favor of the swift's locomotion is nullified. Now, a claw on the heel of the tarsus, functioning as a toe, would enable the swift to maintain its balance in a downward course, or even on a level surface; but lacking such a handy attribute the swift must pitch forward when caught in such positions. The fact that the swift does pitch forward when on a level surface would seemingly account for this bird's inability to rise from the ground as do ordinary birds.

Yosemite, California, January 28, 1926.

AVIAN GONADS AND MIGRATION

By W. H. BERGTOLD

I HAVE VOICED my conviction, in a previous communication (Condor, XXIV, May, 1922, p. 82) that a large amount of valuable data is lost each year through the failure of collectors and preparators to utilize every mensural character of a freshly collected bird. The following contribution is based on an endeavor, made by myself during the recently past few years, to be consistent with this conviction. The data here published form a small but real addition to avian biology, and they have been gathered with ridiculous ease and with the aid of only a little extra equipment, paraphernalia which have served for both table and field purposes. This simple addition to a collector's outfit has been described in the above mentioned prior communication. Beginning in 1916, all male birds collected by me have been utilized to furnish the usual measurements of external characters, and have also contributed the body weight and the weights of the gonads.

The periodic hypertrophy and atrophy of birds' gonads has long been well known to collectors and to students of avian anatomy. Nevertheless the very remarkable increase in size of a bird's spermaries each spring does not cease to be a startling phenomenon; and yet, so far as I have been able to learn, nothing has ever been published which shows just how great this increase may be, when measured by some definite standard. A determination of the extent of this increase is not only of biological value *per se,* but it may shed light on other difficult problems in ornithology.

Table No. 1 gives the body weight and the combined gonads' weight of fifty-eight bird individuals, a series embracing forty-five different species; also the date of collection, the proportion of gonads' weight to body weight, and the "fold" increase (when possible to compute) in weight, of the active over the resting glands.

It is self evident that a considerable period of time is required for the change from complete atrophy (inactivity) to full hypertrophy (activity), and that the season of this period will vary somewhat, according to latitude, altitude and species. It is assumed that, for *most* of the species listed, and occurring in and about Denver during the nidification period, the active gland increase occurs from April to August (inclusive). However, it is more than probable that this does not hold true with such species as the Magpie, Clark Crow, Chickadee, Great Horned Owl, and Screech Owl, some of which may breed as early as February. This fact must be considered in the conclusions to be drawn from the data herein submitted.

The date of collection of a given specimen is recorded because it permits one to judge whether or not the bird had the maximum gonad weight attainable in the breeding period. It is obvious that one must judge, concerning this condition, largely by the date. Twenty-one of these fifty-eight birds exhibited spermaries so small that

they could not be weighed. This extreme shrinkage, found during the non-breeding season, is well known, has often been commented upon, and is frequently a source of error in "sexing" the specimens collected in that season. The difficulty of weighing gonads under these circumstances was not due to the lack of a balance sufficiently delicate to estimate such small quantities, but to the fact that one could not dissect out the minute glands and still be certain that no adventitious tissues were included with the gonads. All these twenty-one specimens are listed as having "plus or minus" gonad weights. However, in attempting to weigh the glands of these twenty-one specimens it was definitely established that every pair of these gonads weighed less than one milligram (3/200 grain + or —).

In weighing ponderable gonads it was done as soon as possible after the collection of the specimen, and only after the glands had been carefully and thoroughly freed of accessory organs and tissues.

In order to determine the relation in weight of the resting to the active gland, and the "fold" increase of the gland from minimum atrophy to maximum hypertrophy, it was of course necessary to have the gland weights in both these stages; unfortunately I have been able to collect but six species for which I have secured these minima and maxima, namely, Mourning Dove, Long-crested Jay, English Sparrow, Virginia Warbler, Pigmy Nuthatch and Robin. In view of this dearth it became necessary to find, or to arbitrarily establish, the resting gland weight for the species in which this was unknown, but for which the maximum weight had been recorded. This was done by *assuming* that the resting gonads of most (if not all) of these species had a weight of one milligram.

