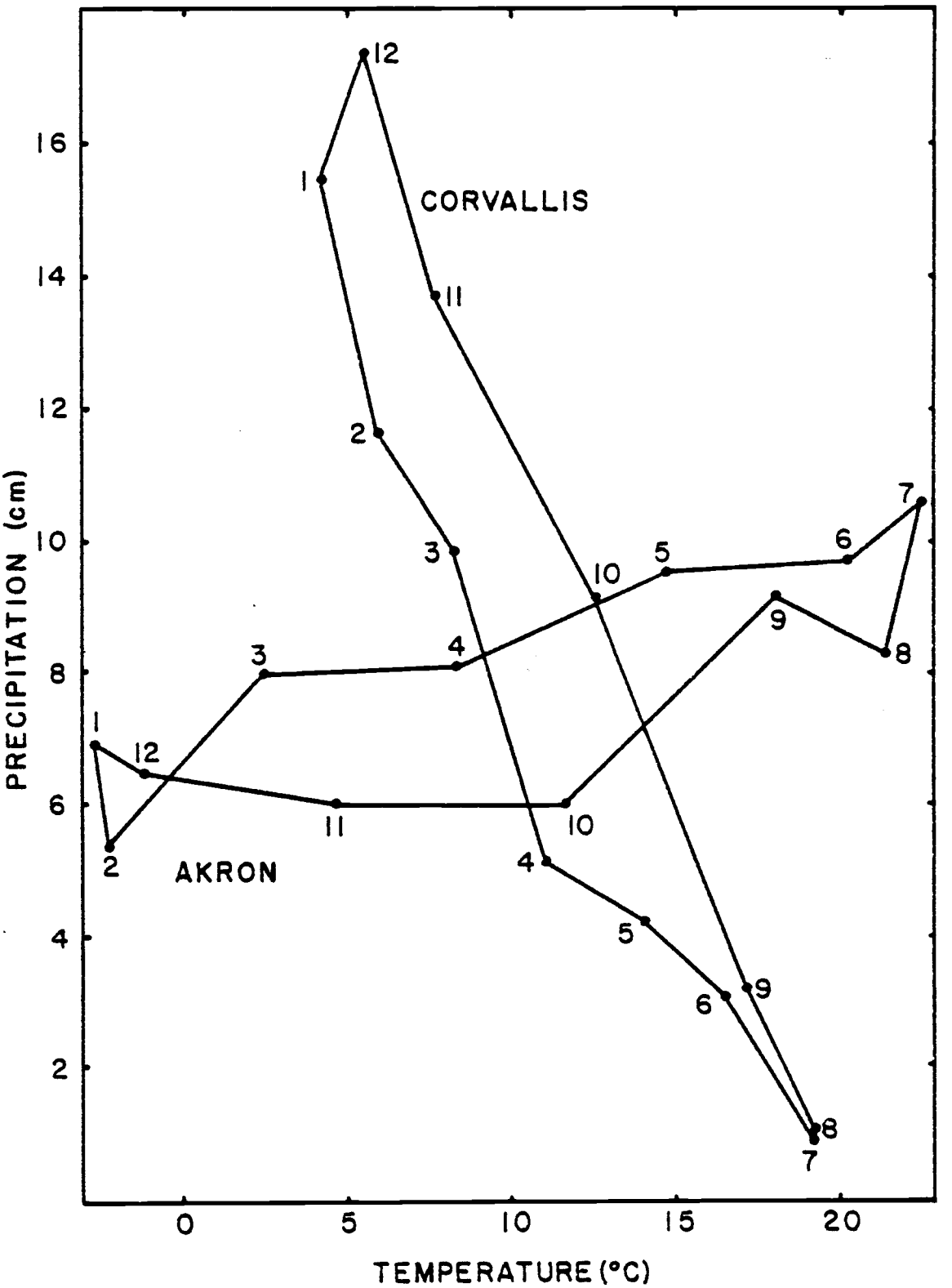

Fig. 1.--Temperature-precipitation climograph for Corvallis, Oregon and Akron (near Kent), Ohio. Numerals represent months.

colored more darkly than conspecifics or congeners that reside elsewhere (Gloger, 1833, as cited by Mayr, 1963). The large proportion of mammal species with more darkly colored subspecies in western Oregon (Nelson, 1909; Goldman, 1910; Jackson, 1928; Howell, 1929; Bailey, 1936) suggests that introduced cottontails might be subjected to forces responsible for dark coloration since introduction. Because introduced eastern cottontails possibly were subjected to these and other selective pressures of the new environment in Oregon, certain adaptive changes likely occurred.

The primary objectives of this research were to determine if the population of eastern cottontails established in Benton County, Oregon differed morphometrically and colorimetrically from samples of cottontails from Ohio and to determine, if possible, when those changes occurred and if similar changes continue in descendants of parental and introduced stocks.

METHODS

Seventy-four eastern cottontails collected in Benton County, Oregon on deposit in the Oregon State University Department of Fisheries and Wildlife Bird and Mammal Collections and 69 cottontails collected throughout Ohio during late winter and early spring 1979 and 1980 through cooperation of David Urban and the Ohio Department of Natural Resources were used in this study. In addition, 22 cottontails collected in Ohio before 1979 were obtained on loan from the Carnegie Museum of Natural History, The Cleveland Museum of Natural History, University of Illinois Museum of Natural History, The University of Michigan Museum of Zoology, and The University of Kansas Museum of Natural History (Appendix). To eliminate effects of size related to growth, only animals at least 170 days old were used; age was determined from ossification of cranial sutures (Hoffmeister and Zimmerman, 1967). All but three were in winter pelage; color band lengths and reflected light measurements in these specimens were consistent with specimens in winter pelage.

Twenty-one of 26 skull characters described by Diersing (1978) were measured to the nearest 0.1 mm with dial calipers (Table 1). In addition, total length, tail

Table 1.--Means, standard errors, coefficients of variation (in parentheses) for skeletal characters (in mm) for five cottontail groups: 1) all Ohio males (n = 36), 2) all Ohio females (n = 23), 3) Oregon females collected 1968-70 (n = 7), 4) Oregon females collected 1979 (n = 32), 5) all Oregon males (n = 33). There were no significant differences between means tested by simultaneous confidence intervals.

