GEOGRAPHIC VARIATION IN THE CLUTCH SIZES OF SEVEN OWL SPECIES

GALE A. MURRAY

GEOGRAPHIC variation in clutch size and its possible adaptive significance have been examined by many authors, most notably Moreau (1944), Lack (1947, 1948, 1954, 1966, 1968), Skutch (1949, 1950, 1967), Wynne-Edwards (1962), and Klomp (1970). Although these authors examined a broad spectrum of orders, the majority of data are for passerines. This paper reports an examination of clutch size in owls.

In many species an increase in mean clutch size is noted as one moves toward the poles and from the coast inland. The north-south trend in the New World has been examined in several species, including Common Eiders (*Somateria mollissima*) (Paynter 1951), Song Sparrows (*Melospiza melodia*) (Johnston 1954), Black-capped Chickadees (*Parus atricapillus*), and Carolina Chickadees (*P. carolinensis*) (Brewer 1963). The east-west trend in North America has been studied in Song Sparrows (Johnston 1954), House Finches (*Carpodacus mexicanus*) (Wagner 1957), and Long-billed Marsh Wrens (*Telmatodytes palustris*) (Verner 1965).

Among the New World Strigidae, Snowy Owl (*Nyctea scandiaca*) clutch size and its relation to food abundance was reported by Pitelka et al. (1955), while the north-south and east-west trends were examined in detail only for the Great Horned Owl (*Bubo virginianus*) by Henny (1972). Other references to geographic trends in the clutch sizes of New and Old World owls were made by Moreau (1944), Lack (1947, 1948, 1954, 1966, 1968), von Haartman (1954, 1971), Klomp (1970), and Foster (1973). von Haartman (1971) presents a graph plotting average clutch sizes of several species against latitude ranging from 70° N to 40° S. His data were obtained "from various local faunas and handbooks." The species examined are not indicated.

The most widely known theory to account for the increase in clutch size with an increase in latitude is that proposed by Lack (1947, 1948) and applies primarily to temperate, r-selected passerines on mainlands. This hypothesis is that clutch size is adapted to the largest brood size for which the parents can find food. Longer daylength in northern latitudes during the breeding season allows more time for food collection, and thereby the support of more young. This explanation is perhaps adequate for diurnal passerines, but would not explain similar trends among nocturnal species. However such trends have been reported (von Haartman 1971), suggesting that the problem is more complex. The

stability of the environment (Ashmole 1963; Cody 1966, 1971), the effect of reproductive strain on individual or species survival (Lack 1954, Wynne-Edwards 1962, Williams 1966), and the energy requirements of the chicks (Royama 1969) also may be important determinants of clutch size.

Geographic variation in an east-west direction as noted by Lack (1947, 1948, 1954) is assumed to be related to climate and its effect on available food. For example, the number of insects is often affected by climate with more insects in the warmer, drier environments. This is true in Central Europe and there the clutch size of the Common Swift (*Apus apus*) has been found to correspond to insect availability (Lack 1954). Some of the smaller owls feed on insects (Earhart and Johnson 1970) and the climate factor could be important in those cases. However rodent populations are more important food sources for most owls and some clutch size variation has been correlated with rodent availability (Lack 1947, 1948, 1954; Pitelka et al. 1955; Klomp 1970; Houston 1971; Henny 1972).

Past studies of these geographic trends in owls are few in number and inadequate in coverage. The existence of the increase in clutch size in some nocturnal birds in northern latitudes and the fact that this aspect of the biology of New World owls has been studied by so few prompted this investigation. Examination of clutches of seven widely distributed owl species provides a closer look at variation within each species and throughout the Strigidae.

Methods

Museums throughout the United States and Canada having egg collections (Banks et al. 1973) were contacted for clutch data. In addition data were obtained from Bent (1938), Grinnell and Miller (1944), Pitelka et al. (1955), Guthrie (1971), Foster (1973) and Harry N. Coulombe (pers. comm.).

From these sources data for 3328 clutches were assembled. These were divided among the seven owl species as follows: 909 Screech Owl (*Otus asio*), 930 Great Horned Owl, 439 Burrowing Owl (*Speotyto cunicularia*), 315 Barred Owl (*Strix varia*), 393 Long-eared Owl (*Asio otus*), 186 Short-eared Owl (*A. flammeus*), 156 Saw-whet Owl (*Aegolius acadicus*). Nocturnal and diurnal species were included to demonstrate any differences as a result of each hunting strategy.