If it be held that the twenty-one "plus or minus" specimens had resting glands weighing one milligram (which is in fact much in excess of the actual weight) and these specimens then averaged with nine others showing varying ponderable gonads during the non-breeding season, we learn that the combined thirty specimens exhibited an average of twenty-eight milligrams as the resting gonads' weight. I am convinced that most, if not all, avian gonads shrink in the middle of the non-breeding season to negligible weights and I therefore feel that all of the above mentioned nine specimens were far from the stage of complete gonad inactivity. Such a thing as belated nestings could easily account for an unexpectedly heavy spermary weight in the fall.

I am sure that seven hundred milligrams, as found in a Clark Crow in October, does not represent completely resting spermaries. Therefore the columns of body-weight to gonad weight, and of gland increase in "fold", have been constructed on the assumption that the completely resting glands do not weigh more than one milligram; except in the cases where the glands were weighed in both the non-breeding and the breeding periods, when, of course, these data were utilized. If the reader chooses to disagree with this assumption, then the figures given in these two columns can be divided by twenty-eight, which will give estimates based on the idea that the resting glands at low tide of activity weigh twenty-eight milligrams. This will not change the conclusions of this study; it merely displaces the levels of comparison*.

Even a casual study of Table No. 1 reveals some interesting, and withal startling, facts. Thus the two resting gonads of a Ferruginous Rough-leg Hawk weighed but 1/57430 of its body weight, while the spermaries of a Virginia Warbler taken close to, or at, the height of breeding weighed 1/19 of its body weight, and in the resting period this warbler's gonads weigh but 1/8500 of the body. From another point of view it can be said that this warbler shows germinal glands which increase five hundred

* I am greatly indebted to Homer Creig of the Department of Mathematics of the University of Colorado for advice concerning questions of averages, etc.

TABLE NO. 1 (weights in grams)