	Ohio		Oregon		
	Group 1	Group 2	Group 3	Group 4	Group 5
Character	$\bar{X}$ ± 1SE (CV)	$\bar{X}$ ± 1SE (CV)	$\bar{X}$ ± 1SE (CV)	$\bar{X}$ ± 1SE (CV)	$\bar{X}$ ± 1SE (CV)
Greatest length of the skull	75.0±0.38 (0.03)	76.5±0.37 (0.02)	73.2±0.54 (0.02)	73.0±0.26 (0.02)	73.0±0.34 (0.03)
Skull depth	31.8±0.14 (0.03)	31.9±0.18 (0.03)	32.0±0.25 (0.02)	31.0±0.13 (0.02)	31.2±0.17 (0.03)
Shield-bullae depth	21.4±0.09 (0.02)	21.6±0.12 (0.03)	20.8±0.18 (0.02)	21.0±0.11 (0.03)	20.9±0.13 (0.04)
Alveolar length of the upper molariform row	14.3±0.09 (0.04)	14.6±0.12 (0.04)	13.7±0.08 (0.02)	13.7±0.09 (0.04)	13.6±0.09 (0.04)
Basal length	59.9±0.33 (0.03)	61.4±0.32 (0.03)	58.2±0.41 (0.02)	58.5±0.32 (0.03)	58.2±0.34 (0.03)

Table 1.--Continued.

Character	Ohio		Oregon		
	Group 1	Group 2	Group 3	Group 4	Group 5
	$\bar{X}$ ± 1SE (CV)	$\bar{X}$ ± 1SE (CV)	$\bar{X}$ ± 1SE (CV)	$\bar{X}$ ± 1SE (CV)	$\bar{X}$ ± 1SE (CV)
Incisive foramina length	18.5±0.16 (0.05)	19.5±0.21 (0.05)	18.1±0.28 (0.04)	17.8±0.13 (0.04)	18.0±0.14 (0.04)
Alveolar width of the upper molariform row at P^3	20.1±0.10 (0.03)	20.6±0.15 (0.04)	19.2±0.32 (0.04)	19.9±0.14 (0.04)	19.5±0.11 (0.03)
Postdental breadth	9.4±0.07 (0.04)	9.4±0.11 (0.06)	9.1±0.14 (0.04)	9.0±0.07 (0.04)	8.9±0.07 (0.05)
Cranial breadth	27.2±0.11 (0.02)	26.7±0.17 (0.03)	26.4±0.32 (0.03)	26.5±0.15 (0.03)	26.6±0.14 (0.03)
Basioccipital length	8.9±0.08 (0.05)	9.1±0.08 (0.04)	8.6±0.19 (0.06)	8.7±0.10 (0.06)	8.5±0.07 (0.05)
Bullae breadth	25.9±0.13 (0.03)	26.1±0.17 (0.03)	25.8±0.26 (0.03)	25.3±0.15 (0.03)	25.0±0.21 (0.05)
Greatest breadth of the nasals	15.1±0.17 (0.07)	15.3±0.20 (0.06)	14.6±0.33 (0.06)	14.0±0.14 (0.05)	14.4±0.14 (0.06)

Table 1.--Continued.

Character	Ohio		Oregon		
	Group 1	Group 2	Group 3	Group 4	Group 5
	$\bar{X}$ ± 1SE (CV)	$\bar{X}$ ± 1SE (CV)	$\bar{X}$ ± 1SE (CV)	$\bar{X}$ ± 1SE (CV)	$\bar{X}$ ± 1SE (CV)
Greatest breadth of the zygomatic arches	36.6±0.20 (0.03)	36.6±0.23 (0.03)	35.0±0.40 (0.03)	36.0±0.18 (0.03)	35.8±0.16 (0.03)
Least interjugal breadth	26.0±0.14 (0.03)	26.6±0.22 (0.04)	25.4±0.47 (0.05)	25.8±0.18 (0.04)	25.6±0.16 (0.04)
Mandibular ramus depth	10.5±0.09 (0.05)	10.8±0.14 (0.06)	10.9±0.21 (0.05)	11.0±0.09 (0.04)	10.8±0.09 (0.05)
Mandibular length	37.0±0.22 (0.04)	37.8±0.22 (0.03)	35.5±0.30 (0.02)	35.5±0.23 (0.04)	35.4±0.22 (0.04)
Alveolar length of the lower molariform row	14.8±0.11 (0.05)	15.1±0.22 (0.04)	13.7±0.16 (0.03)	14.0±0.09 (0.04)	13.9±0.09 (0.04)
Breadth across the infraorbital canals	16.2±0.12 (0.05)	16.2±0.18 (0.05)	15.4±0.34 (0.06)	15.7±0.16 (0.06)	15.8±0.13 (0.05)

Table 1.--Continued.

	Ohio		Oregon		
	Group 1	Group 2	Group 3	Group 4	Group 5
Character	$\bar{X}$ ± 1SE (CV)	$\bar{X}$ ± 1SE (CV)	$\bar{X}$ ± 1SE (CV)	$\bar{X}$ ± 1SE (CV)	$\bar{X}$ ± 1SE (CV)
Alveolar width of both upper incisors	6.5±0.07 (0.06)	6.6±0.07 (0.05)	6.5±0.14 (0.06)	6.8±0.06 (0.05)	6.6±0.06 (0.05)
Hind foot length	96.1±0.87 (0.05)	99.0±0.89 (0.04)	95.0±1.40 (0.04)	95.2±0.82 (0.05)	95.5±0.60 (0.04)

length, hind foot length, and ear length were recorded from specimen labels.

