3 (Ralliformes, Ichthyornithiformes, Charadrii-formes). Bull. Florida State Mus. 11:99–220.

GREGORY, J. T. 1951. Convergent evolution: the jaws of *Hesperornis* and the mosasaurs. Evolution 5:345–354.

GREGORY, J. T. 1952. The jaws of the Cretaceous toothed birds, *Ichthyornis* and *Hesperornis*. Condor 54:73–88.

MARSH, O. C. 1872a. Notice of a new and remarkable fossil bird. Amer. J. Sci., 3rd ser. 4:344.

MARSH, O. C. 1872b. Notice of a new reptile from the Cretaceous. Amer. J. Sci., 3rd ser. 4:406.

MARSH, O. C. 1873. On a new sub-class of fossil birds (Odontornithes). Amer. J. Sci., 3rd ser. 5:161–162.

MARSH, O. C. 1880. Odontornithes: a monograph

on the extinct toothed birds of North America. Yale Univ. Peabody Mus. Mem. 1:1–201.

ROMER, A. S. 1966. Vertebrate paleontology. Third ed. Univ. Chicago Press, Chicago.

ROMER, A. S. 1968. Notes and comments on vertebrate Paleontology. Univ. Chicago Press, Chicago.

STORER, R. W. 1960. The classification of birds, p. 57–93. *In* A. J. Marshall (ed.) Biology and comparative physiology of birds. Vol. 1. Academic Press, New York.

WALKER, M. V. 1967. Revival of interest in the toothed birds of Kansas. Trans. Kansas Acad. Sci. 70:60–66.

TERRITORY SIZE, CLUTCH SIZE, AND FOOD IN POPULATIONS OF WRENS

MARTIN L. CODY

Department of Zoology
University of California
Los Angeles, California 90024

AND

CHRISTOPHER B. J. CODY

Hope Hall,
Bramham, Boston Spa
Yorkshire, England

Island populations of nonmarine birds at high latitudes characteristically show a reduced clutch size over their mainland counterparts (Cody, Ecological Aspects of Reproduction, p. 461. *In* Farner and King [eds.] Avian Biology. Vol. 1. Academic Press, New York. 1971). The Wren (*Troglodytes troglodytes*)[1] is one species which well illustrates this, as it has reached just about every North Atlantic island. Information on clutch size is reasonably complete and quite intriguing (fig. 1). The usual correlation with latitude exists; further, clutch size decreases with population isolation and the inverse of population size (as measured by distance from the mainland and island size, respectively). In order to evaluate the hypothesis that changes in clutch size are due to geographic differences in food supply, we examined various populations of Wrens during the 1970 breeding season: (a) *T. t. troglodytes*, Hope Hall, Yorkshire, England, early June and late July; (b) *T. t. troglodytes*, Dunvegan, Isle of Skye, Scotland, early July; (c) *T. t. hebridensis*, Isle of Lewis, Outer Hebrides, late June; (d) *T. t. zetlandicus*, Mainland and Mousa, Shetland Islands, mid-July; (e) *T. t. islandicus*, Vaglaskógur, Akureyri, Iceland, early August. We wished to discover if changes in food supply which correspond to changes in habitat and numbers of competitors were compensated by changes in territory size. We also hoped to shed light on an often cited and equally often denied inverse relation between territory size and food density. The data are presented and discussed below.

METHODS

In each locale, we selected, where possible, areas of uniform habitat in which Wrens held contiguous territories. The Wrens of Lewis and Shetland Islands

were very patchy in their local distribution, and of these we included some Wrens whose territories were not or were only partly contiguous with those of neighbors. In this case, we used the foraging area as a territory size. All Wrens were in vigorous song and defended their territories against interlopers; most were feeding young in the nest or juveniles within the territory, while one or two may have been unmated. Territories were plotted by accumulating activity records on a map, and no area was included which was rarely or never used by foraging Wrens.

The density of all other passerine species in territories of Wrens was noted, and the feeding heights and behaviors of each of these potential competitors were measured as described by Cody (Amer. Nat. 102:107, 1968). This information was used to calculate competition coefficients a_i between each Wren and the other species with which it shared its territory. The product of four overlap factors—horizontal overlap a_H, vertical overlap a_V, bill measurement overlap a_B, and feeding behavior overlap a_F—gives an estimated competition coefficient a. The factors by which densities of Wrens might be increased if each competitor were removed can then be calculated. The carrying capacity of Wrens in the absence of $(n-1)$ competitors is given by the vector product $[1 \ a_2 \ a_3 \ \ldots \ a_n]$ $\{N_1 \ N_2 \ N_3 \ \ldots \ N_n\}$ where N_1 is the observed density of Wrens and N_2-N_n the densities of its competitors. Wrens had between zero (in the walls and ruins of Mousa) and 13 (in Yorkshire woods) competitors, 23 different species in all, whose effect was thus evaluated.