Species	Date	Body weight	Gonad weight Resting	Gonad weight Active	Gonad ratio to body	Fold increase	Remarks
Avocet	Oct. 20	493.60	±	.....	.....	.....	.....
Killdeer	May 5	90.00	.....	0.12	1/750	120	too early
Scaled Quail	Aug. 5	202.50	.....	0.20	1/1012	200	.....
Mourning Dove	Jan. 23	127.50	0.012	.....	.....	.....	.....
	May 5	120.20	.....	0.628	1/191	52	too early
Marsh Hawk	Sept. 11	342.00	0.017	.....	.....	.....	too early in autumn
American Rough-leg Hawk	Dec. 29	822.14	0.021	.....	.....	.....	.....
Ferruginous Rough-leg Hawk	Nov. 26	1445.82	±	.....	.....	.....	.....
Sparrow Hawk	Mch. 31	123.50	.....	0.47	1/263	470	.....
Screech Owl	Mch. 17	142.00	.....	0.71	1/200	710	.....
Hairy Woodpecker	Nov. 11	68.40	±	.....	.....	.....	.....
Lewis Woodpecker	Sept. 14	111.50	0.029	.....	.....	.....	delayed nesting?
Orange-shafted Flicker	Dec. 9	173.00	0.009	.....	.....	.....	.....
Wood Pewee	June 23	13.30	.....	0.10	1/133	100	.....
Traill Flycatcher	Sept. 3	13.60	±	.....	.....	.....	.....
Desert Horned Lark	Sept. 30	33.50	±	.....	.....	.....	.....
Magpie	Mch. 31	221.50	.....	0.95	.....	950	.....
	May 5	192.60	.....	0.87	1/221	870	.....
Long-crested Jay	Mch. 24	132.00	±	.....	.....	.....	.....
	May 30	108.00	.....	0.345	1/313	345	.....
Clark Crow	Oct. 14	136.00	0.70	.....	.....	.....	late breeding?
Red-winged Blackbird	Nov. 11	70.50	±	.....	.....	.....	.....
Meadowlark	Sept. 2	123.10	0.013	.....	.....	.....	late breeding
Mexican Crossbill	May 19	40.60	.....	0.02	1/2030	20	too early
Pale Goldfinch	May 30	13.90	.....	0.015	1/926	15	too early
English Sparrow	Oct. 11	27.90	±	.....	.....	.....	.....
	Dec. 12	28.00	±	.....	.....	.....	.....
	Feb. 10	28.70	0.014	.....	.....	.....	.....
	May 3	28.50	.....	0.45	.....	450	.....
	June 4	25.40	.....	0.445	1/57	445	.....
McCown Longspur	Sept. 30	27.40	±	.....	.....	.....	.....
Tree Sparrow	Nov. 11	19.30	±	.....	.....	.....	.....
Chipping Sparrow	May 19	13.80	.....	0.36	1/38	365	too early
Clay-colored Sparrow	May 8	13.20	.....	0.215	1/61	215	too early
Brewer Sparrow	Sept. 10	13.40	±	.....	.....	.....	.....
Slate-colored Junco	Nov. 11	19.50	±	.....	.....	.....	.....
Arctic Towhee	Dec. 2	39.00	±	.....	.....	.....	.....
Long-spurred Towhee	May 5	42.90	.....	0.587	1/73	587	.....
Black-headed Grosbeak	May 30	46.00	.....	0.97	1/47	970	.....
Lark Bunting	May 14	43.60	.....	0.66	1/66	660	.....
	May 20	43.70	.....	0.678	1/66	678	.....
Cassin Vireo	Sept. 10	16.70	±	.....	.....	.....	.....
Plumbeous Vireo	May 19	17.90	.....	0.07	1/256	70	too early
Virginia Warbler	May 19	7.80	.....	0.092	.....	92	too early
	July 8	9.50	.....	0.50	1/19	500	.....
	July 8	9.50	.....	.....	1/19	.....	.....
	Sept. 10	8.60	±	.....	.....	.....	.....
	Sept. 14	8.50	±	.....	.....	.....	.....
Yellow Warbler	May 30	8.40	.....	0.127	1/66	127	too early
Audubon Warbler	Sept. 16	12.20	±	.....	.....	.....	.....
Pileolated Warbler	Sept. 2	9.00	±	.....	.....	.....	.....
House Wren	May 19	11.40	.....	0.12	1/95	120	too early
Slender-billed Nuthatch	Mch. 10	18.50	±	.....	.....	.....	.....
Pigmy Nuthatch	May 19	10.50	.....	0.095	1/110	.....	too early
	Sept. 12	11.20	±	.....	.....	.....	.....
Long-tailed Chickadee	May 5	12.00	.....	0.16	1/75	160	.....
Catbird	May 30	37.00	.....	0.22	1/168	220	.....
Robin	May 19	80.00	.....	1.14	1/70	1140	.....
	Sept. 12	79.00	0.011	.....	.....	.....	.....

fold in weight in passing from the inactive to the active stage. A glance at the "fold" increase column discloses other situations equally surprising. The gonads of a Robin when active are eleven hundred and forty times heavier than when resting. The increase with a Pigmy Nuthatch is but ninety-five fold.

These investigations show that small birds have relatively or actually larger spermaries than larger birds; the active gonads of a Robin weigh more than those of a Magpie; while those of a Virginia Warbler exceed in weight those of a Long-crested Jay by almost forty-five per cent, and even actually exceed those of so large a bird as a Scaled Quail. This accords with the greater prolificity found in small birds, a condition probably demanded by their greater mortality. A study of gonad hypertrophy in birds is valuable not only *per se* but also, as just said, because this enlargement may have important bearings on activities in birds other than those of breeding. To get a correct idea of such collateral effects one must have some knowledge of what has been learned during the past few years concerning the physiology of the gonads and other glands which produce a so-called "internal secretion" or "hormone".

A brief review of such matters will therefore be apropos at this time. It is now well known that there are a number of secreting organs in vertebrates which have no ducts (or channels) through which their secretions can be delivered to a body cavity or externally. The thyroid, the pituitary and the adrenals are good examples, since they all are true ductless glands. Such glands are often termed the "endocrines".