Latitudinal and longitudinal sectioning of North America produced a grid of cells (Fig. 1) into which the data were partitioned. Clutches examined fell between 20° and 74° N. Longitudinal regions were determined on the basis of topographic similarity: region 1 east of the Central Plains excluding the Appalachian Mountains; region 2 the Appalachian Mountains; region 3 the Central Plains to the Rocky Mountains; region 4 the Rocky Mountains; region 5 characterized by the Great Basin; region 6 the Coast, Cascade, and Sierra Nevada Mountains west to the Pacific Coast.

Mean clutch size for each species was computed within each cell using a statistical

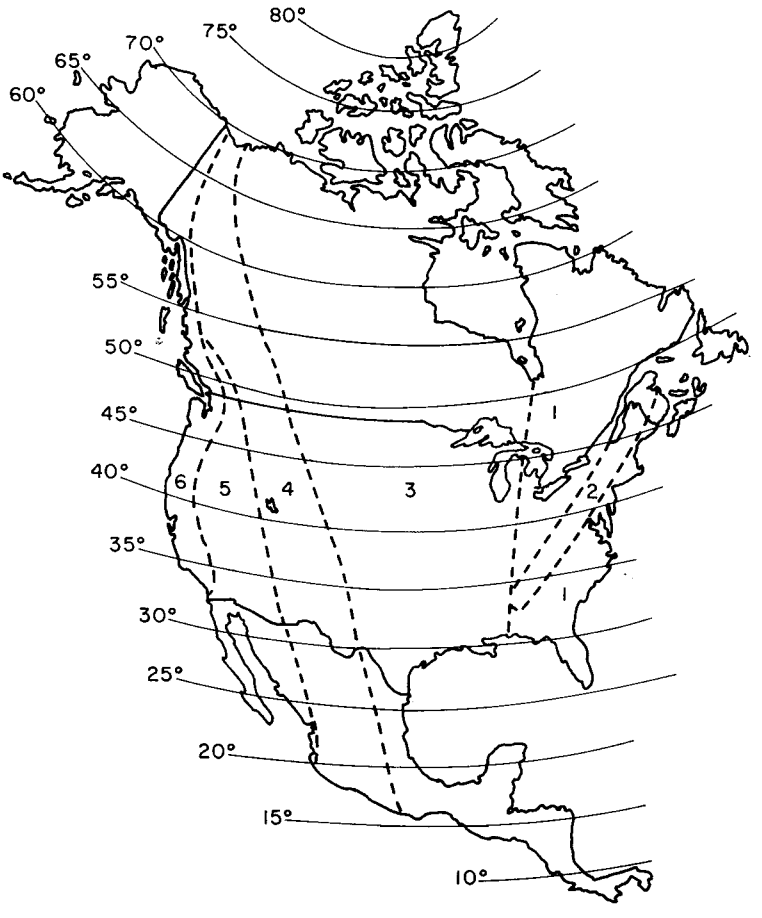

Fig. 1. Regional and latitudinal subdivisions of North America used in the analysis of clutch size data.

analysis system (SAS) program. An analysis of variance (ANOVA) program was used to examine the means by latitude and region identifying the direction of significant variation within each species. The significance of visible trends was tested by Chi-square analysis.

RESULTS

Mean clutch size for each location coordinate, by species, is presented in Tables 1 through 7. Overall means by region, latitude, and species are recorded as well as the low and high clutch for each latitudinal group.

