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## THE DIVING AND FEEDING ACTIVITY OF THE WESTERN GREBE ON THE BREEDING GROUNDS

By GEORGE E. LAWRENCE

These observations on the subsurface feeding habits of the Western Grebe (*Aechmophorus occidentalis*) were made to determine how this species is able to compete successfully in the underwater community as a predator. The methods of food capture, the time of day of greatest activity, and the specific food sources, were general objectives of the study. Field work was conducted in the breeding area at Clear Lake, Lake County, California, from April through September, 1947.

Clear Lake is an irregularly shaped volcanic lake over seventeen miles long and six and one-half miles wide; it is constricted at the middle to a passage less than one mile in width and fifty-six feet deep. Mountains of the Coast Range surround it on all sides, and the surface is 1325 feet above sea level. The lake is ideal as a breeding grounds for grebes because of the extensive stands of common tule (*Scirpus acutus*), which border much of the lake. These tule belts are several hundred feet in width in some marginal areas, the individual stems standing six to nine feet high. Presence of submerged sand bars is often revealed by dense growths of tules which form islands of swaying stems and floating plant material. The water temperature readings taken three feet beneath the surface showed a range of summer temperatures from 52°F. to 81°F. The air temperature readings in the same period were 42°F. minimum and 95°F. maximum.

### DIVING BEHAVIOR

In watching the diving behavior of the Western Grebe, it became apparent that the pattern of movement was not always the same. Dependent upon the stimulus which caused the diving reaction, there appeared to be five or more distinct patterns. The most common type of dive is what will be referred to as the "feeding dive." This basic pattern occurs only when the surface of the water is smooth and unbroken by large waves. It involves a deliberate, forward and downward thrust of the head and a vigorous stroke of the feet, which propels the grebe beneath the surface in an effortless appearing dive. This type of dive is evident throughout the diurnal feeding period. It causes a minimum of splashing and allows the grebe to approach the underwater prey with little surface disturbance.

The second type, the "springing dive," is employed most widely under conditions of strong wind and rough water. All dives by the grebes observed in the San Francisco Bay area and on the ocean off Tomales Point, Marin County, in February, March and April of 1947, were of this springing type. On the breeding grounds at Clear Lake this type of dive would often be evident in the late afternoon when the water surface was ruffled by moderate winds. The movement consists of a vigorous leap forward and downward into the water. The head is arched upward slightly, then forward and downward, accompanied by a strong thrust of the hind limbs, causing the forepart of the body to spring entirely clear of the surface and reenter the water more than twelve inches forward of the original position. The considerable surface disturbance and splashing which is involved in this springing dive is nullified by the already disturbed water surface and whitecaps. An additional feature of the springing dive is the orientation into the wind; all the dives are made directly into the waves. This orientation does not influence the direction of underwater exploration, however, as the diving of a grebe at 4:45 p.m., on July 16 at Clear Lake illustrated. This large adult consistently dived toward the westerly afternoon wind, but would reappear at the surface at right angles or occasionally behind the point of entry.

The third type, or "alarm dive," was observed only rarely. It represents a part of an elaborate pattern of escape movement from a vulnerable, exposed, surface position. An observation at 10:50 a.m., on May 21, 1947, demonstrated this alarm diving pattern. The observer was sitting on an exposed rock at the lake margin watching a pair of grebes, when a particularly long, 61-second dive carried the nearest grebe within 20 feet of the observer's position. Shortly after surfacing, a movement alarmed the grebe, causing the frightened bird to thrust its wings outward and virtually push the body beneath the surface. Thus with considerable splashing the grebe disappeared almost instantaneously. As the alarmed grebe dived, it was possible to see several wing beats of the partly folded wings. The murky water of Clear Lake obscured vision more than thirty inches beneath the surface.

The fourth pattern of diving was observed on June 16, 1947, in a narrow backwater at the northern end of Clear Lake. A single grebe was diving at the inner reaches of the narrow channel when it became aware of the approach of the observer in a canoe at the mouth of the backwater. The grebe suddenly appeared near the canoe. It then dived in an effort to reach the open lake with a minimum of exposure of its body on the surface. This "surface dive" was a porpoise-like action. The grebe was able to continue its escape, not exposing the hind part of the body at any time but simply breaking the surface of the water with the head and neck, which allowed rapid inhalation for the continued rapid swimming.