To measure food, we set out in territories of Wrens sets of grease-covered plaques, 10 cm × 10 cm, at various heights which spanned feeding activity of Wrens. Between 42 and 308 plaque-days were recorded at each location. The insects caught on the plaques were removed every 24 hr and classified according to length. A unit of food was taken to be an insect of ¼ inch body length (= ⅛ of a ½ inch insect, $\frac{1}{27}$ of a ¾ inch insect), and density of food has the units "number of ¼ inch insects/plaque/day." Each feeding site of Wrens, from cracks in banks and walls to tree trunks and foliage, was sampled. A final figure of food density was determined by weighting the insect catch at different heights according to the proportion of its time the Wren fed there.

There are potential sources of error in this estimate of food abundance of Wrens: immobile food items are not sampled; some of the food items caught will be perhaps unusable or unavailable to Wrens; the plaques may be differentially effective in different habitats.

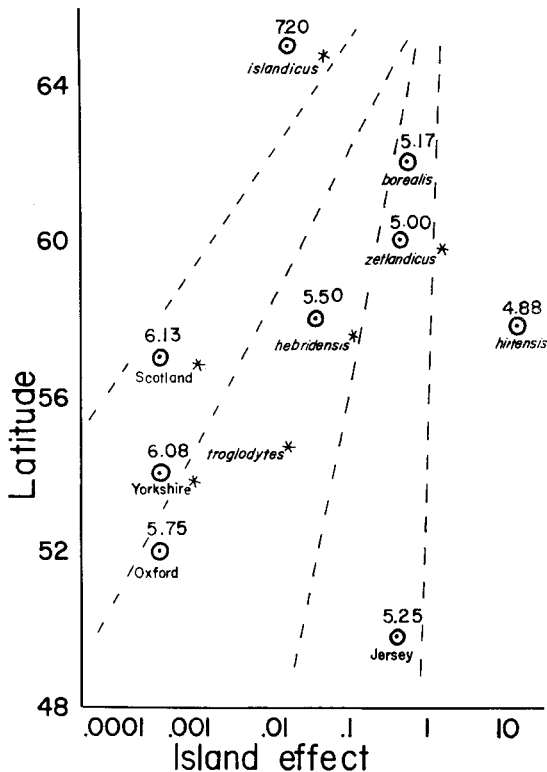---

[1] = Winter Wren of N.A.

FIGURE 1. Variation in clutch size in the populations of wrens of northeastern Atlantic islands. Both latitude and "island effects" are involved. Island effect is measured by the ratio of distance from mainland (mi.)/island size (sq. mi.). This effect is more pronounced at high latitudes than at low latitudes, as shown by the contours which cannot be drawn parallel to each other while still delimiting clutch sizes similar within 0.5 eggs. Information on clutch sizes comes from published information and from collections in the British Museum, the Royal Scottish Museum, and the National Museum of Iceland. The one exception is the clutch size of *hebridensis* obtained here by interpolation but in agreement with the few data in Armstrong (Brit. Birds 46:37, 1953). Populations marked with asterisks were studied in 1970.

We believe the method remains useful and accurate for the present purposes despite such difficulties. Of course, we cannot know just what the Wren perceives and hence cannot measure the abundance of only those food items the Wren would see and capture. We do know that, like most insectivorous passerines, Wrens eat a great variety of prey and seem to be opportunistic in their use of insect food. Our measure of the abundance of insects should at least be proportional to the abundance of the perhaps rather different insects the Wren actually catches (including immobile and completely mobile prey items). And habitats selected by Wrens are often very similar in the structure of vegetation below 10 ft, where the Wren actually forages, even though above that height they may differ. Differential plaque effectiveness among habitats might in the future be combatted by the deployment of several different sorts of insect traps (Malaise traps, CO_2 foliage traps, etc.) whose catches could be correlated. Inaccuracies are minimized by using many plaques over several different
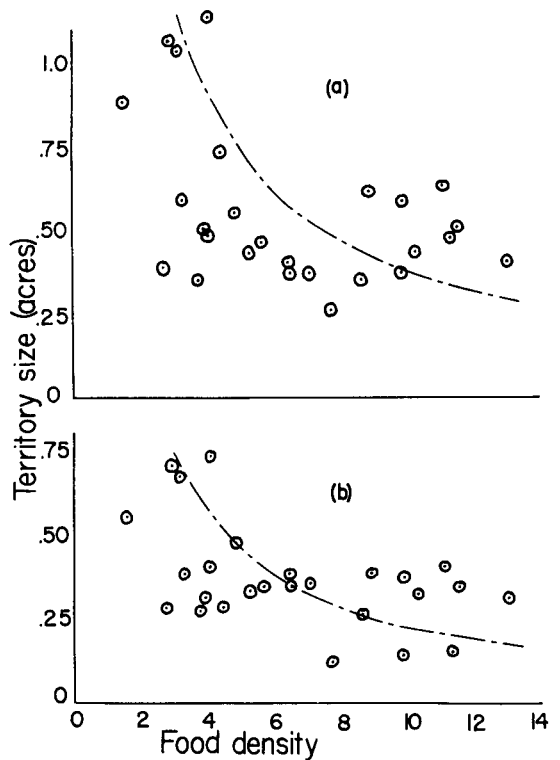

