A GENERAL THEORY OF CLUTCH SIZE

MARTIN L. CODY

Leidy Laboratory of Biology, University of Pennsylvania, Philadelphia

Accepted June 11, 1965

It is possible to think of organisms as having a certain limited amount of time or energy available for expenditure, and of natural selection as that force which operates in the allocation of this time or energy in a way which maximizes the contribution of a genotype to following generations. This manner of treatment of problems concerning the adaptation of phenotypes is called the “Principle of Allocation” (Levins and MacArthur, unpublished), and of its applications might be the formulation of a general theory to account for clutch size in birds. At this stage we will assume that clutch size is a hereditary phenotypic characteristic which can be affected to a greater or lesser extent by the prevailing environmental conditions and which exhibits the normal variability of such characteristics. Lack (1954) discusses the validity of several hypotheses which attempt to account for clutch size and its variation under different circumstances and conditions, all of which were rejected in favor of his now widely accepted theory that clutch size is adapted to a limited food supply. This paper is an attempt to show that this and other existing hypotheses when taken singly are inadequate in some respect to account for all the data, that each holds for some particular set of conditions, and that each is but a part of the complete explanation. The theories will be dealt with individually and it will be shown that as environment varies so will the factors which determine clutch size.

PRESENTATION OF THE THEORY

It is known that in temperate regions, because periodic local catastrophes reduce and maintain populations below the carrying capacity, \( \bar{K} \), of the habitat, natural selection is proceeding to maximize \( r \), the reproductive rate (Fisher, 1929, whose fundamental theorem is density independent). In these regions any phenotypic variation which enables parents to leave more offspring will be selected for. Any increase in clutch size, up to a limit determined by natural resources, would suffice to increase the reproductive rate. In the tropics, however, with a more climatically stable environment where the advent of such catastrophes is rare, populations will be at saturation densities, and any adaptive variations which will increase the carrying capacity \( \bar{K} \) will usually be favored by natural selection (MacArthur, 1962). Increasing \( \bar{K} \) is equivalent to increasing the population density with the same resources, or maintaining the population density with decreased resources. Whereas in unstable regions all energy was perform utilized to increase \( r \), an individual living in a stable environment well suited to the needs of the species would need to spend much less energy on maximizing \( r \) than individuals living elsewhere. By the “Principle of Allocation,” maximum contribution to future generations will be achieved by those individuals which utilize, to increase \( \bar{K} \), some of the energy conserved by reducing \( r \). Such individuals will be favored by natural selection over others which do not allocate surplus energy to this end. We can guess suitable recipients for the conserved energy, possible candidates for its use being predator avoidance, more successful intraspecific competition (i.e., reduction in resource density necessary for maintained existence), or perhaps devoting more energy per individual to the raising of the young. All these considerations could serve to increase the contribution to future generations. Such energy requirements or drains, together with the number of eggs laid, may
Fig. 1. Three-dimensional graph showing the point of intersection $P$ of the surface of phenotypes $S$ with the “adaptive function” $\pi$. The phenotype $P$ receives benefits proportional to its intercepts on the axes $X, X_1,$ and $X_2$, resulting from dividing its energy between clutch size, avoiding predators and competitive ability respectively.