From each cottontail collected in 1979 and 1980, 10 secondary guard hairs were plucked and mounted on glass slides with clear fingernail polish. Secondary guard hairs were measured because overall color in rabbits is determined mostly by lengths of their color bands (Castle and Sawin, 1932) and because the long primary guard hairs are black shading to gray at their bases. Lengths of the terminal (black) and subterminal (brown) color bands on secondary guard hairs were measured to the nearest 0.1 mm with a stage micrometer and a dissecting microscope. Hairs were not plucked from borrowed specimens but were embedded temporarily in rubber cement on a glass slide and measured in situ. These hairs could not be measured with the stage micrometer because of physical limitations of the device so were measured with dial calipers. The two methods produced comparable results on test hairs ($t = 0.3709$; 39 d.f.; $P > 0.6$) so were considered to be equivalent. Reflected light was measured from five equidistant points between the posteriorly extended ear tips and the base of the tail with a Model 610 reflectometer (Photovolt Corp., New York) calibrated from absolutely no reflected light (0.0 units) to 5YR 4/3, reddish brown (Anonymous, 1973) (10.0 units).

All computer analysis was accomplished on the Control Data System Cyber 70/73 computer at Oregon State University with the Statistical Interactive Programming System (Rowe and Brenne, 1981).

Samples were defined as groups of specimens of identical sex and with similar localities and dates of collection. Samples with fewer than two individuals were not used in the analysis. Measurements for missing skeletal characters were estimated with multiple regression techniques from measurements of other individuals in the same sample (Frane, 1976). The regression model for each missing measurement was constructed by adding variables with forward selection and dropping variables with backward selection (Neter and Wasserman, 1974).

Mean lengths of the terminal and subterminal color bands and all five reflectance measurements comprised the seven pelage characters used in the analysis. A portion of the analysis was limited to 20 variables. Therefore, five skeletal characters were eliminated: total length and tail length on the basis of probable lack of precision in measurement by different researchers (B. J. Verts, pers. comm.); ear length on the basis of numerous missing values; least length of the palatal bridge and diameter of the external auditory meatus on

the basis of similar measurements between groups. Those remaining consisted of 1 external and 19 skull measurements. Pelage and skeletal characters were analyzed separately because many individuals were represented by either skin or skull.

Multivariate analysis of variance (MANOVA) (Roy, 1953, 1957; Morrison, 1976) was used to determine if there were significant differences between sample mean vectors. When MANOVA indicated significant differences, Hotelling's T^2 statistic (Hotelling, 1931; Morrison, 1976) was used on all possible pairs of samples to determine which were similar and which contained differences detected by MANOVA. Samples with no significant differences were combined. With two such groupings, T^2 tests failed to reveal significant differences when MANOVA indicated such. Because calculated probabilities in these instances were within 3% of the critical values required by the conservative Bonferroni alpha level (Morrison, 1976), they were accepted as significant. The resulting homogeneous groups were used in the remainder of the analysis.

Simultaneous confidence intervals (Roy and Bose, 1953; Morrison, 1976) were used to determine which between-group differences in character means were significant in MANOVA's of homogeneous groups. A form of

discriminant function analysis (Fisher, 1938; Binet and Watson, 1956; Kshirsager and Arseven, 1975; Morrison, 1976) was applied to the cottontail groups. Characteristic roots were used to determine the number of discriminant functions necessary to distinguish between groups (Binet and Watson, 1956; Heck, 1960; Pillai, 1965; Morrison, 1976). Correlations between discriminant scores and original variables (Pimentel, 1979) were used to indicate their relationship. Wald-Anderson W statistics (Wald, 1944; Anderson, 1951; Morrison, 1976) were used to classify individual cottontails into groups according to their discriminant scores.

The level accepted as significant for all analyses was $P < 0.05$ except $P < 0.25$ was used with multiple regression as the critical value to drop variables.

RESULTS AND DISCUSSION

Morphometric Analysis.--Five groups of cottontails based on skeletal characters were: 1) All Ohio males (n = 36), 2) All Ohio females (n = 23), 3) Oregon females collected 1968-70 (n = 7), 4) Oregon females collected 1979 (n = 32), and 5) All Oregon males (n = 33). Plots of cottontail group centroids (Fig. 2) and distributions of discriminant scores (Fig. 3) revealed that, in general, differences between Ohio and Oregon rabbits were greater than the magnitude of sexual dimorphism in either state. Oregon cottontails generally were smaller (Table 1).

Oregon females collected 1968-70 were considerably different from all other groups (Figs. 2 and 3), possibly an indication that female cottontails in Oregon were still changing morphologically in response to the Oregon environment, or that the sample size of that group was too small to be representative.

Although overall differences between groups were significant, the Roy-Bose simultaneous confidence interval technique failed to reveal a single character responsible for the differences (Table 1). However, all 20 characters were correlated significantly with the first discriminant score and 6 with the second score