Screech Owl.—An increase in clutch size to the north is seen in all regions except region 6 where there is a decrease. The trends are sig-

TABLE 1
CLUTCH SIZES FOR THE SCREECH OWL

Latitude °N[1]	Region 6	Region 5	Region 4	Region 3	Region 2	Region 1	$\bar{x}$ by latitude	Low	High
50–54	(1.00–1)[2]	—	(4.00–4)	(3.60–5)	—	—	(3.50–10)	1	7
45–49	3.04–41	3.57–38	—	(3.33–3)	—	(3.66–3)	3.31–85	1	6
40–44	(3.23–13)	(4.20–5)	4.24–29	4.15–111	(4.46–13)	4.06–96	4.10–267	1	8
35–39	3.38–119	(3.60–5)	(3.71–7)	3.50–26	(4.00–1)	(3.27–11)	3.42–169	1	6
30–34	3.63–111	3.21–41	—	3.76–38	—	3.09–21	3.52–211	1	6
25–29	—	(3.33–6)	(3.60–5)	3.27–37	—	3.09–109	3.15–157	1	7
20–24	—	(3.00–1)	(3.77–9)	—	—	—	(3.70–10)	3	4
$\bar{x}$ by region	3.42–285	3.43–96	4.01–54	3.83–220	(4.42–14)	3.49–240	3.59–909[3]		

TABLE 2
CLUTCH SIZES FOR THE GREAT HORNED OWL

Latitude °N[1]	Region 6	Region 5	Region 4	Region 3	Region 2	Region 1	$\bar{x}$ by latitude	Low	High
65–69	(2.20–5)[2]	—	—	—	—	—	(2.20–5)	2	3
60–64	(2.66–3)	—	—	(2.66–3)	—	—	(2.66–6)	1	4
55–59	(3.00–1)	—	—	(2.00–3)	—	(3.00–1)	(2.40–5)	1	3
50–54	—	—	(2.00–1)	2.57–40	—	(2.25–8)	2.51–49	2	4
45–49	(2.41–17)	2.52–46	(3.00–1)	(2.28–14)	—	(2.42–7)	2.45–85	1	4
40–44	(2.57–7)	(2.52–17)	2.09–21	2.31–102	(2.37–16)	2.10–47	2.27–210	1	5
35–39	2.59–186	(3.00–5)	(2.33–6)	2.41–24	—	(2.16–12)	2.55–233	1	5
30–34	2.63–156	2.51–49	(2.66–3)	2.42–21	—	(2.00–7)	2.57–236	1	5
25–29	—	—	—	2.50–56	—	1.86–43	2.22–99	1	4
20–24	—	—	(3.00–2)	—	—	—	(3.00–2)	3	3
$\bar{x}$ by region	2.59–375	2.53–117	2.26–34	2.41–263	(2.37–16)	2.05–125	2.44–930[3]		

[1] No samples were obtained above 54° N for the Screech Owl or above 69° N for the Great Horned Owl.
[2] First number represents mean clutch size; second number represents sample size. Samples of fewer than 20 clutches are enclosed in parentheses.
[3] Mean and sample size for entire species sample.

TABLE 3
CLUTCH SIZES FOR THE BURROWING OWL

Latitude °N[1]	Region 6	Region 5	Region 4	Region 3	Region 2	Region 1	x̄ by latitude	Low	High
55–59	(8.00–1)[2]	—	—	—	—	(8.00–1)	(8.00–2)	8	8
50–54	—	—	—	(5.66–6)	—	—	(5.66–6)	1	11
45–49	(3.00–1)	(5.82–17)	—	(8.25–16)	—	—	6.88–34	2	11
40–44	(5.50–2)	(5.40–5)	(7.77–9)	(7.41–17)	—	(3.50–2)	6.88–35	2	10
35–39	6.83–60	(8.00–1)	—	7.89–28	(2.00–1)	—	7.12–90	2	10
30–34	7.06–101	5.37–27	—	(7.55–9)	—	(7.00–2)	6.76–139	1	11
25–29	(4.00–1)	—	—	—	—	5.56–132	5.54–133	1	10
x̄ by region	6.92–166	5.58–50	(7.77–9)	7.64–76	(2.00–1)	5.56–137	6.48–439[3]		

TABLE 4
CLUTCH SIZES FOR THE BARRED OWL

Latitude °N[1]	Region 6	Region 5	Region 4	Region 3	Region 2	Region 1	x̄ by latitude	Low	High
45–49	—	—	—	(2.00–1)[2]	—	(2.00–5)	(2.00–6)	1	3
40–44	—	—	—	2.55–73	(2.83–6)	2.43–64	2.51–143	1	5
35–39	—	—	—	(2.18–16)	(2.00–2)	2.60–35	2.45–53	1	4
30–34	—	—	—	2.23–21	—	(2.16–6)	2.22–27	2	3
25–29	—	—	—	2.32–50	—	2.30–36	2.31–86	1	9
x̄ by region	—	—	—	2.40–161	(2.62–8)	2.41–146	2.41–315[3]		

[1] No samples were obtained above 59° N for the Burrowing Owl or above 49° N for the Barred Owl.
[2] First number represents mean clutch size; second number represents sample size. Samples of fewer than 20 clutches are enclosed in parentheses.
[3] Mean sample size for entire species sample.