all be operating simultaneously and can be considered as acting along the axes of a multidimensional graph. Distance along the axes represents not the actual amount of energy spent, but the advantage gained by the individual who spends that amount of energy on that particular requirement. Measurable quantities such as clutch size can be substituted as units for the purpose of this argument. Representing increasing clutch size along the $X$-axis, two other energy drains can be represented along $X_1$ and $X_2$ in a three-dimensional figure (Fig. 1). All possible allocations of energy to these three requirements—clutch size, predator avoidance, and competition—can be represented as points comprising a surface $S$ and the volume under it in the figure. Every point of the surface $S$ can be considered as a phenotype having the strategy indicated by the proportions of the available energy to be spent on the factors represented by the three axes. Using the coordinates shown in the figure, phenotypes at the vertices of the solid farthest out along the axes, will be concentrating their energy on either laying many eggs, avoiding enemies, or competing more efficiently for resources. Since a jack-of-all-trades policy often brings greater returns than a specialist policy, the ability to avoid predators will rise appreciably when a large clutch is sacrificed for a slightly smaller one. Reasoning likewise with the other two combinations of axes, we deduce the convex nature of the surface $S$ which, together with the enclosed space, represents all possible phenotypes. We can now consider the strategy which maximizes the number of descendants for a particular species and environment and is favored by natural selection over the many alternatives as that point where a surface $\pi$ touches $S$ tangentially. $\pi$ is an “adaptive function” for the environmental conditions, the position of which varies in relation to the surface as...
the relative importance of the coordinates changes. \( \pi_f \) consists of all points of equal fitness, \( f \) (see Levins, 1962), and the most fit phenotype, or most apt strategy, is that represented by a point \( P \) which lies both on \( S \) and the \( \pi_f \) with largest \( f \). The fitness or suitability, \( f \), of a phenotype for certain conditions increases with the perpendicular distance of \( \pi_f \) from the origin, because the farther out a point is on lines radiating from the origin, the greater are the advantages obtained along the axes (bigger intercepts) and the more fit becomes the phenotype. So the point which lies farthest from the origin on \( S \) and on the farthest \( \pi \) indicates the best strategy. Different environments will select different optimum phenotypes. As the relative importance of one coordinate, say competitive ability, increases, the adaptive surface \( \pi \) will rotate toward that coordinate, resulting in an optimal phenotype which has sacrificed some egg-laying ability for increased competitive ability. So the position of \( P \) and hence clutch size, the intercept of \( P \) on the \( X \)-axis, will vary with the environmental conditions.

**Existing Theories of Clutch Size**

That a bird is limited physiologically from laying more eggs is a view which finds little acceptance today. There are numerous instances of birds laying more eggs than their normal clutch when eggs are removed at laying. And yet there are groups, e.g., Procellariformes, which lay one egg and usually do not replace it if lost. This seems a great waste of reproductive potential, and this theory might be the correct answer to account for the low \( r \), especially as petrels lay eggs notably large for the size of the bird. But then, if natural selection has brought the ruddy duck (\textit{Oxyura jamaicensis}) to lay a clutch three times its own weight (Kortright, 1943), surely the same could apply to a petrel given the same environmental conditions if it were advantageous to the species. It is apparent that this group of birds, living in the most stable coastal environment, are at a fairly constant maximum density as determined by the resources, and the importance of increasing \( r \) is small. Denoting \( X_1 \) and \( X_2 \) as shown in Fig. 1, large \( X_2 \) and small \( X_1 \) (predation being low) intercepts indicate strategy \( P_1 \) as shown, having a very small \( X \) intercept (clutch size).

The second hypothesis, again not a popular one, states that clutch size is limited by the number of eggs a parent can cover. This seems plausible when we consider that many ground-nesting birds have large clutches, this being a nest-site obviously conducive to holding many eggs. However, most of the large clutches of ground-nesters belong to gallinaceous birds, in which the young are not heavily dependent on the parents for food. Therefore, the largest number of eggs which can be covered, or young which can be brooded (shelter probably being very important), whichever is the lower, will determine clutch size. This being a limitation which does not vary with environment, we expect clutch size to be invariably high (large \( X \) intercept). Ground-nesters which do feed young have much smaller clutches (\textit{Caprimulgus, Sterna, Alauda}).

A third theory is that clutch size is adjusted "to balance mortality," but it has been pointed out by Lack (1947, 1949, 1954) that there is no proven mechanism to carry out this adjustment, convenient though such a system would be. The "balancing mortality" theory implies altruism, that birds possess a self-regulatory mechanism whereby recruits just compensate for losses. We cannot see how natural selection could operate in successive years to favor that clutch which would bring the population back to its optimum. Birds which laid larger clutches would naturally come to predominate, if conditions allowed the survival of these clutches, to the detriment of any or all altruistic members of the population which lay the supposedly optimal clutch for that season. There is perhaps one conceivable way in which a population could balance its mortality, and that is a behavioral one. There have been certain cases documented in which popula-
tion density has been shown to be inversely proportional to clutch size, but it is just as difficult to see how natural selection could accomplish this. Kluijver (1951) showed this relation for Parus major, and also that the same inverse relation holds for numbers of broods and density. Given that this relationship obtains, and is adhered to by all members of the population, here is a possible and sufficient mechanism to ensure a constant optimum density, on the average. Thus a greatly depleted population will have a correspondingly high clutch size, and as density increases under the influence of this high clutch, the latter will decrease accordingly. Large or small overwinter losses can be accommodated in this way. Many examples of density-fecundity relationships are given by Wynne-Edwards (1962), observed both in laboratory and field populations. We would now interpret this as follows, that as population density increases, numbers approach $\bar{K}$, and advantage is removed from high $r$ with a corresponding reduction in clutch size. The greatest difficulty in assessing the value of such relationships is that of divorcing density and food supply, and it is undoubtedly the latter which is the more appropriate factor in many cases; the inversely proportional density and clutch size may be an incidental result of the directly proportional food supply and clutch size.