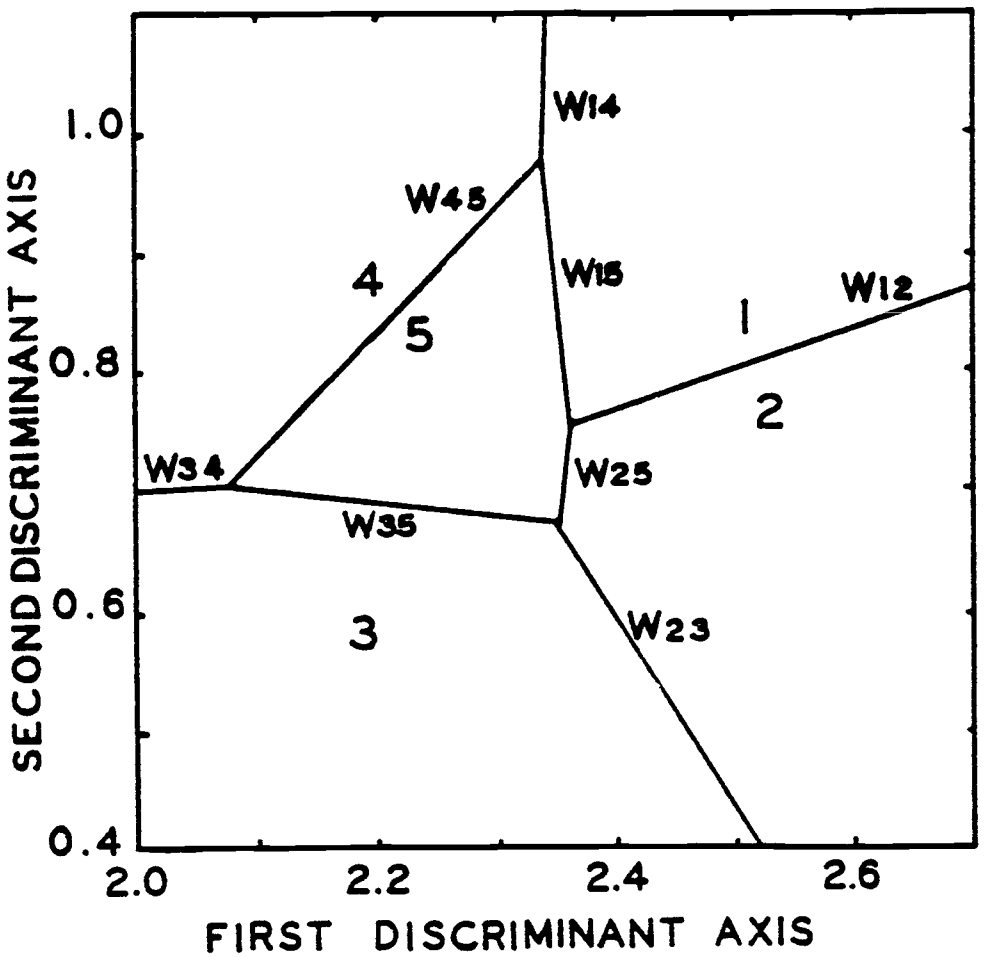

Fig. 2.--Group centroids and classification regions for discriminant analysis of cottontail skeletal character groups: 1) All Ohio males (n = 36), 2) All Ohio females (n = 23), 3) Oregon females collected 1968-70 (n = 7), 4) Oregon females collected 1979 (n = 32), and 5) All Oregon males (n = 33). Numerals represent centroids and boundaries are the appropriate Wald-Anderson W statistics. Of the total variation, 72.0% was accounted for by the first discriminant axis and 13.4% by the second. In general, larger scores on both axes indicate larger skeletal size.

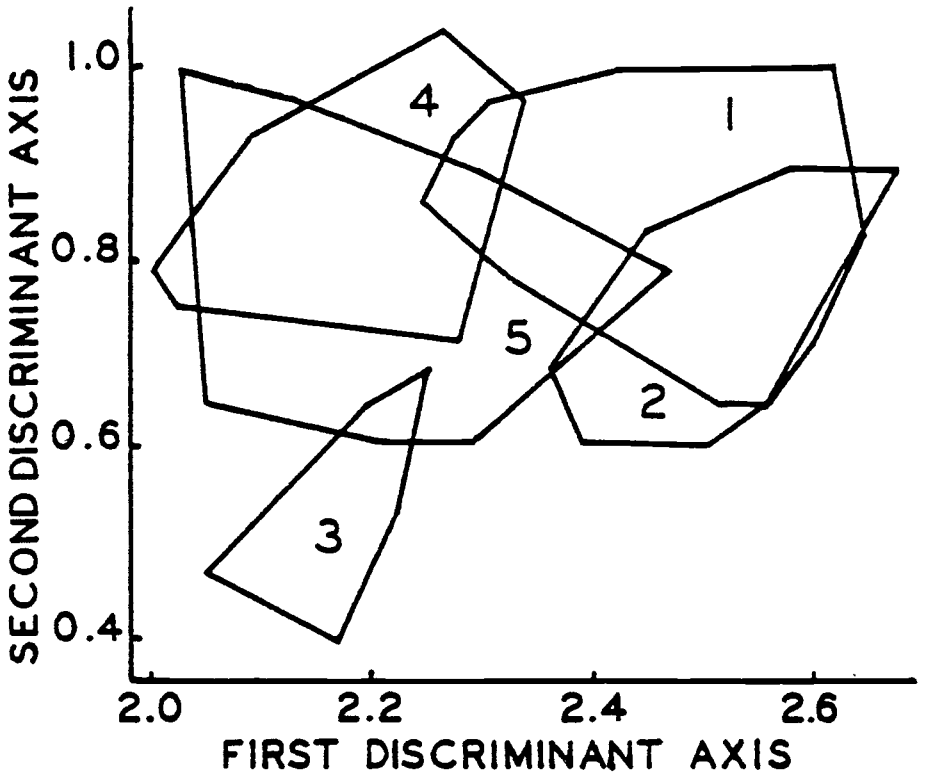

Fig. 3.--Distribution of discriminant scores for cottontail skeletal character groups: 1) All Ohio males (n = 36), 2) All Ohio females (n = 23), 3) Oregon females collected 1968-70 (n = 7), 4) Oregon females collected 1979 (n = 32), and 5) All Oregon males (n = 33).

(Table 2) indicating that both size and shape of the skull contributed to the separation of cottontail groups; Oregon cottontails generally had shorter skulls in relation to overall skull size (Table 1).

Classification of cottontails into groups according to their discriminant scores misclassified only 8 (6.1%) of 131 Ohio and Oregon rabbits as to the state in which they were collected (Table 3). Differences in the five groups of cottontails detected nearly exclusively from skull allometry may not be as great as overall structural differences because of the high ontogenic priority on skull development (Marshall and Corruccini, 1978).

Colorimetric Analysis.--Four groups of cottontails resulted from analysis of the pelage characters: 1) All Ohio cottontails except females collected 1979-80 (n = 57), 2) Ohio females collected 1979-80 (n = 20), 3) Oregon females collected 1968-70 (n = 7), and 4) All Oregon cottontails except females collected 1968-70 (n = 65). Ohio females collected in 1979-80 were significantly darker than all other rabbits; whether this indicates a temporal change in color, or simply an example of sexual dimorphism (only 8 of 57 other cottontails from Ohio were females) is unknown. Oregon cottontails generally were lighter in color than Ohio cottontails (Table 4), but there was some overlap between

Table 2.--Correlations between discriminant scores and cottontail skeletal characters. Correlation coefficients greater than 0.170 are significant.