TABLE 5
CLUTCH SIZES FOR THE LONG-EARED OWL

Latitude °N[1]	Region 6	Region 5	Region 4	Region 3	Region 2	Region 1	$\bar{x}$ by latitude	Low	High
50–54	—	—	—	(4.50–14)[2]	—	—	(4.50–14)	2	7
45–49	(6.00–2)	(5.38–18)	—	(4.70–17)	—	(4.33–6)	5.00–43	2	8
40–44	—	(4.37–8)	(4.55–18)	3.96–58	(5.50–4)	3.86–23	4.12–111	2	8
35–39	4.97–43	(4.75–4)	(4.00–1)	(4.18–11)	—	(4.25–4)	4.76–63	2	10
30–34	4.80–132	(4.22–9)	—	(2.62–8)	—	—	4.65–149	2	7
25–29	—	—	—	(2.50–8)	—	(3.60–5)	(2.92–13)	2	5
$\bar{x}$ by region	4.85–177	4.84–39	(4.52–19)	3.96–116	(5.50–4)	3.94–38	4.49–393[3]		

TABLE 6
CLUTCH SIZES FOR THE SHORT-EARED OWL

Latitude °N	Region 6	Region 5	Region 4	Region 3	Region 2	Region 1	$\bar{x}$ by latitude	Low	High
70–74	6.36–22[2]	—	—	—	—	—	6.36–22	4	8
65–69	(3.00–3)	—	—	(4.00–1)	—	—	(3.25–4)	2	4
60–64	(7.50–8)	—	—	(7.00–1)	—	—	(7.44–9)	5	11
55–59	(7.00–4)	—	—	(5.66–3)	—	(6.00–1)	(6.37–8)	5	8
50–54	—	—	—	(6.00–9)	—	—	(6.00–9)	3	9
45–49	(4.66–3)	(6.61–13)	—	5.65–35	—	(5.24–4)	5.80–55	1	10
40–44	(5.00–1)	(5.27–11)	5.66–21	4.83–24	(5.50–4)	(3.00–3)	5.14–64	1	8
35–39	(5.33–9)	—	—	(6.00–2)	—	—	(5.45–11)	3	7
30–34	(3.50–2)	—	(2.00–1)	—	—	—	(3.00–3)	2	5
25–29	—	—	—	(3.00–1)	—	—	(3.00–1)	3	3
$\bar{x}$ by region	5.98–52	6.00–24	5.50–22	5.50–76	(5.50–4)	(4.50–8)	5.61–186[3]		

[1] No samples were obtained above 54° N for the Long-eared Owl.
[2] First number represents mean clutch size; second number represents sample size. Samples of fewer than 20 clutches are enclosed in parentheses.
[3] Mean sample size for entire species sample.

TABLE 7
CLUTCH SIZES FOR THE SAW-WHET OWL

Latitude °N	Region 6	Region 5	Region 4	Region 3	Region 2	Region 1	$\bar{x}$ by latitude	Low	High
70–74	(6.50–2)[1]	—	—	—	—	—	(6.50–2)	6	7
65–69	—	—	—	—	—	—	—	–	–
60–64	(4.00–1)	—	—	—	—	—	(4.00–1)	4	4
55–59	(4.00–1)	—	—	—	—	—	(4.00–1)	4	4
50–54	—	—	(6.00–1)	(4.87–8)	—	—	(5.00–9)	4	6
45–49	(2.25–4)	—	—	(5.00–7)	(4.00–1)	(4.85–7)	(4.31–19)	1	7
40–44	—	(3.83–6)	(4.75–4)	(4.33–3)	(5.14–14)	(5.14–14)	4.81–38	2	7
35–39	3.82–39	(1.00–1)	—	(5.83–6)	—	—	4.02–46	1	10
30–34	3.76–30	(4.33–3)	—	—	—	—	3.81–33	2	9
25–29	—	—	—	(2.66–3)	(4.50–4)	(4.50–4)	(3.71–7)	2	5
$\bar{x}$ by region	3.79–77	(3.70–10)	(5.00–5)	4.81–27	4.96–25	4.96–25	4.28–156[2]		