FIGURE 2. Territory size in acres versus food density in units of one-quarter inch insects/plaque/day. (a) Territory size plotted as observed. (b) Territory size corrected for presence of competitors. The dashed lines are fitted hyperbolae.

days, placing them over the variety of locations and heights the Wren uses as foraging sites, and adjusting the final figure in accordance with the time distribution of foraging heights favored by the Wrens. The outcome is a measure which should have at least relative value (among territories and among habitats), and is employed in only this relative way.

RESULTS

Territory size and food density. Table 1 summarizes the information gathered on actual territory size and food density. In any one habitat-type territory, sizes differed by up to a factor of 3 (in the heather and bracken of Lewis), but smaller variations were more usual (a factor of 2.2:Skye gully; 1.6:Skye wood; 1.2: Shetland burnside; 1.1:Shetland cliff and burnside; and 1.8:Yorkshire woods). The product of territory size and food density can be taken as a crude index of the food available to feed parents and young; as can be seen from figure 2a, this index remains roughly constant over a fivefold variation in territory size of Wrens and a twelvefold range of food density. The relation is hyperbolic and has the form territory size $(Y) \times$ food density $(X) =$ constant, supporting the theory that territory sizes are expanded or contracted to compensate for local and geographic variations in food supply. The residual sums of squares to the fitted equation $XY = 3.75$ total 5.094. Other data exist which show a similar relation, but these are less complete (e.g., Holmes *in* Animal populations in relation to their food resources. Blackwell, Oxford. 1970, and other papers and references in that work).

Table 1.   Territory sizes and food density of Wrens.

Location	Wren(s)[a]	Food[b] density	Territory size[c] with/without competitors		No. of competitors
Lewis	10 (Heath)	2.92	1.06	0.70	2–5
	W5	4.08	0.48	0.39	2
	W1	3.19	1.03	0.67	3
	W2	4.11	1.13	0.73	2
Skye	6 (Gully)	3.98	0.50	0.31	5
	3 (Wood)	10.31	0.43	0.32	5–6
	W1	5.31	0.43	0.33	5
	W2	2.74	0.39	0.28	5
	W3	4.46	0.78	0.28	5
	W4	3.31	0.59	0.38	5
	W5	3.79	0.35	0.27	5
→	W1	13.05	0.40	0.31	6
	W11	8.86	0.35	0.26	5
Shetland	2 (Burn/Bldg)	4.87	0.55	0.47	2–3
	3 (Cliff)	6.46	0.40	0.35	2–4
	W2	5.69	0.46	0.37	3
	W3	7.11	0.37	0.34	2
	W4	6.57	0.37	0.34	4
	M1	1.55	0.88	0.55	1
Yorkshire	4 (Garden)	9.88	0.37	0.14	11–14
	W1	11.37	0.47	0.15	13
	W2	7.75	0.26	0.11	12
Iceland	6 (Woods)	9.91	0.58	0.37	3
	W1	11.13	0.63	0.39	3
	W2	8.93	0.61	0.38	3
	W7	11.58	0.50	0.34	3

[a] First row or rows in each location are averages of number of pairs of Wrens indicated.
[b] Units: number of $\frac{1}{4}$-inch insects/plaque/day.
[c] Units: acres.