Character	Correlation: First discriminant score	Correlation: Second discriminant score
Greatest length of the skull	0.657	-0.127
Skull depth	0.426	-0.336
Shield-bullae depth	0.463	0.063
Alveolar length of the upper molariform row	0.674	-0.083
Basal length	0.577	-0.065
Incisive foramina length	0.577	-0.246
Alveolar width of the upper molariform row at P^3	0.473	0.172
Postdental breadth	0.550	-0.068
Cranial breadth	0.338	0.161
Basioccipital length	0.437	0.039
Bullae breadth	0.411	-0.211

Table 2.--Continued.

Character	Correlation: First discriminant score	Correlation: Second discriminant score
Greatest breadth of the nasals	0.549	-0.212
Greatest breadth of the zygomatic arches	0.408	0.283
Least interjugal breadth	0.307	0.018
Mandibular ramus depth	-0.286	-0.106
Mandibular length	0.704	-0.076
Alveolar length of the lower molariform row	0.733	0.103
Breadth across the infraorbital canals	0.325	0.154
Alveolar width of both incisors	-0.189	0.137
Hind foot length	0.253	-0.100

Table 3.--Classification of skeletal character groups by Wald-Anderson W statistics. Groups: 1) all Ohio males (n = 36), 2) all Ohio females (n = 23), 3) Oregon females collected 1968-70 (n = 7), 4) Oregon females collected 1979 (n = 32), and 5) all Oregon males (n = 33).

Classified as coming from group	Known group: Ohio 1	Ohio 2	Oregon 3	Oregon 4	Oregon 5	Totals
1	18	7	0	1	1	27
2	13	16	0	0	1	30
3	0	0	6	0	4	10
4	2	0	0	19	12	33
5	3	0	1	12	15	31
Totals	36	23	7	32	33	131

Table 4.--Means, standard errors, and coefficients of variation (in parentheses) for pelage characters for four cottontail groups: 1) all Ohio cottontails except females collected 1979 (n = 57), 2) Ohio females collected 1979 (n = 20), 3) Oregon females collected 1968-70 (n = 7), and 4) all Oregon cottontails except females collected 1968-70 (n = 65). Similar letters in the same row indicate means were not significantly different tested by simultaneous confidence intervals.

	Ohio		Oregon	
	Group 1	Group 2	Group 3	Group 4
Character[1]	$\bar{x}$ ± 1SE (CV)	$\bar{x}$ ± 1SE (CV)	$\bar{x}$ ± 1SE (CV)	$\bar{x}$ ± 1SE (CV)
Terminal color band	5.4±0.09a (0.12)	5.5±0.15a (0.12)	5.9±0.19a (0.08)	5.1±0.08a (0.13)
Subterminal color band	4.0±0.07a (0.14)	3.7±0.09a (0.12)	4.6±0.17ab (0.10)	4.9±0.06b (0.09)
First reflectance measurement	6.1±0.09a (0.10)	5.5±0.12a (0.09)	7.5±0.18b (0.06)	7.4±0.08b (0.09)
Second reflectance measurement	5.7±0.09a (0.12)	5.0±0.15a (0.13)	6.5±0.21ab (0.09)	7.0±0.10b (0.12)
Third reflectance measurement	5.6±0.09ab (0.12)	5.1±0.14a (0.12)	6.6±0.26bc (0.10)	6.6±0.09c (0.11)
Fourth reflectance measurement	5.8±0.09ab (0.12)	5.0±0.21a (0.19)	6.4±0.35ab (0.14)	6.4±0.10b (0.13)
Fifth reflectance measurement	6.3±0.10a (0.11)	6.0±0.16a (0.12)	6.8±0.37a (0.14)	6.6±0.13a (0.16)

[1]Color bands measured in mm and reflected light measured on an arbitrary scale from absolutely no reflected light (0.0 units) to 5YR 4/3, reddish brown (Anonymous, 1973) (10.0 units).

groups (Fig. 4).

Both Roy-Bose simultaneous confidence intervals (Table 4) and correlations of original variables with discriminant scores (Table 5) indicated that the mean length of the brown subterminal color band and the anterior four reflectance values could be used to distinguish between groups of cottontails. The length of the black terminal color band and reflected light from the rump also were correlated significantly with discriminant scores although the relationship was weaker (Table 5). Only 12 (8.1%) of 149 specimens were misclassified as to the state in which they were collected (Table 6).

Possible Explanations for Morphometric Changes.--Introduced mammals, especially those introduced on islands, commonly become smaller in size (Foster, 1964; Marshall and Corruccini, 1978). Because the Willamette Valley is markedly different physiographically, geologically, edaphically, and vegetatively from surrounding areas (Franklin and Dyrness, 1969), and because eastern cottontails do not seem to occupy habitats above the valley floor (Verts and Carraway, in press), the Willamette Valley population of eastern cottontails may be responding as if it were an insular population.