The last pattern of diving behavior is linked with the final phase of the courtship behavior for which this species is widely noted. Following the shrill *kreeeee kreeeee* notes of the mating grebes, and the second phase of ballet nodding movements, the two grebes rise upward on the water, with necks outstretched. They rush across the surface erect with rapidly beating feet and wings, then disappear beneath the surface at the end of the 150-foot rushing action. The final movement in this elaborate and impressive nuptual behavior pattern is the "courtship dive" which terminates the surface rushing action. Folding the wings simultaneously, the grebes disappear into the water, the head being the last part of the body to sink from view.

On May 29, 1947, in the tule-bordered northern Clear Lake area, a single pair was observed to complete this courtship pattern seven times within the hour from 9:40 to 10:40 a.m. Through the months of July and August when the birds were nesting, this courtship pattern was continually observed but with less frequency. The final record of this behavior occurred on September 2, 1947, when a pair of grebes displayed the same spectacular behavior of the mating period.

## DAILY ACTIVITY CYCLE

The position of the Western Grebe in the aquatic community is restricted by specific physical factors within the diurnal period of activity. The time-community relationships of this species have been studied intensively to find out the periods in which the grebes are most active and what environmental factors determine the increased or decreased activity.

After measuring the length of time spent in each dive and the time of each resting period, it became convenient to express these periods in a ratio, which will be termed the dive-pause ratio. The dive-pause ratio for any particular period, therefore, will be the ratio of the time spent beneath the water, to the time pausing on the surface of the water in any series of dives. This diving activity was recorded over a seven-month period. Over 1700 dives were noted, representing different times of day, different individuals, and activity in varying depths of water (table 1).

Table 1

Compiled Data of Diving Activity of the Western Grebe

| Inclusive dates | Number of individuals observed | Total minutes of readings | Number of dives recorded |
|---|---|---|---|
| April 1-30 | 12 | 231 | 114 |
| May 1-31 | 19 | 547 | 284 |
| June 1-30 | 31 | 973 | 473 |
| July 1-31 | 26 | 696 | 345 |
| August 1-31 | 23 | 589 | 322 |
| September 1-30 | 14 | 422 | 209 |
| Totals | 125 | 3,548 | 1,747 |

The arithmetical average for all dives recorded reveals an underwater time of 30.4 seconds while the average of all pause periods shows 21.3 seconds. The average dive-pause ratio for all periods is 1.41.

Figure 1 illustrates the dive-pause activity of individual grebes feeding at different periods of the day. The bar graph is designed to indicate by dark areas above the divid-

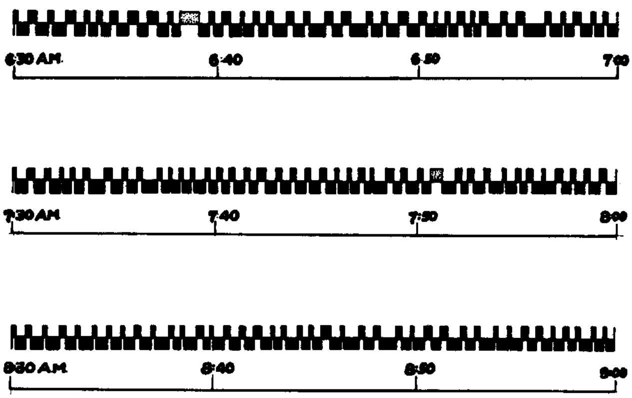


Fig. 1. Dive-pause activity of three adult grebes feeding at the same location on May 15, 1947. Blocks above median line indicate pause periods, blocks below line dive periods; dotted areas indicate rest periods.

ing line the time spent resting or pausing; the time spent diving beneath the surface is shown below the line. The long pauses or resting pauses or resting periods are included in the graph and influence the dive-pause ratio correspondingly. The first series from 6:30 a.m. to 7:00 a.m. recorded on May 15, 1947, give an average dive-pause ratio of 1.97. The readings from 7:30 a.m. to 8:00 a.m. show a 2.13 ratio and the period from 8:30 a.m. to 9:00 a.m. reveals the highest recorded ratio, 2.73. This comparison of samples points to a peak of feeding activity between 8:30 a.m. and 9:00 a.m., when the time submerged is almost three times the pause time on the surface.

The dive-pause ratio may be used as the index of activity of any period during the activity cycle of the species, and it becomes useful to determine this figure for each hour of the day. The earliest morning activity recorded was on June 20, 1947, when a pair of adults was observed paddling slowly about near the tules at 4:22 a.m. No diving activity was observed until nearly 5:00 a.m. when the dives were spaced between long pauses. This feeding activity before sunrise was exploratory, as no instances of successful food capture were observed.