The influence of competitors on food availability. Next, the influence of various numbers and kinds of competitors on the scatter of points in figure 2a can be determined. A detailed example follows which illustrates the calculations involved in producing a vector of competition coefficients and a new figure for the territory size of Wrens. Table 2 lists the six species with which W_I in the Skye wood shares its territory. Their densities vary from 0.60 pair per acre in the Whitethroat (*Sylvia communis*) to 2.32 pair per acre in the Willow Warbler (*Phylloscopus trochilus*), which is almost as dense as the Wren. The horizontal overlaps a_H are computed from territorial maps, with slight overlap in the whitethroat to almost complete overlap with the Blue Tit (*Parus caeruleus*). Each species spends its time feeding between certain heights according to the percentages given in the table, and from these a vertical overlap figure, a_V, is computed. Feeding behavior is characterized by three figures: average speed while feeding, v ft/sec; duration d in seconds of the average feeding stop; per cent of time stationary while feeding, t. Zero overlap occurs between a pair of species when $t_1 - t_2 = 100$ or, by convention, when $v_1 - v_2 \geqslant 1.0$ and $d_1 - d_2 \geqslant 60.0$; complete overlap is recorded when these differences are zero. These three overlap figures are averaged to give a_F, an index of similarity in feeding behavior. When bill lengths differ by 25.4 mm and the ratios

bill depth/bill length differ by 1.0 or more, overlaps of zero are recorded; two overlaps of bill measurement are averaged to give a_B. The product $a_H \cdot a_V \cdot a_F \cdot a_B \cdot$ gives an estimated competition coefficient between the Wren and each of these six species in this habitat. The carrying capacity for the Wren W_I is then calculated to be [1 0.13 0.09 0.29 0.04 0.08 0.08] {2.51 0.67 2.32 0.96 0.60 0.90 0.75} = 3.246 pairs per acre. Thus a new territory size of the Wren of 0.31 is recorded (table 1). Figure 2b shows a plot of competitor-corrected territory sizes and food density; the fitted hyperbola $XY = 2.26$ minimizes the residual sums of squares which now total 1.687. This indicates that Wrens compensate for food differences related to habitat and the presence of more or fewer competitors by holding larger or smaller territories, and thereby secure constant amounts of food for themselves and their broods.

Clutch size and food availability. Can any of the remaining scatter in figure 2b be attributed to the known variations in clutch size among populations? The product XY and clutch size (in fig. 1) certainly show some interaction ($F = 5.764$; $p < 0.02$ that XY, or availability of food, is not a significant factor in the determination of clutch size). However, with a correlation coefficient of only 0.44, just 20% of the observed variability in clutch size is accounted for by availability of food. When latitude and body size are

TABLE 2. Competition coefficients of Wren W_I, Skye Wood

| Competitor $i = 1-6$ | Density[a] | α_{II} | Distribution of feeding heights | | | | | | | | α_v | Feeding[b] behavior | | | α_F | Bill measurements[b] | | α_R | $\alpha_i \dfrac{W_I}{B} = \pi a_k$ $k = H$ |
			$<$gd	gd	gd $-6''$	$6''$ $-1'$	$1'$ $-2'$	$2'$ $-4'$	$4'$ $-10'$	$>10''$		v	d	t		l	p/l		
Wren W_I *Troglodytes troglodytes*	2.51		0	21	18	18	15	15	13	0		0.402	1.74	83.7		13.0	0.23		
Chaffinch *Fringilla coelebs*	0.67	0.70	0	0	0	0	0	20	80	0	0.28	0.017	11.74	92.8	0.79	13.5	0.51	0.85	0.13
Willow warbler *Phylloscopus trochilus*	2.32	0.80	0	0	0	0	0	0	50	50	0.13	0.504	2.54	74.8	0.93	11.0	0.22	0.96	0.09
Robin *Erithacus rubecula*	0.96	0.80	0	45	2	2	5	14	32	0	0.57	1.152	7.33	88.5	0.70	14.3	0.35	0.92	0.29
Whitethroat *Sylvia communis*	0.60	0.10	0	0	0	5	20	50	25	0	0.48	0.261	4.37	86.5	0.93	12.8	0.32	0.95	0.04
Blue tit *Parus caeruleus*	0.90	0.95	0	0	0	0	0	0	68	32	0.13	0.573	2.01	81.3	0.93	8.3	0.73	0.66	0.08
Blackbird *Turdus merula*	0.75	0.60	29	71	0	0	0	0	0	0	0.21	0.667	3.05	81.8	0.90	25.0	0.35	0.70	0.08

[a] Units: pairs per acre.
[b] Units and explanation in text.

entered as variables, 34% of this variability is then explained. We are forced to reject the hypothesis that the availability of food is the major determinant of clutch size in these populations. Certainly some factor is missing from this analysis on which much of the variation in clutch size is dependent. From inspection of figure 1, this factor seems to be associated with the axis termed island effect, and therefore with the population size and its isolation. Cody (op. cit.) associated low clutch sizes of islands at temperate latitudes with the combined effects of (a) increased year-to-year survival of the adult population and, only partially in consequence of this, and (b) the decreased survival of offspring to reproductive age. The necessary life table information to test this hypothesis is lacking for the island Wrens.