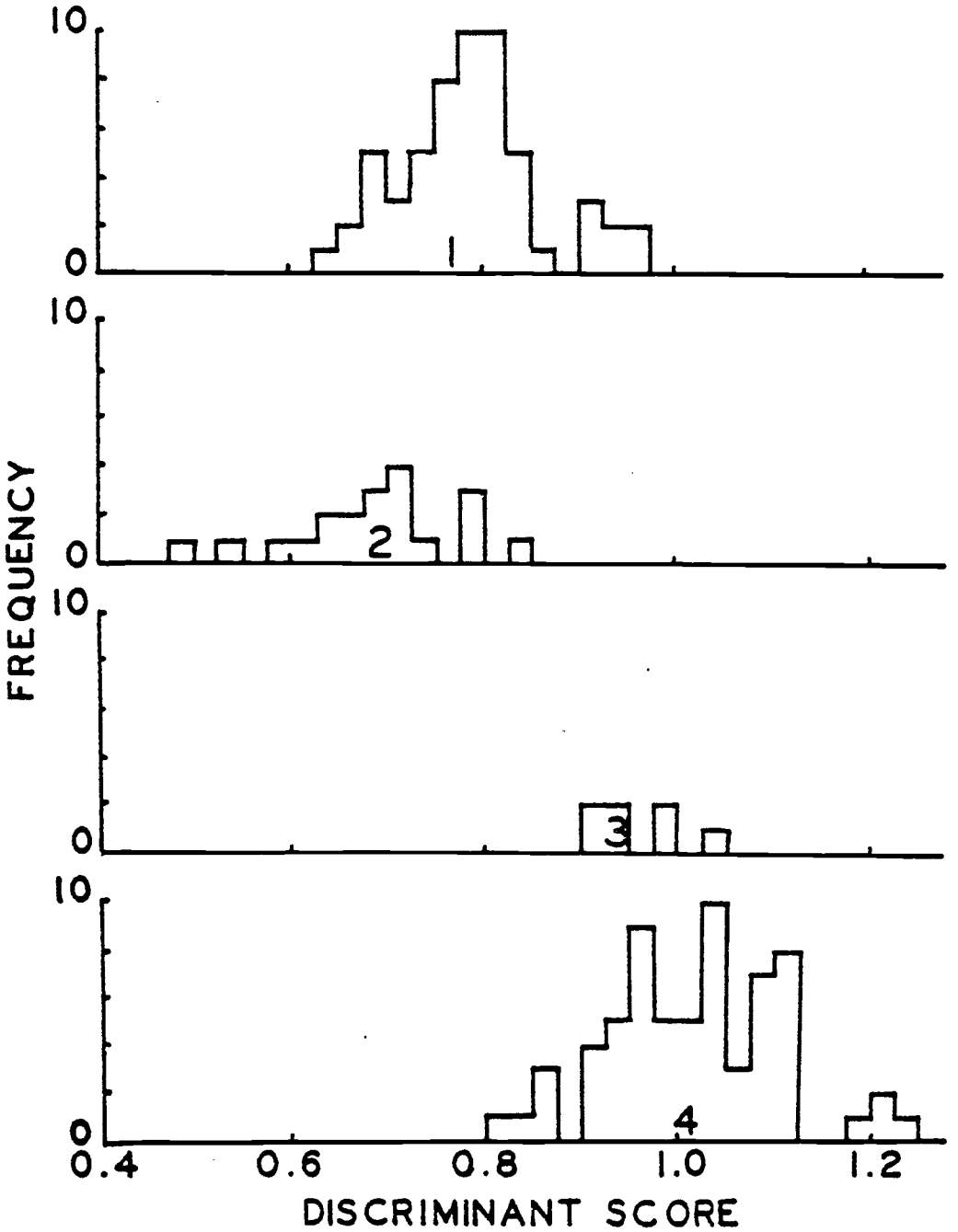

Fig. 4.--Histograms of discriminant scores for cottontail pelage character groups: 1) All Ohio cottontails except females collected 1979 (n = 57), 2) Ohio females collected 1979 (n = 20), 3) Oregon females collected 1968-70 (n = 7), and 4) All Oregon cottontails except females collected 1968-70 (n = 65). Numerals are at group centroids. Of the total variation, 94.3% was accounted for by the first discriminant axis. In general, larger scores indicate lighter pelage color.

Table 5.--Correlations between discriminant scores and cottontail pelage characters. All correlation coefficients are significant.

Character	Correlation: Discriminant score
Terminal color band	-0.290
Subterminal color band	0.836
First reflectance measurement	0.914
Second reflectance measurement	0.851
Third reflectance measurement	0.752
Fourth reflectance measurement	0.606
Fifth reflectance measurement	0.256

Table 6.--Classification of pelage character groups by Wald-Anderson W statistics. Groups: 1) all Ohio cottontails except females collected 1979 (n = 57), 2) Ohio females collected 1979 (n = 20), 3) Oregon females collected 1968-70 (n = 7), and 4) all Oregon cottontails except females collected 1968-70 (n = 65).

Classified as coming from group	Known group: Ohio 1	Ohio 2	Oregon 3	Oregon 4	Totals
1	37	5	0	5	47
2	13	15	0	0	28
3	7	0	5	19	31
4	0	0	2	41	43
Totals	57	20	7	65	149

Reduction in body size of introduced mammals may be the result of genetic drift related to the small number of colonizers, introgression of genetic material from a smaller closely-related native species, phenotypic dwarfing in response to less abundant or less available food resources, or selective forces in the new environment (Wright, 1921, 1931; De Vos et al., 1956; Foster, 1964; Berry et al., 1978; Marshall and Corruccini, 1978; Futuyma, 1979). Intraspecific and interspecific competition may be a source of selection in a new environment (MacArthur and Wilson, 1967; Pianka, 1970; Stearns, 1977).

The brush rabbit, a smaller congener of the eastern cottontail, occurs throughout the Willamette Valley (Hall, 1981) and commonly occupies the same coverts as eastern cottontails (Chapman and Verts, 1969). Verts and Carraway (1980) reported on two rabbits from the Willamette Valley thought to be hybrids between these two species. However, the apparent infrequency of individuals with intermediate characters among samples and differences in numbers of chromosomes (Palmer and Armstrong, 1967; Worthington, 1970) that likely would interfere with gamete formation in hybrid offspring indicates that the reduction in size of eastern cottontails probably was not related to introgression of

genetic material from brush rabbits.