On the other hand, there are secreting organs with true ducts through which the gland product is carried to the outside world, or to a body cavity, there to assist in other physiological processes; the pancreas, the ovaries and the spermaries illustrate this type of "internal secretion" gland. The purely ductless glands are vital to the growth, proper development and health maintenance of the containing body. This was known before it was definitely determined that the same thing is more or less true of those duct equipped glands, which were found also to throw into the circulation (not through the duct) a product of vast importance, in various ways, to the body. It was known that the sperm-forming glands, while not ductless, in some way produced maleness and all its manifestations in a bird, and that birds, if caponized early, failed to develop maleness in its fullest bloom. It was not understood, however, that this failure of development arose, not through the absence of spermatazoa, but to the body receiving none of the internal secretion which would have accrued to it had the gonads remained.

The internal secretion or hormone originating in the spermaries causes not only the growth of antlers in the elk, for example, but it also, at the period of greatest breeding activity, changes the whole action and demeanor of the animal. After one has watched any of the Cervidae during the mating season, even for a brief time, one realizes that a variety of veritable insanity possesses the creatures; the impulses engendered during this season are irresistible and indubitably proceed from the activities of the gonads and their correlated glands.

With most, if not all, mammals there is little if any increase in the size of the gonads at any time, but there may be a decided enlargement of some other organs, glands which are more or less closely related to the spermaries, the parotids in the Cervidae. All internal secretion glands act and interact in such a way as to stimulate, control, or repress each other. When one (or more) temporarily overacts, or becomes depressed in function, alterations in the animal's physiology occur. If these abnormal endocrine actions are of any long continued duration, functional or organic disease supervenes. One can gather from these facts that the endocrines are agents powerful enough to produce almost unbelievable activities and effects.

The vernal enlargement of the gonads in birds results in a progressive increase in their internal secretions, which starts the chain of events in motion leading finally to the rearing of the young. Without the gonadal hormone this series of events is wholly lacking, the spermary secretions being to the wonderful breeding displays and activities, as is the spark to gunpowder. Now *part* of the physiology of breeding in birds finds expression in the marvels of migration, which commonly is held to have two main groups of causes, the *extrinsic* and the *intrinsic*.

The first group does not concern us here, nor are we here discussing the *origin* of migration. The gonads belong in the second group and it seems impossible to escape the conclusion that they have a great deal to do with the activities of migration. It does not seem unreasonable to believe that migration may depend, more or less, on the spermaries when we recall that their secretions can bring into being striking differences in plumage and even in the structural characters of birds. If one could emasculate and then liberate migrating birds, their subsequent recapture might give direct evidence on the question of the relation of the gonads to migration. Unfortunately this is impracticable, and the problem must be approached in a more indirect manner.

However the migrating habit arose in birds, it can be said with safety that a present factor in its causation, a factor of enormous force, is the increase of certain hormones in birds' bodies caused by vernal spermary and ovarian hypertrophy. Gonad hypertrophy in male birds is not only the precursor of the formation of spermatozoa, but it also initiates, or accelerates, the pouring into the body of internal secretions which influence all of the bird's activities, engendering song, mating displays and belligerency, and the *activities* of *migration*. Physiologists are agreed as to the principle that the hormones act on various organs, and also on the body as a whole. It is the secretions from the endocrines which help guide the body during its development along the road to perfect maturity, and then in adult life act and interact on the various parts of the body to maintain not only the individual's health and existence but also the persistence of the species. That the periodic enlargement of the sperm glands in birds has a more or less direct causative relation to their migrations is not a new thought. It has been mentioned many times in the past, but, so far as I know, this relation has never been quantitatively demonstrated.

Chapman says that individuals found south of their breeding area, during the nesting season, are generally barren (Auk, XI, 1894, p. 14); and Alexander Wetmore, who has given a great deal of attention to avian anatomy and physiology, writes "that some of these [ducks] may remain in southern localities, lacking the physiological incentive for the flight to the breeding ground in the north" (Auk, XXXVII, 1920, p. 229).

There can be little question of the tenableness of the following points:

A. That there is an enormous vernal hypertrophy of avian gonads.
B. That this increase in size entails a greater and greater pouring of gonadal hormones into the body tissues.
C. That these hormones cause many, if not all, of the breeding activities in the males, probably *including the activities of migration.*

There are several well known facts which support this last view. The spermaries enlarge earlier than do the ovaries, and coincidently the males begin migrating earlier (with many species) than do the females. It is also well known that the vernal migration is immensely more urgent and impetuous than the autumnal. The first coincides with progressively increasing gonadal internal secretions, and the second with a waning condition in their hormone outpouring.