SUMMARY

Clutch size is reduced in the endemic populations of Wrens of the northeastern Atlantic islands, perhaps in response to reduced food supply of the islands. Yet a plot of territory size against food density in three insular and two mainland populations of Wrens is close to rectangular hyperbolic, indicating that the Wrens compensate for reduced densities of food by increasing territory size. The relation is even closer to that stated when the effects of various numbers of competitors are removed. The product territory size × food density is a measure of the availability of food, and accounts for only 20% of the variation in clutch size among populations. Latitude and body size of Wrens increase this figure to only 34%, leaving major factor(s) of island clutch size undetermined.

AREAL VERSUS LINEAL TERRITORIES IN THE WREN, *TROGLODYTES TROGLODYTES*

MARTIN L. CODY

Department of Zoology
University of California
Los Angeles, California 90024

AND

CHRISTOPHER B. J. CODY

Hope Hall
Bramham, Boston Spa
Yorkshire, England

In summer 1970 we studied the relation between territory size and its food value in insular and mainland populations of the Wren (*Troglodytes troglodytes*)[1] in the British Isles (Cody and Cody, Condor 74:473). In one of these populations, *T. t. zetlandicus* of the Shetland Islands, we found that pairs included in defended territories dry-stone walls, as well as more usual foraging habitat such as bushes, stream banks, and cliff faces. In particular, we found Wrens to be common on Mousa, an island off the east coast of Mainland Shetland, where the only available foraging habitat is either dry-stone wall or the faces of sea cliffs. Only one of the six Wrens whose territories we plotted there was limited to cliff face (M_1 of Cody and Cody, loc. cit.); the others fed partially or completely in stonework and were not mentioned in our other paper.

Our data on the Wrens of Mousa are particularly apt for demonstrating the relative value to Wrens of two quite different sorts of feeding habitat, quasi-planar cliff face and stone walls in a linear configuration. The stone walls of Mousa are in various degrees of disrepair, so we converted the walls to an area measure, length × (variable) height; thickness is roughly constant at around 2.5 ft. In this way we can also include in the measure of territory size the walls of ruined buildings. Thus the six territories of Wrens are scored in two components, area of cliff face and area of dry-stone wall. These are plotted in figure 1.
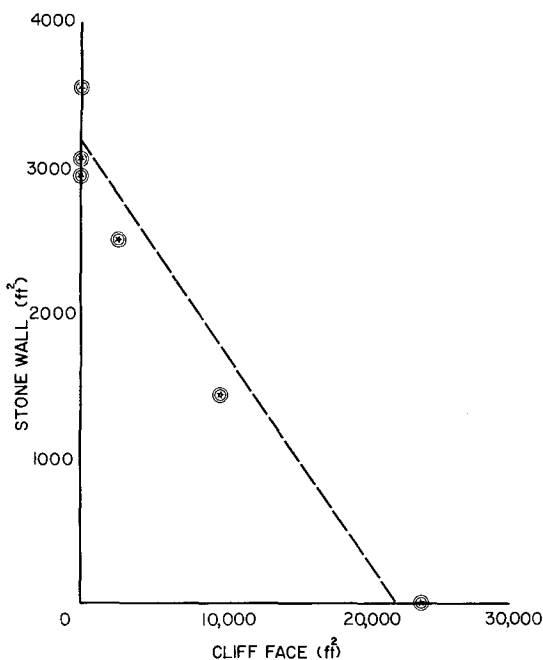
---

[1] = Winter Wren of N.A.

FIGURE 1. Two components of territory size in Wrens on Mousa, area of stone wall and area of cliff face, are shown to be complementary to each other. The six pairs of Wrens whose territories are plotted and which are mentioned in the text are, from lower right to upper left, M_1, M_2, M_7, M_3, M_4, and M_6.

As can be seen from the figure, the territory area of dry-stone wall and that of cliff face complement each other in a precise way, in such a way that area not available in one habitat type is made up from the other. More interesting is the discovery that dry-stone wall is worth much more to the Wren per unit area, apparently, than is cliff face, about 12 times more. We believe the reason for this is that the walls present a much greater area over which the Wrens can forage than do the more planar cliff faces. The walls are constructed sufficiently loosely that the birds forage within them with much freedom; a Wren