If interspecific competition involving eastern cottontails were to occur, its congener, the brush rabbit, likely would be the competitor. However, despite some overlap in use of habitats, eastern cottontails occur in areas rarely frequented by brush rabbits (Chapman and Verts, 1969). Also, productivity of eastern cottontails (Trethewey and Verts, 1971) was approximately twice that of brush rabbits on the same area (Chapman and Harman, 1972). If, indeed, competition between these species occured, the more productive and behaviorally dominant eastern cottontail (Chapman and Verts, 1969) likely could out-compete the smaller brush rabbit. Thus, interspecific competition probably is not a strong selective force and did not affect body size of eastern cottontails.

Phenotypic dwarfing related to inadequate nutrition during development was not believed to have caused the observed nanism in Oregon cottontails. Bailey (1969) found that cultivated legumes and several wild forbs were prime foods of young cottontails in feeding trials conducted in Illinois. Some of these same legumes have escaped from cultivation and grow along roadsides and on uncultivated lands in the Willamette Valley, and many of the introduced forbs typically found in the Willamette

Valley also occur within the native range of eastern cottontails (Fernald, 1950; Franklin and Dyrness, 1969). Certainly, most of these plants mature and dry during summer droughts in the Willamette Valley; however, cottontail reproduction ceases during dry summers (Trethewey and Verts, 1971). Also, in arid sagebrush-steppe communities, survival of juvenile Nuttall's cottontails (S. nuttallii) is reduced in summer during exceptionally dry years (McKay and Verts, 1978; Skalski and Verts, in press); juvenile eastern cottontail survival likely is affected similarly (Trethewey and Verts, 1971). Therefore, few young likely are born at the critical season or survive to be subjected, during their development, to inadequate nutrition caused by desiccation of succulent plants. Consequently, intraspecific competition, if operative, likely would affect juvenile survival during summer droughts.

Climographs for Oregon and Ohio (Fig. 1) indicate that cottontails introduced into Oregon were subjected to a grossly different physical environment; especially pronounced was the strongly seasonal rainfall pattern. McKay and Verts (1978) thought juvenile survival in Nuttall's cottontails during drought, when plants were desiccated, likely was related to loss of a source of

water rather than alteration of food resources. Skalski and Verts (in press) believed that shifts in allele frequencies for a cryptomorphic character (transferrin polymorphism) were related to juvenile survival, thus were regulated by rainfall and plant succulence. If absence of younger individuals noted in eastern cottontails in Oregon after a severe drought (Trethewey and Verts, 1971) was produced as much by juvenile mortality as by early cessation of breeding, rainfall might be a selective force of considerable magnitude for eastern cottontails. Of course, whether selective forces that operated through changes in juvenile survival in relation to available moisture would affect body size is unknown.

Because only 12 individuals were brought to Oregon from Ohio, the observed overall smaller size of Oregon cottontails possibly resulted from inadvertent choice of small individuals to comprise the founding population or from random drift toward small size after introduction. I cannot reject the possibility that both factors were involved or that selection played a role throughout the establishment of the Oregon population.

Possible Explanations for Colorimetric Changes.--Based on logic similar to that to develop possible mechanisms for changes in body size, mammals

introduced into new environments could become lighter in color by random processes such as genetic drift (Wright, 1921, 1931; Foster, 1964; Berry et al., 1978; Futuyma, 1979), introgression of genetic material from a lighter colored related species native to the new environment, or by selective forces in the new environment.

Hybridization of eastern cottontails with species other than the brush rabbit likely is impossible (Van Gelder, 1977).

Based on the extensive list of darkly colored taxa of mammals native to the Willamette Valley (Nelson, 1909; Goldman, 1910; Jackson, 1928; Howell, 1929; Bailey, 1936), the occurrence of eastern cottontails in Oregon lighter in color than descendants of parental stock from Ohio within 40 years indicates that introduced eastern cottontails were not subjected to the same selective pressures as native species, if, indeed, such selective pressures were operative. Selection for dark color in native species does not necessarily require that introduced species be subjected to the same selective pressures. For example, introduced cottontails might be selected for light color for greater concealment against light-colored backgrounds of dry vegetation and dry, light-colored soils in summer, whereas, native species might be selected for dark-colored pelage for better

concealment against dark-colored vegetation and wet, dark-colored soils in winter.

As with the size character, lighter colored cottontails in Oregon possibly resulted from a larger than representative proportion of light-colored individuals in the small founding population or from random shift toward greater frequency of light-colored individuals after introduction.

CONCLUSIONS

Small size and light color in eastern cottontails in Benton County, Oregon probably cannot be explained as the result of merely a single mechanism but rather as the result of a combination of selective and random processes (Jones et al., 1977).

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APPENDIX

APPENDIX: SPECIMENS EXAMINED

Most of the following specimens are on deposit in the Oregon State University Department of Fisheries and Wildlife Bird and Mammal Collections. Exceptions are noted after each specimen. (Carnegie Museum of Natural History, CaMNH; The Cleveland Museum of Natural History, ClMNH; University of Illinois Museum of Natural History, IMNH; The University of Michigan Museum of Zoology, UMMZ; and The University of Kansas Museum of Natural History, KU).

Ohio females collected 1936-43. Ashtabula Co.: 4 mi N Geneva, 1 (CaMNH); Mechanicsville, 1 (KU). Cuyahoga Co.: South Euclid, 1 (UMMZ). Lake Co.: Mentor, 1 (ClMNH); Kirtland Hills Village, 1 (ClMNH).

Ohio males collected 1935-45. Adams Co.: 1 (UMMZ). Clermont Co.: Union Twp., 1 (UMMZ); Union Twp., 2 (ClMNH). Cuyahoga Co.: Beechwood Village, 1 (ClMNH); South Euclid, 1 (ClMNH); Cleveland Heights, 1 (KU). Hamilton Co.: California, 1 (CaMNH). Lake Co.: Kirtland Hills, 1 (ClMNH); Daniels Knob, Kirtland Twp., 1 (ClMNH).

Ohio females collected 1948-50. Clermont Co.: William's Corner, 1 (IMNH). Hamilton Co.: California, 1 (IMNH); Lunken Airport (Cincinnati), 1 (IMNH).