Lack's (1954) views that parents rear the average maximum number of young possible, given the prevailing conditions and food supply, that one clutch size is optimal for a species in a locality in any particular year, and that this is the clutch size that will be favored by natural selection in that year is supported by much data for temperate passerines and near-passerines. It is also supported indirectly by observed variances in clutch size with food supply (Table 1). Evidence does show one optimum clutch size per season, as revealed either by the greatest number of fledglings reared from intermediate clutch size (as in Apus apus, Lack and Lack, 1951) or by the greatest post-fledging survival from an intermediate clutch size in those species which show approximately the same fledging success for several clutch sizes (Sturnus vulgaris and Parus major, Lack, 1954). Examples of variation in clutch size with food supply are assembled in Table 1, which illustrates how independent of rigid genetic control clutch size may become. Influence of food-gathering conditions, not on clutch size but on differential survival, is seen in swifts (Lack and Lack, 1951) in which c/3 and c/2 yield 0.9 and 1.0 fledglings, respectively, in a bad year (below average sunshine) and 2.3 and 1.9 fledglings, respectively, in a good year. Non-passerines are also subject to a food limitation, as is seen in the case of the short-eared owls (Asio flammeus), snowy owls (Nyctea nyctea) and pomatorhine skuas (Stercorarius pomarinus), all of which prey on lemmings (Dicrostonyx) in northern Alaska. Population density is one

<table>
<thead>
<tr>
<th>Species</th>
<th>Conditions average or below</th>
<th>Conditions above average</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nutcracker, Nucifraga caryocatactes</td>
<td>poor nutcrop previous year, av. clutch = c/3</td>
<td>good nutcrop av. clutch = c/4</td>
<td>Swanberg, in Lack, 1954</td>
</tr>
<tr>
<td>Barn owl, Tyto alba</td>
<td>normal clutch = c/3 in this part of Africa</td>
<td>clutch size during mouse plague = c/7</td>
<td>Fuggles-Couchman, in Moreau, 1944</td>
</tr>
<tr>
<td>Ploceus velatus</td>
<td>dry season, 10% c/4, 90% c/3</td>
<td>good rainfall, 90% c/4, 10% c/3</td>
<td>Hoesch, in Moreau, 1944</td>
</tr>
<tr>
<td>Bay-breasted warbler, Dendroica castanea</td>
<td>non-budworm years 4 c/4, 8 c/5, 5 c/6 av. = c/5.1</td>
<td>budworm years 1 c/4, 5 c/5, 15 c/6, 3 c/7, av. = c/5.8 (significantly higher)</td>
<td>MacArthur, 1958</td>
</tr>
</tbody>
</table>
per three to four square miles, one per two to four square miles, and 18 per square mile, respectively, in peak lemming years, zero, one per two to four square miles, and four per square mile in intermediate years, and no breeding takes place in years of low density (Pitelka et al., 1955). It is agreed here that because of the adaptive nature of clutch size, parents are rearing as many young as will maximize their contribution to the next generation and that in the above cases the limiting factor is food.