[1] First number represents mean clutch size; second number represents sample size. Samples of fewer than 20 clutches are enclosed in parentheses.
[2] Mean and sample size for the entire species sample.

nificant in regions 1, 3, and 6 at the $P < 0.01$ level and in region 5 at the $P < 0.05$ level. The overall latitudinal trend of an increase to the north is somewhat obscured but nonetheless significant ($P < 0.01$). In an east-west direction the largest means are in regions 3 and 4 with a decrease toward the coasts. The variation in this direction is significant ($F < 0.05$).

Great Horned Owl.—No obvious trends appear to the north or south in the overall data in any region, except for an insignificant but observable increase in region 1. East to west clutch size shows an increase, but with an irregularity in region 3. The regional variation is significant at the $P < 0.01$ level.

Burrowing Owl.—A weak trend of increase to the north appears in the overall data, but is absent in the regional data. Some evidence suggests that the trend is reversed in region 6. In an east-west direction the largest clutches are seen in regions 3 and 4 with a decrease towards the coasts, though on the Pacific Coast (region 6) clutch size increases over that of region 5. This east-west variation is significant at the $F < 0.01$ level.

Barred Owl.—A small, but significant increase in clutch size to the north appears in region 1 ($P < 0.02$) and in region 3 ($P < 0.05$). This trend also appears in the data for the combined regions but is not significant. Samples in an east-west direction span only three regions with no visible trend.

Long-eared Owl.—A small increase is seen to the north in all regions but is obscured in the overall data. An increase in clutch size also occurs to the west. The overall increases to the north and west are both significant ($F < 0.01$).

Short-eared Owl.—An increase in clutch size to the north is seen in those regions with sufficient data and overall by latitude. The trends for the combined data and for region 6 are significant at the 0.01 level. Clutch size also increases slightly to the west but the trend is not significant.

Saw-whet Owl.—An overall increase occurs to the north ($F < 0.05$). Samples by region are too small to demonstrate a consistent trend. A significant decrease in clutch size is seen to the west ($F < 0.01$).

Discussion

An increase in clutch size with latitude, though sometimes small, is seen in all species except possibly the Great Horned Owl. A reversal of this trend occurs in region 6 in the Screech Owl and to a somewhat lesser degree in the Burrowing Owl. Large clutch size in the Short-eared Owl has been attributed by others to the availability of small rodents

(Rendall 1925; Lack 1947, 1948, 1954, 1966, 1968; Marsden 1964; Cody 1971). An increase in clutch size to the north in this species and others feeding on rodents that demonstrate the trend, such as the Great Horned, Barred, Long-eared, and Saw-whet Owls, suggests that more food is available for the young at high than at low latitudes. It should be noted that among these species are both nocturnal and diurnal hunters. The Great Horned, Long-eared, and Saw-whet Owls are nocturnal and the Short-eared Owl is diurnal. The Barred Owl is primarily nocturnal over most of its range but is more active by day than most other species. The existence of the trend in clutch size in the nocturnal species suggests that they have abandoned exclusively nocturnal activity in the northern parts of their range. Observations of diurnal or crepuscular activity in owls living at high latitudes by Campbell (1969) and mention of this behavior by Storer (1971) suggest a common diurnal feeding strategy. This type of activity pattern would account in part for the similar magnitude of the trend seen in most species.

The two species showing trend reversals in region 6, the Screech Owl and Burrowing Owl, are insectivorous (Earhart and Johnson 1970). It was found in Europe that insect numbers are correlated with humidity, with the lowest numbers in the most humid locations (Lack 1947, 1948, 1954). Smaller clutch sizes were found for insectivorous birds in these humid areas. If the same relationship applies in North America, it would explain the decrease in clutch size on the Pacific Coast where the humidity increases with latitude.

