VARIATION IN CLUTCH SIZE AT DIFFERENT LATITUDES

BY H. O. WAGNER

MORE than 100 years ago the South American explorers Prince Wied (1830) and Schomburgk (1848) pointed out that the clutch size of tropical song birds was smaller than that of European song birds. The fact that the number of eggs per clutch generally increases with the latitude has been confirmed repeatedly. This applies to species which originated in the tropics and have extended their range to the temperate zones, as well as to those which, on the contrary, have extended their breeding grounds across the tropics to the equator. It also applies in regions of hot climates and in high mountains.

Hesse (1922) was the first to attempt to interpret this phenomenon. He assumed that the length of the day-light period, and hence the time available for seeking food for the nestlings, determines the clutch size. Starting with this hypothesis Lack (1947a, 1947b, 1948a, 1950) developed a whole complex of questions by means of careful and extensive investigations. He was of the opinion that clutch size at any time is determined by heredity, and that environmental influences are of only subordinate significance. In my opinion, Lack has not given due attention to one important factor, namely living conditions at the time the eggs are laid. Genetically, there is a fixed upper limit for each species; however, it is reached only in optimum living conditions, particularly when the clutch size in itself is fairly large.

During my many years' residence in Mexico, I was continually concerned with the questions of the causes of the smaller clutch size and why smaller clutches are compensated for by increased numbers of broods. The experiments I began were interrupted by my return to Germany. These were intended to determine, by combining two broods, whether Lack's assumption—which runs like a red thread through his writings—that no more nestlings can be reared between the tropics, could be maintained. House Finches (*Carpodacus mexicanus*), which breed prolifically in the neighborhood of the Mexican capital and have a usual clutch size of two eggs (17 clutches had two eggs; three clutches had three eggs), and the Yellow-eyed Junco (*Junco phaeonotus*) with clutches of two or three eggs, were chosen as the test material. Their geographical representatives have larger clutches further north (House Finch up to 7, Yellow-eyed Junco up to 5 eggs). Of eight combined nests two were prematurely destroyed, and one youngster disappeared from one. Of the remaining five (three of House Finches, two with four eggs and one with five) and (two of Yellow-eyed Juncos, both with four eggs), no influence attributable to the duplication could be detected on the duration of development or the condition of the nestlings. If the number of tests is too small to produce anything conclusive, at least they show that the hypothesis of Hesse and Lack is probably incorrect. It is to be hoped that such experiments, which can be carried out without great difficulty, will be repeated. A few research workers who have lived in the tropics for many years cannot support the theory that the feeding time for the nestlings is of decisive significance. Moreau (1950) after many years of experience in Africa, became convinced that food supply was the critical factor, as it is so seldom fully exploited. The biologist Alexander Skutch, who has been active in Costa Rica for 25 years, also doesn't follow Lack's attempted interpretation (1949 and 1950). Particularly telling among his arguments is the fact that there is no difference in the number of nestlings in species where the female alone, or the parents jointly, feed the progeny. His statement (1950) on the clutch size of the Tyrannidae shows that the females of *Pipromorpha oleaginea*, who look after their nestlings alone, usually feed three young instead of two like the other species mentioned, in which the males share in the care of the brood. Skutch attempts to explain the advantage of small clutches by referring to the danger which snakes represent to broods in the tropics. He assumes that the danger is reduced where the number of young is less, as the frequency of approach of the parents bringing food and the number of young are in a fixed ratio, and so their position is more or less easily betrayed. This attempted explanation is not very convincing, as in seeking for their prey (according to a statement by Prof. H. Kahmann, Munchen) snakes are guided mainly by their sense of smell. As far as we know today, their power of sight is too weak to recognize a bird flying to its nest as such. The other argument with the same drift, that the general danger of discovery increases with the number of nestlings owing to the increase in the noise of begging for food, has yet to be proved. In such cases selection, which originates with the nestlings, would have to reduce the preceding number of eggs, a conception which can hardly be reconciled with our present knowledge. Paynter (1951), and Lack (1948 a and b) attempt to prove this hypothesis in the case of Starlings by showing statistically that the young of small clutches have improved life expectancies. This selective advantage, however, is not so great as to produce by selection a reduction of, for example, from 5 to 4 eggs, i.e. 20 per cent. Since the interpretations of Lack and Skutch do not appear satisfactory, there is given an added general interest to the question. It is probable that the cause must be looked for in a completely different direction, namely in the physical constitution of the individual at the time of laying.