**Clutch Size and Latitude**

The increase of clutch size with latitude is a phenomenon which has been recognized by ornithologists for many years (Moreau, 1944, pp. 286–287). The only reasonable attempt to account for this trend is that of Lack (1947) who maintained that food supply is limiting in the tropics as in the temperate zones. He accounted for the increase in clutch size by considering that increasing day length from the equator gave parents a longer time per day to find food, and consequently larger broods could be reared. Support for this was forthcoming from data on the raven (Corvus corax) and the crossbill (Loxia curvirostra), both of which nest before the March equinox in northern Europe and show an increase in clutch size toward the equator. The theory does not easily account for species which feed young and do not increase clutch size with latitude (many Corvidae, Sulidae, Falconiformes, Charadriiformes), or species which do not feed young and do increase clutch size with latitude (Anatidæ — see Fig. 2.4, Rallidæ). Even more interesting are the tropical species which nest before the equinox (many tropical Passerines nest in the dry season, January to March). These show a large increase in clutch size from the equator northward, although day length decreases with north latitude (Skutch, 1954, 1960). It is also interesting that nocturnal mammals show increased litter size with latitude (Lord, 1960).

The more stable an environment is for a species, the greater the incidence of selection for $\bar{K}$ in populations of that species, and the more inter- and intraspecific competition will occupy the time and energy of the species, with a consequent reduction in clutch size. We therefore expect that clutch size will be inversely proportional to the climatic stability of the habitat, and as this stability decreases on moving north or south from the equator, clutch size will increase correspondingly. The latitude/clutch size graphs in Fig. 2 illustrating this relationship have been compiled from sources listed in the bibliography. A discussion of the individual examples mentioned in the figure footnote will be found below, as well as discussion of differences in the distribution of points and steepness of slopes. We may now relate these graphs to the theoretical model presented earlier. Degree of environmental stability, as we infer this to be directly proportional to energy spent on competition, may be represented along the $X_2$ axis in Fig. 3, and all points of equal stability on $S$ are given by the intersection of $S$ and a plane perpendicular to $X_2$ and parallel to $X$ and $X_1$. Before we can denote the path described on $S$ by the optimal phenotype as the adaptive function changes from one suitable at high latitudes to one suitable at low latitudes, we need to know the relationship between $X_2$ and $X_1$, the axis along which energy spent avoiding predation is represented. Students of tropical birds have often remarked on the heavy predation losses sustained by their subjects at breeding. Skutch (1949, 1954, 1960), perhaps the most experienced observer in this field, emphasized that nest predation in the tropics is far greater than in temperate counterparts, to the extent that he has postulated the necessity for a reduced number of trips to the nest with food for the young, and hence a better chance of escaping the detection of a watching predator, as a possible reason for low clutch size in the tropics. He further observed that the habit, apparently widely developed among forest birds, of bringing to the nest large morsels seldom and thereby cutting visits to a minimum, might be an adaptation
FIG. 2. Graphs of clutch size (ordinate) against latitude (abscissa).

2.1—the genus Emberiza. ○ = species nesting in Africa south of the equator; ● = species nesting in Europe and Asia. The two sets of points fit the same line.

2.2—the family Tyrannidae. ○ = South American species; ● = North American species (p << 0.001 that the lines fitting these two sets of points have the same slope); ○ = the genus Myiarchus (hole nesters); ○—○ = Myiarchus tuberculifer.

2.3—the family Icteridae. ▲ = North American species; △ = South American species.

2.4—the genus Oxyura (family Anatidae), worldwide distribution.

2.5—the “superfamily” Thraupidae plus Parulidae, in Central and North America. ●—● = Myioborus miniatus; ○—○ = Tanagra lauta (hole nester); ○ = Tanagra luteicapilla (niche nester); □ = Prothonotaria citrea (hole nester).

2.6—the family Troglophilidae. ○ = South American species; ● = North American species; ▲—▲ = Trogldytes aedon.
to reduce nest predation. The work of Snow (1962) on *M. manacus*, in which the young of only 19 per cent of 227 nests reached fledgling over five years of observation confirms this high rate of loss to nest enemies, as at least 158 of these failures could be attributed to predation. Such losses from this cause are not nearly so great in temperate regions (Lack, 1954). If we now let $P'$ be the strategy of a species nesting in the temperate, with low predation, low stability, and therefore a high clutch, the optimal phenotype will describe a curve $PP'$, where $P$ represents the strategy in the tropics, a region of high predation and high stability, resulting in a small intercept on $X$ and a low clutch size.