In an east to west direction an increase in clutch size is seen in the Great Horned, Long-eared, and Short-eared Owls. These three species are primarily rodent predators (Earhart and Johnson 1970). Daylength is not a factor in an east-west variation. This suggests that the food supply increases to the west, although I have no data to support this view.

In contrast, a decrease to the west is seen in the Saw-whet Owl, which is also a rodent predator. Perhaps this species has ecological requirements such as habitat preferences, energetic necessities, or preferred prey items that are below optimum in the west and cause the observed decrease in clutch size.

In the Screech and Burrowing Owls the largest clutches occur in regions 3 and 4. This appears to be a function of food supply. These species are primarily insectivorous. In keeping with the relationship seen by Lack (1947, 1948, 1954) in Europe, the warmer and drier central areas of the continent would be expected to have the greatest quantity of insects resulting in the largest clutch sizes in these regions.

Some of the remaining variation in the data presented here may be

related to the variables of habitat and altitude that others have shown to be important (Moreau 1944; Lack 1947, 1948, 1954, 1966, 1968; Cody 1966; Klomp 1970). When comparing clutch size variation in species that feed on similar prey, the species' body size and the variety of prey taken also may be important. The possibility of periodic nesting in relation to population cycles of rodents was not examined. In some species of owls clutch size is reduced or birds do not attempt to breed during lows of rodent populations (Bent 1938, Austing and Holt 1966). The regional patterns found in this study could have been affected by variations in clutch size from this source if sampling was biased with respect to the timing of rodent cycles. However the sample sizes and their distribution through time suggest that this is unlikely. The expansion of clutch size studies to include analysis by habitat, altitude, and local rodent abundance would serve to clarify and accentuate observed trends.

ACKNOWLEDGMENTS

I wish to express most sincere gratitude to Harry N. Coulombe and the following institutions for their cooperation in providing clutch data: American Museum of Natural History; Buffalo Museum of Science; Burke Memorial Washington State Museum, University of Washington; California Academy of Sciences; Carnegie Museum; Charles R. Conner Museum, Washington State University; Charleston (South Carolina) Museum; Chicago Academy of Sciences; Clemson University; Cleveland Museum of Natural History; Cornell University; Davenport (Iowa) Museum; Delaware Museum of Natural History; Denver Museum of Natural History; El Paso Centennial Museum; Florida State Museum; Life Science Museum, Brigham Young University; Los Angeles County Museum; Milwaukee Public Museum; Museum of Comparative Zoology, Harvard University; Museum of Natural History, Oregon State University; Museum of Natural History, University of Kansas; Museum of Science, Boston; Museum of Vertebrate Zoology, University of California, Berkeley; National Museum of Canada; Neotropical Ornithological Museum, Tucson; Ohio State Museum; Peabody Museum, Yale University; Royal Ontario Museum; Santa Barabara Museum of Natural History; Sespe Museum of Comparative Oology, (California); State Museum, University of Nebraska; Strecker Museum, Baylor University; Tillamook (Oregon) Pioneer Museum; University of Arkansas; University of Massachusetts; Western Foundation of Vertebrate Zoology, Los Angeles.

A most hearty thanks is extended to Richard E. Johnson for his continual guidance, encouragement, and suggestions in revision of this manuscript and who, with Rolla V. Ward, suggested the problem. John H. Larsen and Don E. Miller are gratefully acknowledged for their encouragement and advice. I greatly appreciate the assistance of Thomas S. Russell and Wayne S. Tate in statistical programming and interpretation. Sievert A. Rohwer made helpful comments on the manuscript.

This study was partially funded by the Department of Zoology, Washington State University.

SUMMARY

Geographic variation in the clutch sizes of seven widely distributed owl species in North America was examined. Increasing clutch size to

the north was seen in all species. Two insectivorous species demonstrated a reversal of this trend along the Pacific Coast. Longitudinally two species showed an increase in clutch sizes to the east, two species showed an increase to the west and one demonstrated no trend. The largest clutches in the two primarily insectivorous species were seen in the central portion of the continent with a decrease towards each coast. Possible explanations for these trends are discussed.

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Department of Zoology, Washington State University, Pullman, Washington 99163. Accepted 1 April 1975.