The production of a clutch entails a considerable physical effort for the bird. The structural materials required are derived from the daily consumption of food, possibly supplemented by the reserve materials stored in the animal. The proportions of the two components at any time can differ considerably. Whenever stored reserves are utilized, the percentage of the total reserve going into the production of each egg can determine the total number of eggs, because when the reserve materials are used up the bird is compelled to cease laying. If, for example, each egg requires 25 per cent of the female's reserve material, the clutch size cannot exceed four eggs. However, the proportion of the reserves can be much greater, and if these are not available or are present only in inadequate quantities owing to unfavorable feeding conditions, they can lead to the complete cessation of reproduction, as is known in the Arctic and in arid and semi-arid regions of the tropics (Hoesch, 1936; Leopold, 1933; Serventy and Whittell, 1948; and Sumner, 1935). The opposite situation, a heavy increase in egg production under exceptionally favorable feeding conditions, also occurs. In years having a plethora of mice and lemmings, owls and birds of prey double the number of their eggs, as the required supply of material for egg production is more than compensated for by the ample supply of prey. Finches from tropical regions are frequently bred in Europe, and when kept under optimum conditions in a cage, the clutch size and number of eggs per year can be considerably higher than in natural conditions.

For species, the production of whose eggs utilizes just or considerably more than the daily consumption of food, there is a danger that the bird will lay more than it can hatch. This is prevented by the cessation of laying as soon as all the brood spots comes in contact with the eggs. Paludan (1951) has investigated experimentally the relationships between brood spot and number of eggs. According to Witschi (1950) the clutch size is probably regulated by the female evidently sensing the extent to which the nest is filled by means of the tactile papillae in the skin of the breast. This sensory perception probably passes via the spinal cord and the cerebral stem to the posterior lobe of the hypophysis, from where the impulse is transmitted on to the secretory anterior lobe to modify the hormone production so as to inhibit the development of the egg and ovulation and to cause the already grown oocytes to degenerate.

Birds which do not use their reserve materials or use them only in part continue laying after the eggs have been removed from the nest until these materials are exhausted, or become permanent layers (Stresemann, 1934) like domestic poultry. In view of the generally small number of eggs laid, it is not possible to carry out satisfactory investigations in the tropics on the ability to continue laying. In the environs of Mexico City, Brown Towhees (*Pipilo fuscus*) and American Robins (*Turdus migratorius*), whose northern races hatch 4 to 5 eggs as against 2 to 3 in the region investigated, did not make up their clutch after one egg had been removed. Accordingly, the clutch size at any time is probably determined by the food potentialities existing at the time of reproduction in conjunction with the degree of ability to store reserve material, independently of any hereditarily fixed factor. It is possible that the usually smaller number of eggs in warm countries is related to more unfavorable ecological conditions and lessened tendency to store fat as compared with the inhabitants of temperate latitudes. Both are confirmed by my investigations. The ability to form generous reserves of fat seems to be limited to the residents of higher latitudes. This is understandable, as reserves are a prerequisite to the survival of long winter nights and the exertions of spring and autumn migrations.

The reserves for the eggs need not be available in the form of fat. At the time of breeding, female hummingbirds store material for the second egg in the form of supernumerary egg follicles. About six grow to a certain size, one of which developes in a few days into an egg ready for laying. Within 48 hours after it has been laid, a second is formed from the remaining follicles. In a Black-billed Azure-crown (*Amazilia verticalis*) killed immediately before the laying of the second egg, the remaining oocytes were not only completely utilized, but the ovary was so much worn that no one could have guessed its activity of a few hours previously. As I have shown elsewhere (Wagner, 1952), in the case of hummingbirds, clutches of three belong to two birds, where a female whose own nest has been destroyed has laid its developed egg in a strange one.

The relatively poor feeding conditions at breeding time in the tropics are not merely a consequence of the short days, but also of a limited exploitation of them. As soon as a certain degree of heat is exceeded, the instinct to look for food fails, even where a feeling of hunger predominates. In the semi-arid cactus deserts, savannas, dry and pine groves of Mexico, it is useless to look for birds a few hours after sunrise, and the same applies in Australia (Finlayson, 1935). Only toward evening do they again become active. Exceptions prove this rule. The number of eggs of quail which inhabit the semi-arid regions of Mexico south of the Tropic of Cancer, is not smaller than in the United States. The ability of these birds to store food in the crop makes them independent of high midday temperature. In Caderyta, Queretaro (2100 m. elevation) even the crops of Scaled Quail (*Callipepla squamata*) killed at midday were filled with cactus seeds which had been gathered in the cool hours of the morning. This supply ensures a uniformly continuous metabolism which permits the laying of an egg each day without making demands on the reserve materials. My attention was drawn to their qualities as permanent layers by boys looking after goats in the cactus and stony desert, who brought me a few eggs every couple of days but never a full clutch. Questioning revealed that they always left a few eggs in any nest they found, so as to exploit the ability to lay continuously and increase the yield. Up to the time of my departure one female laid 17 and another 19 eggs, whereas the normal clutch in nearby Hidalgo fluctuated between 10 and 13.