**Predictions from the Theory**

Let us first consider stable environments. We have asserted above that reduced clutches in the tropics are the indirect result of climatic stability. If this is indeed so, and we have correctly deduced the most pertinent factors involved, then we should be able to predict that reduced clutch sizes will be found in any environment characterized by its stable conditions. Moreau (1944), when comparing species inhabiting evergreen forests in equatorial Africa with close relatives occupying more seasonal habitats at the same latitude (and therefore receiving the same amount of light per day), found that in eight cases the forest birds had lower clutches, in two cases the opposite, and in 12 instances no change in clutch size could be detected (by $t$-test, these data have a 75 per cent probability of significance). Specifically, a caprimulgid which nests in the forest lays one egg, while all other members of its family in the Old World and in North America lay two eggs.

Oceanic islands, well known for the great climatic stability they enjoy, ought to show decreased clutches from the mainland at the same latitude, and indeed this is the case (Table 2). See also Lack (1947, pp.

---

**Fig. 3.** Paths traced by the adaptive function from temperate to tropical latitudes for mainland open-nesting passerines ($P'\ldots P'$), predation-free species ($P''\ldots P'''$), hole-nesters ($H'\ldots H$) and island-nesting species ($Q\ldots Q'$).
Table 2. Differences between island and mainland clutch sizes at the same latitude.

<table>
<thead>
<tr>
<th>Species or genus</th>
<th>Average mainland clutch</th>
<th>Average island clutch</th>
<th>Species or genus</th>
<th>Average mainland clutch</th>
<th>Average island clutch</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anas</td>
<td>8 (3 sp.)</td>
<td>3.5 (1 sp.)</td>
<td>Saltator albicollis</td>
<td>2.0</td>
<td>2.5</td>
</tr>
<tr>
<td>Bowdleria punctata</td>
<td>3.1</td>
<td>2.5</td>
<td>Tangara gyrola</td>
<td>2.0</td>
<td>2.0</td>
</tr>
<tr>
<td>Gerygone</td>
<td>4.5 (1 sp.)</td>
<td>4.0 (1 sp.)</td>
<td>Habia rubica</td>
<td>2.3</td>
<td>2.0</td>
</tr>
<tr>
<td>Petroica macrocephala</td>
<td>3.5</td>
<td>3.0</td>
<td>Cacicus cela</td>
<td>2.0</td>
<td>2.0</td>
</tr>
<tr>
<td>Miro australis</td>
<td>2.6</td>
<td>2.5</td>
<td>Coereba flaveola</td>
<td>2.5</td>
<td>2.5</td>
</tr>
<tr>
<td>Anthornis melanura</td>
<td>3.5</td>
<td>3.0</td>
<td>Empidonax eulieri</td>
<td>2.0</td>
<td>3.0</td>
</tr>
<tr>
<td>Cyanoramphus novaezelandiae</td>
<td>6.5</td>
<td>4.0</td>
<td>Elaenia flavogaster</td>
<td>2.3</td>
<td>2.5</td>
</tr>
</tbody>
</table>

1 Species considered were either indigenous to the offshore islands and had a mainland relative in the same genus, or were subspecifically distinct on the island. The difference between the mainland and island means is 90 per cent significant, by t-test.

2 Species on isolated West Indian islands are compared to the mainland, and also the extreme southern Lesser Antillean islands (isolated) are compared to Trinidad, which is very close to the mainland. The means are not significantly different.

308–309). To exhibit an “island effect” (i.e., reduced clutch size), the island must be sufficiently isolated that mainland immigrants, which lay a larger clutch, do not swamp the island population, and the typical island clutch size is kept at the lower level. I have taken the subspeciation of island forms as an indication of sufficient isolation to fulfill this requirement. As well as possessing an impoverished fauna in general, most islands have no predators whatsoever, either on adult birds (most island bird lists are without accipiters or falcons) or on nests (snakes and mammals, among the chief nest predators at lower latitudes, are poor colonizers and are absent from most islands), a fact which probably accounts for the evolution of many flightless species (rails and ducks) on islands. Lack of predation puts island strategies in the XX₂ plane in the figure, and if Q represents the strategy on an island at the same latitude as the temperate mainland but having a much milder, fairly stable climate, and Q′ the strategy on a tropical island, perhaps even more stable than the opposite mainland, Q′Q is the path of optimum strategies of island birds from high latitudes to the equator. Consequently, although temperate islands should have reduced clutch sizes, tropical island clutch sizes, if different at all, will be only slightly higher or slightly lower than those on the mainland, depending on the relative increase of predation on the mainland which determines the X-intercept of P, or the relative increase of stability on the island which will alter the X-intercept of Q. This prediction is also verified in Table 2 which shows that in some cases lack of predation permits a larger clutch size on tropical islands not compensated for by increased stability on the island. In many others the difference in clutch size will be perhaps only fractional (of an egg), requiring a detailed study of many nests to reveal it.