Ohio males collected 1948-50. Clermont Co.: near Elk Lick, 1 (IMNH); 2 mi N East Glen Este, 1 (IMNH). Hamilton Co.: Lunken Airport (Cincinnati), 2 (IMNH).

Ohio females collected 1979-80. Athens Co.: Athens, Athens Twp., 1; St. Rt. 33, 4 mi SE Athens, Lodi Twp., 1. Brown Co.: St. Rt. 505, 0.5 mi N Freesburg, Lewis Twp., 1. Butler Co.: St. Rt. 63, Monroe, Madison Twp., 1. Darke Co.: Richland Twp., Sec. 30, 1. Delaware Co.: 9 mi N Delaware, Delaware Wildlife Area, Marlboro Twp., 1; 12 mi N Delaware, Delaware Wildlife Area, Marlboro Twp., 1; 1 mi W Delaware, Delaware Twp., 1; U. S. 37 intersection in Berkshire, Berkshire Twp., 1. Franklin Co.: St. Rt. 33 in Columbus, Marble Cliff Twp., 1. Greene Co.: 5 mi N Yellow Springs, Miami Twp., 1. Hancock Co.: St. Rt. 68 in Findlay, Liberty Twp., 1. Logan Co.: St. Rt. 336 in Russells Point, Stokes Twp., 1. Morgan Co.: St. Rt. 78, 3 mi W Malta, Morgan Twp., 1; 1 mi W Wolf Creek Wildlife Area, Union Twp., 1. Morrow Co.: 1.5 mi S Mt. Gilead on St. Rt. 42, Gilead Twp., 1; 0.5 mi N Cardington, Cardington Twp., 1; St. Rt. 746, 4 mi SW Cardington, Westfield Twp., 1; Co. Rd. 149, 3 mi SW Cardington, Cardington Twp., 1. Pickaway Co.: 4 mi N New Holland, Perry Twp., 1; St. Rt. 56, 3 mi N Laurelville, Saltcreek Twp., 1. Portage Co.: 5 mi E

Ravenna on St. Rt. 5, Charlestown Twp., 1. Preble Co.: St. Rt. 503, 1 mi N Lewisburg, Harrison Twp., 1. Putnam Co.: St. Rt. 613, 2 mi E Leips, Van Buren Twp., 1. Sandusky Co.: Ballville Twp., 1; York Twp., 1. Seneca Co.: 1 mi N McCutchenville, Seneca Twp., 1. Stark Co.: Tuscarawas Twp., Sec. 16, 1.

Ohio males collected 1979-80. Champaign Co.: 5 mi NE Urbana, Salem Twp., 1. Clark Co.: St. Rt. 68, 1 mi N Hustead, Green Twp., 1. Crawford Co.: 4 mi SW Sulfer Springs, Liberty Twp., 1. Defiance Co.: Oxbow Wildlife Area, 5 mi N Defiance, Tiffin Twp., 1. Delaware Co.: 4 mi N Delaware, Troy Twp., 1; 4 mi N Delaware, U. S. D. A., Troy Twp., 5; 14 mi E Delaware, Trenton Twp., 1; 5 mi N Delaware, Delaware St. Park, Troy Twp., 1; 4 mi E Delaware, Rt. 36, Co. Rd. 10, Delaware Twp., 1; 1 mi N Delaware, Delaware Twp., 1; 0.5 mi E Delaware, Delaware Twp., 1; 12 mi N Delaware, Delaware Wildlife Area, Marlboro Twp., 1; Delaware, Delaware Twp., 1; 4 mi N U. S. 42 on Co. Rd. 220, Troy Twp., 1. Fairfield Co.: 4 mi S Lancaster, Berne Twp., 1; 3 mi S Lancaster, Berne Twp., 1. Hardin Co.: Goshen Twp., 1. Highland Co.: near Hillsboro, Liberty Twp., 1. Holmes Co.: Berlin Twp., 1; Walnut Creek Twp., 1. Huron Co.: 0.5 mi W Norwalk, Norwalk Twp., 1; 0.5 mi W Clarksfield, Clarksfield Twp., 1. Mercer Co.: 12 mi S

Celina, Franklin Twp., 1. Morgan Co.: St. Rt. 78, 4 mi W Malta, Union Twp., 1. Morrow Co.: Co. Rd. 156, S Westfield, Westfield Twp., 1. Sandusky Co.: Fremont, Sandusky Twp., 1. Seneca Co.: 3 mi N Fostoria, Jackson Twp., 1; 1 mi N McCutchenville, Seneca Twp., 1; Twp. Rd. 76, 2 mi SW Green Sprs., Pleasant Twp., 1. Stark Co.: Lawrence Twp., Sec. 10, 1; Sugar Creek Twp., Sec. 22, 1; Bethlehem Twp., Sec. 13, 1. Wyandot Co.: 2 mi NE Upper Sandusky, Crane Twp., 1; Co. Rd. 115, 3 mi S Upper Sandusky, Crane Twp., 1.

Oregon females collected 1968-70. Benton Co.: E. E. Wilson Game Mgmt. Area, 1; E. E. Wilson Game Mgmt. Area, 7 mi N Corvallis, 2; 2.5 mi S, 1 mi W Corvallis, 1; confluence of Mary's and Willamette Rivers, 1; E. E. Wilson Game Mgmt. Area, 9 mi N Corvallis, 1; 2 mi N Corvallis on Elliot Circle, 1.

Oregon males collected 1968-70. Benton Co.: E. E. Wilson Game Mgmt. Area, 7 mi N Corvallis, 1; 1 mi S Corvallis, 1; 1.5 mi S, 1 mi E Corvallis, 1; 8 mi N, 2 mi E Corvallis, 1; E. E. Wilson Game Mgmt. Area (North), 9 mi N Corvallis, 1; 10 mi N, 0.5 mi E Corvallis, 2.

Oregon females collected 1979. Benton Co.: 7 mi N Corvallis, E. E. Wilson Game Mgmt. Area, 32.

Oregon males collected 1979. Benton Co.: 7 mi N Corvallis, E. E. Wilson Game Mgmt. Area, 26.