The exceptional behavior, which has often been discussed, of nightjars whose clutch size increases as the latitude decreases, can be accounted for by the possibility of searching for food for a longer period than in the temperate latitudes, owing to the brighter tropical nights. Birds of twilight in the north, in the south they hunt for insects even at night. Why swifts on the other hand produce an equal number of eggs in the United States and in equatorial Brazil is problematic: *Chaetura andrei*, 4 to 5 in Brazil (Sick, 1948), *Chaetura pelagica*, 4 to 5, and *Chaetura vauxi*, 4 to 6 in the United States (Bent, 1940).

The type of food can also be influential. Corn-eating Scaled Quail with their large number of eggs form a contrast to the Spotted Wood-quail (*Odontophorus guttatus*) and Long-tailed Wood-quail (*Dendrortyx leucophrys*) of the cool, tropical moist and mist forests, which live on insects, worms, and other small animals and have clutches of four to six eggs. With the wood-quail the search for food lasts the whole day, so that the general basal metabolism is greater than with the blue quails (*Lophortyx* and *Callipepla*) which rest in the shade for the main part of the day and so have less food material available for the production of eggs.

The difference in composition of the food probably also helps to determine the different numbers of eggs of Ocellated Turkeys (*Agriocharis ocellata*, wt. 2260 g.; 2026 g.) which lay six to eight eggs and the Purplish Guan (*Penelope purpurascens*, wt. 2430 g.) which lay only two. Turkeys, which have a crop, live on seeds (they are fond of raiding maize fields), berries, insects, and young plant shoots, whereas the stomachs of Mexican guans, *Penelopina nigra, Penelope purpurascens*, *Oreophasis derbianus*, and *Crax rubra* which I have examined, were filled with leaves, young shoots, and berries (Wagner, 1953 a and b). It is therefore not surprising that the fleshy turkeys are tasty, whereas the thin guans are dry and stringy. The argument that the extra hazards of turkeys, which nest on the ground, compared with guans, which nest in trees, necessitates a larger number of eggs is untenable, as ground breeders among the guans such as *Penelopina nigra* and *Oreophasis derbianus* do not rear more than two chicks.

To sum up, we can state that in the overall constellation the upper limit of the number of eggs of a brood is fixed genetically. The fertility potential can be reduced by environmental influences as has been proved in numerous experiments in entomology. The effects of external factors are more obvious in the tropics than in temperate latitudes where the birds cannot afford such a close dependence.

In any case, the opinion of Lack (1947a and 1948a) and of Lack and Arn (1947), that the number of eggs in a clutch is generally fixed genetically for the species, is in my opinion not universally valid. The statistically proved differences in propagation of English, Dutch, and Swiss starling and quail populations are probably conditioned by the environment, as are the fluctuations in individual years (Lack, 1947b, 1948b, 1949, and Silva, 1949). The relatively large number of eggs in the clutch which occurs within a population in the spring and the smaller clutches of the second brood are conditioned by the physical constitution and age of the female. This view will appear erroneous to those who cannot give up the idea that slight differences in the reproductive rate are not significant for the preservation of the species. Figures for increases and losses are not as clearly balanced as is often assumed. Otherwise external circumstances could only too easily lead to the extinction of a species. Nature employs a considerable surplus as a safety factor, so as to cope with any possible threats of extermination (Wagner, 1953c) or to bridge the gap caused by the loss of a reproductive period.

Resistance to the environment, which constantly aims at increasing the propagation rate, is less in the seasonally balanced regions of the tropics than in areas with contrasting seasons. To counter unfavorable environmental influences (northern winter, aridity of the desert, etc.), all possible methods of progressive adaptation to the given environmental conditions are adopted to improve the prospects of life for the individual and to increase the propagation rate. Under favorable living conditions this has led to larger broods and clutches, or in the arid regions of Australia, to the ability to procreate at the age of two months as with the Zebra Finch (*Taeniopyga castanotus*). Thus in the case of the Zebra Finch, an additional generation within a reproductive period helps to bridge gaps created by failure to breed for some time or by the extinction of large swarms where a water-hole dries up and there is no possibility of reaching another (MacGillivray, 1932). In contrast to this, many smaller birds of the damp, warm tropical forests, such as representatives of the thrushes, tyrant flycatchers, finches, swifts, trogons, and other families, do not breed until the age of two years and more. No reason can be given for this late breeding.

Further experiments must show whether the variable clutch size can be accounted for by the preceding conclusions. Only a consideration of the whole problem will enable us to understand correctly a process as complicated as the one we have discussed, while at the same time we should not deceive ourselves that causal explanations are always defective, as we do not and never shall know the conditions well enough to understand them perfectly.

LITERATURE CITED

BENT, A. C. 1940. Life histories of North American cuckoos, goatsuckers, hummingbirds, and their allies. U. S. Natl. Mus. Bull. 176: 1–506.