Coastal areas of continents are more stable climatically than central regions, and as we would expect if the theory is correct, clutch size increases from the coast inland (Lack, 1947, for Europe). This phenomenon is well observed in the United States, which has an extremely mild west coast, in contrast to the center of the continent where violent storms are of common occurrence. Thus, many birds (see, for example, Bent, 1938, p. 302, for the great horned owl, Bubo virginianus) lay their largest clutches in the midwest (between about 86° and 96° east longitude), an area which includes those states most familiar with severe winters and storms. A study by Johnston (1960) of clutch size in song sparrows, Melospiza melodia, revealed not
only a gradual latitudinal increase from Baja California (3.05 eggs) to Alaska (4.17), but an increase from the Pacific coast east to Ohio (4.15) at which latitude the coastal sparrows lay 3.65 eggs. Presumably by taking advantage of the coastal climate, a few hummingbirds (Trochilidae) reach British Columbia, while one species, Selasphorus rufus, reaches Alaska (61° N). Mountainous areas are more unstable and unpredictable in their climate than adjacent lowlands, which accounts for the general trend for species nesting at high altitudes to lay larger clutches. In the Sierra Nevada, song sparrows (Johnston, 1960) at a median latitude of 38° N lay an average clutch of 3.99 eggs, which would not be found on the coast south of about 58° N.

A further instance of climatic stability affecting clutch size is found in South America, whose narrow and tapered configuration, especially below the tropics, where the influence will be most important, allows the closer proximity of inland areas to the surrounding oceans and results in a considerably milder more stable climate in this country compared to similar latitudes in North America. The Humboldt current up the west coast will have an additional ameliorating influence. We expect that the slope of the latitude clutch size graph will be steeper in North America than in the southern half of the continent, and this is exactly the situation which exists (Fig. 2). Africa, on the other hand, has a much larger and wider land mass, and Fig. 2 shows an equal slope for both north and south of the equator there. Large sea-birds live in coastal and hence quite stable environments, and have few predators, and so in tropical and temperate waters alike there will be a tendency to increase $\bar{K}$ not $r$, because of the stable conditions in which these birds live. Implications that this might be the case come from the work of Nelson (1964) on Sula bassana, which suggests (but does not prove as yet) that food is not the limiting factor of clutch size. It is possible that the $X_3$ axis in Fig. 1 might more appropriately denote effort spent on an individual chick, measurable as weight at fledging, as even slightly smaller chicks at fledging would perhaps be at a disadvantage in its competitive ability during the next few years.

The Peruvian booby, Sula variegata, is a guanay-producing species which feeds in the waters of the Humboldt current off western South America. Every seven years or so the cold waters of this current are met by warm waters ("El Niño") from the northeast at a time when these birds are feeding young, and a food shortage results during which colonies are abandoned and the young boobies starve (Murphy, 1936). So far as this species is concerned conditions are unstable, and selection will be proceeding for $r$. In fact this species lays one to four eggs, and six out of seven years rears three young as often as two (other species of Sula which lay two eggs seldom rear both young). This is no doubt made possible by the rich food supply of the Humboldt current, and is seen graphically as equivalent to moving from $P_1$ to $P_2$ in Fig. 1.

The bay-breasted warbler, Dendroica castanea, Cape May warbler, D. tigrina, and the Tennessee warbler, Vermivora peregrina, are the North American warblers which depend on an unstable food supply. These species are largely dependent on irregular spruce-budworm outbreaks (Mac-Arthur, 1962) for food during their breeding season, and as we would expect lay larger clutches (of five to six, five to seven, and five to six eggs, respectively) than other member of the Parulidae (normal clutch size four, rarely five, eggs). Another exception to the usual four eggs is the prothonotary warbler, Prothonotaria citrea, which is a hole-nester and lays a six-egg clutch.