If migration in the male be more or less dependent on the intensity of spermary activity we ought to find this greater in the highly migratory than in the non-migratory species, which will be revealed by greater increase of gonad size. Manifestly the amount of material submitted in this study is too small upon which to base hard, fast and sweeping deductions relating to this point. Nevertheless a tabulation of the "fold" increase in size of the gonads of eleven non-migrating species compared with that of thirteen markedly (or highly) migratory birds shows a decidedly greater enlargement in the latter, enough to give color to the statement that migratory male birds have the greatest breeding gonad hypertrophy.

Table no. 2 gives the data on which this statement is based. With the eleven non-migrants there are but two species having five hundred fold (or more) increase, while with the thirteen migrants there are five having an increase of this amount or more. This situation would be altered in greater favor of the migrants had not six of these thirteen been collected a considerable time before the full physiological increase of the gonads could be attained. In other words, I believe most, if not all, of these thirteen migrants would have exhibited a gonad hypertrophy of five hundred fold or more had they been collected later on in the breeding season. If one compares the fully enlarged breeding gonads with the containing body, it is found that the proportion is much higher with the migratory than with the non-migratory birds. Thus, table no. 2 also shows that of ten non-migrants but two exhibited gonads which attained 1/75 (or more) of the body weight, while of the migrants eight reached or surpassed this level of increase, notwithstanding that five of these thirteen migrants were not at the highest breeding pitch. It would doubtless throw much light on this question were we in possession of data relating to gonad and body weights of such marvelous migrants as the Golden Plover and the Arctic Tern.

TABLE NO. 2

Non-migratory			Migratory		
Species	Fold increase	Gonad-body	Species	Fold increase	Gonad-body
Pale Goldfinch	15	1/926	Plumbeous Vireo	70	1/256
Mexican Crossbill	20	1/2030	Wood Pewee	100	1/133
Pigmy Nuthatch	95	1/110	House Wren	120	1/95
Killdeer*	120	1/750	Yellow Warbler	127	1/66
Long-tailed Chickadee	160	1/1012	Clay-colored Sparrow	215	1/61
Scaled Quail	200	1/75	Catbird	220	1/168
Long-crested Jay	345	1/313	Chipping Sparrow	360	1/38
English Sparrow	450	1/57	Virginia Warbler	500	1/19
Sparrow Hawk*	470	1/263	Long-spurred Towhee	587	1/73
Screech Owl	710	1/200	Mourning Dove	52	1/191
Magpie	950	1/221	Lark Bunting	678	1/66
			Black-headed Grosbeak	970	1/47
			Robin	1140	1/70

* Feebly migratory within Colorado.

I have elsewhere (Journal of Mammalogy) recorded a few data relating to the body weights and the spermary weights of some mammals. The highest ratio between these two different weights was found to obtain with guinea pigs, namely, a gonad weight of 1/6 of the body, and the lowest (1/1073) with the domestic cat. These data are, of course, too few to be anything but of comparative interest. With the five species of mammals recorded in this list the gonad weight to the body weight only once attained a ratio of 1/100 or better, while with the thirteen migratory birds, as aforesaid, it occurred nine times.

Can one doubt what the effect would be on the breeding activities of a mammal, a deer for example, if its physiology brought about an increase, in weight, in its gonads during the rut, of a five hundred or a thousand fold multiplication! It is

highly probable that there is an increase of the hormones coming from glands other than the gonads, in the Cervidae for example, during rut which may be the equivalent of the increase of internal secretions in vernal migrating birds; but so far as I know this has not yet been demonstrated.

SUMMARY

A. The gonads of most birds shrink to imponderable states during the non-breeding season; even when ponderable the spermaries in this season may weigh only 1/57430 of the bird's body.

B. The gonads may grow in the nesting season to be 1/19 of the body weight.

C. The males of smaller birds have relatively larger gonads than do males of larger birds.

D. A small male migratory bird may exhibit gonads actually heavier than those of a large non-migrating bird.

E. There is some evidence that the males of migratory birds have heavier gonads than do those of non-migrating birds.

Denver, Colorado, September 22, 1925.