FINLAYSON, H. H. 1935. The Red Centre; Man and Beast in the Heart of Australia. Angus & Robertson Ltd., Sydney, Australia.

HESSE, R. 1922. Die Bedeutung der Tagesdauer für die Vögel. Sitzber. Nathist. Ver. Bonn for 1922–1923, pp. A 13–17.

HOESCH, W. 1936. Nester und Gelege aus dem Damaraland, II. Journ. für Ornith., **84**: 3–20.

LACK, D. 1947a. The significance of clutch-size, I. Ibis, **89**: 302–352.

LACK, D. 1947b. The significance of clutch-size in the partridge (*Perdix perdix*). Journ. Anim. Ecol., **16**: 19–25.

LACK, D. 1948a. The significance of clutch-size, III. Ibis, **90**: 25–45.

LACK, D. 1948b. Natural selection and family size in the Starling. Evolution, **2**: 95–110.

LACK, D. 1949. Family size in certain thrushes (Turdidae). Evolution, **3**: 57–66.

LACK, D. 1950. Family-size in titmice of the genus *Parus*. Evolution, **4**: 279–290.

LACK, D., and H. ARN. 1947. Die Bedeutung der Gelegegrösse beim Alpensegler. Ornith. Beob., **44**: 188–210.

LEOPOLD, A. 1933. Game Management. C. Scribner's Sons, New York.

MACGILLIVRAY, W. D. K. 1932. The Flock Pigeon (*Histriophaps histrionica*). Emu, **31**: 169–174.

MOREAU, R. E. 1950. The breeding seasons of African birds—1. land birds. Ibis, **92**: 223–267.

PALUDAN, K. 1951. Contributions to the Breeding Biology of *Larus argentatus* and *Larus fuscus*. Munksgaard, Copenhagen.

PAYNTER, R. A., JR. 1951. Clutch-size and egg mortality of Kent Island eiders. Ecology, **32**: 497–507.

PEARSON, O. P. 1950. The metabolism of hummingbirds. Condor, **52**: 145–152.

RICHDALE, L. E. 1949. The effect of age on laying dates, size of eggs, and size of clutch in the Yellow-eyed Penguin. Wilson Bull., **61**: 91–98.

SCHOMBURGK, M. R. 1847–48. Reisen in British-Guiana in den Jahren 1840–1844. J. J. Weber, Leipzig.

SERVENTY, D. L., and H. M. WHITTELL. 1948. Birds of Western Australia. Pattersons Press Ltd., Perth, W. A.

SICK, H. 1948. The nesting of *Chaetura andrei meridionalis*. Auk, **65**: 515–520.

SILVA, E. T. 1949. Nest records of the Song-Thrush. Brit. Birds, **42**: 97–111.

SUMNER, E. L., JR. 1935. A life history study of the California Quail, with recommendations for conservation and management. Calif. Fish and Game, **21**: 167–342.

SKUTCH, A. 1949. Do tropical birds rear as many young as they can nourish? Ibis, **91**: 430–455.

SKUTCH, A. 1950. The nesting seasons of Central American birds in relation to climate and food supply. Ibis, **92**: 185–222.

STRESEMANN, E. 1927–34. Aves. In Kükenthal u. Krumbach, Handbuch der Zoologie. Vol. 7, pt. 2. De Gruyter, Berlin.

WAGNER, H. O. 1952. Beitrag zur Biologie des Blaukehlkolibris *Lampornis clemenciae* (Lesson). Veröff. Mus. Bremen, Reihe A, **2**: 5–44.

WAGNER, H. O. 1953a. Beitrag zur Biologie und Domestizierungsmöglichkeit des Pfauentruthuhnes (*Agriocharis ocellata* Cuvier). Veröff. Mus. Bremen, Reihe A, **2**, 2: 135–140.

WAGNER, H. O. 1953b. Die Hockohühner der Sierra Madre de Chiapas/Mexiko. Veröff. Mus. Bremen, Reihe A, **2**, 2: 105–128.

WAGNER, H. O. 1953c. Zur Populationsdynamik der Kleinnager in den Tropen und ihre Ursachen. Bonner Zool. Beitr., **4**: 1–12.

WAGNER, H. O., and E. STRESEMANN. 1950. Über die Beziehungen zwischen Brutzeit und Ökologie mexikanischer Vögel. Zool. Jahrb. Jena (Syst.), **79**: 273–308.

WIED, MAXIMILIAN PRINZ ZU. 1825–33. Beiträge zur Naturgeschichte von Brasilien. Landes-Industrie-Comptoirs, Weimar.

WITSCHI, E. 1950. Zur biologischen Charakterisierung der gonadotropen Hormone. Naturwissenschaften, Berlin, **37**: 81–85.

Übersee-Museum, Bremen, Germany.