A second prediction concerns predation-free species. It can be seen from Fig. 3 that if a species does not experience the increased predation in the tropics that most passerines do, the line $PP$ would be altered to $PP'$, $P'$ having the same $X_3$-intercept as $P$, but an intercept on $X_4$ equal or nearly equal to that of $P'$ and an $X$-intercept
closer to that of $P'$. Thus we can predict that species which are relatively free from predators will have a smaller temperate-tropical increase in clutch size. This is exactly the situation observed by Lord (1960) in North American mammals, in which no statistically significant increase in litter size with latitude could be found in predatory species (*Vulpes, Felis, Mustela*).

Hibernating animals would manage to avoid predation during winter and showed a less steep slope than did non-hibernating prey species, all these being statistically significant.

A third and final prediction may be made for hole nesters. Hole-nesting birds would escape much of the predation suffered by species nesting in open or exposed situations. For instance in the red-breasted merganser (*Mergus serrator*), which in Europe commonly nests in holes in banks, rocks, and tree roots, 91 per cent of hatched young survived, whereas for six species of open-nesting ducks this figure averages 58 per cent (from data in Lack, 1954). We can predict not only that clutch size will be higher in the tropic and temperate zones alike, but also that, as nest predation is higher in the tropics and the relative advantage of hole-nesting over open nests is greater there, the latitude/clutch size slope will be less steep for these hole nesters than for the open nesters. As this has been represented in Fig. 3, $P$ and $P'$ move down curves of points of equal stability to strategies $H$ and $H'$; but $PH$ will be greater than $P'H'$ due to the greater relative advantage gained in the more stable-greater predation region. Lack (1948) showed not only that hole nesters lay a larger clutch by nearly two eggs on the average, for mid-European passerines, but that strategies between $P'$ and $H'$ exist, as intermediate stages of nest exposure, i.e., roofed and niche sites, between hole and open sites, which expose the nest to more predation and a higher chance of failure, result in intermediate clutch sizes. Tropical hole nesters also have higher clutches. The genus *Myiarchus* comprises the only tyrannid flycatchers to nest in holes in decayed stumps (Skutch, 1960, p. 398), and these species are responsible for the higher clutches of the family (Fig. 2.2). Similarly, of the Central American Thraupidae the only member for which clutch data exist and which nests in a hole is the Bonaparte euphonia, *Tanagra lauta*. While the other members of its genus, and indeed its family, lay two to three and rarely more eggs in this region (Skutch, 1954, p. 249), this species lays five to six eggs. The hole-nesting Ramphastidae (toucans) lay three to four eggs, compared to the two eggs which comprise a full clutch for the vast majority of tropical birds and likewise with the jacamars Galbulidae laying an average of 2.6 eggs (Skutch et al., *in litt.*). Indications that the slope of the graphs for hole-nesters is more gradual are obtained from limited data, but hole-nesting Alcenidae increase their clutch size from four to five or six (ratio 1 : 1.4) from Central America to the United States, while most of the graphs given show a ratio of 1 : 2.5 for that range of latitude.

**Summary**

The principle of allocation of time and energy is used to formulate a general theory to account for clutch size in birds. "Advantages" are figured as the axes of a three-dimensional graph, and phenotypes allocating their energy in particular ways as points in space forming a surface and enclosed solid.

In the temperate zones most energy is used to increase the reproductive rate $r$. In the tropics the carrying capacity of the habitat is more important, resulting in a smaller clutch size. Different phenotypes will be more fit in different environments, as optimum allocation of energy differs.

Previous theories of clutch size are discussed, and incorporated into this general theory. Increase of clutch size with latitude is analyzed, and accounted for by the theory.

Predictions are made that all stable environments, the tropics, islands, coasts, will favor reduced clutches. Examples are quoted in which instability of conditions results in increased clutch size. The situa-
tion of predation-free species is examined, and it is predicted that the clutch size of such species will remain relatively unchanged with latitude changes. These predictions seem to be verified in all cases where data are available to test them.

ACKNOWLEDGMENTS

I am deeply indebted to Dr. Robert MacArthur for his assistance throughout the preparation of this paper. I am also grateful to Dr. Mike Rosensweig and Dr. Harry Recher for reading the manuscript and offering many useful suggestions.

LITERATURE CITED


Skutch, A. F. 1949. Do tropical birds rear as many young as they can nourish? Ibis, 91: 430-455.