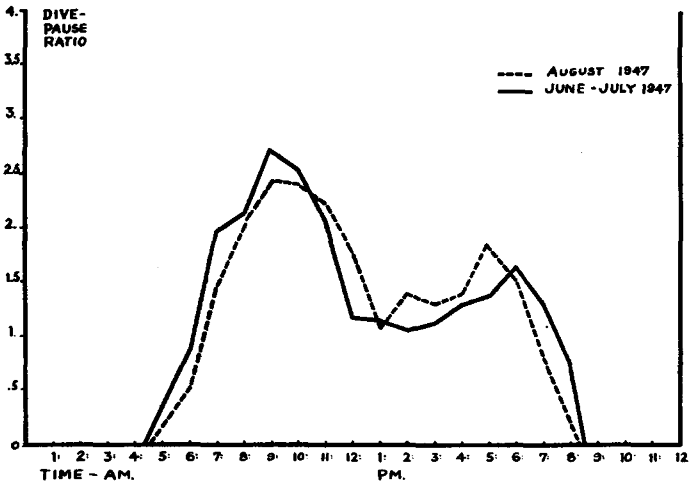


Fig. 2. Average dive-pause ratios for June, July and August, 1947.

This morning feeding activity did not reach a peak until three and one-half hours later when the sun was well up over the water of the lake. Figure 2 illustrates the average hourly variation in the daily activity cycle of the Western Grebe. The rapid increase in activity is evident before 9:00 a.m., after which time there is a gradual decrease in feeding and diving until 2:00 p.m. This decrease is then replaced by another late afternoon peak at 6:00 p.m. when the ratio reaches 1.61. This ratio indicates only that the period spent below the surface was one and one-half times longer than that spent above. After 6:00 p.m. in midsummer, the ratio decreases very rapidly as the light fades and the latest observed diving grebe was seen at 8:33 p.m., on June 22, 1947.

The method used in compiling the graph of this activity cycle was to time the individual dives and pauses of many different birds over the entire seven-month period from March to September. These figures were grouped by the hour and hourly ratios determined by dividing the total time below water by the total time above water.

Dewar (The Bird as a Diver, 1924) has presented a principle called the time-depth rule. He studied some 6000 dives of many species and concluded that the length of the dive was directly correlated with the depth of the water; dives of one fathom or less require twenty seconds. For each additional fathom in depth an additional ten seconds are added. The rule would be interpreted, then, to mean that all dives of twenty seconds would occur in water of six feet or less in depth, while in water of two fathoms depth thirty-second dives would be used, and in three fathoms of water forty seconds would be required.

The data on the Western Grebe do not confirm the rule. First, the grebes did not dive invariably to the bottom in search of food, although small white pebbles which served as the evidence for bottom feeding were present in the stomachs, as reported also by Dewar. An instance which reveals the depth to which the grebes often dive follows: On May 27, 1947, observations were being made from a bridge over the northern tip of Clear Lake when a feeding grebe dived near the bridge and swam for a distance of thirty feet while less than three feet submerged. The total depth of water was six to seven feet at this point, and the grebe appeared to be exploring the mid-depths. The method of swimming was by regular strokes of the hind limbs; the leg movements were at a rate of fourteen strokes every ten seconds. The neck was not fully extended and the wings were folded at the sides, as they were not employed in this unhurried progression.

The second line of evidence which does not corroborate the time-depth rule is related to the fact that the average depth of water near the tules where the greatest amount of feeding is accomplished, is six feet, varying from four and one-half feet to nine feet. Most of the dives recorded were in water of these depths, and there appeared to be no correlation between length of dive and water depth. The longest dive recorded was 63 seconds and soundings revealed the water to be only five and one-half feet deep. In a shallow lagoon extending north of Clear Lake, on June 12, 1947, 10:20 a.m., a series of thirty dives was recorded in water only four feet deep. The time spent beneath the surface did not vary from that of dives in water eight or nine feet in depth. These dives in the shallow water averaged thirty-one seconds and ranged from twenty-two seconds to forty-six seconds. The Dewar time-depth rule would indicate dives of less than twenty seconds in this water only two-thirds of a fathom deep.

Such a physical factor of the environment as the afternoon wind, which ruffles the surface of the water, tends to cause a general movement of the diving birds several hundred yards out into the lake, where preening and resting replace feeding activity. During this period of the daily cycle a tendency to form loose aggregations is evident, and as many as ten or twelve individuals may be observed far out on the lake within a radius of 80 feet. In such a group there are always two or three grebes which are alert to the approach of disturbances; the other individuals may be preening, resting, or sleeping with the head tucked back under one wing. This sleeping position makes the individual especially vulnerable because the grebe appears to float very high in the water and the amount of white along the flanks is conspicuous. The loose flocking behavior of the early afternoon periods therefore appears to serve a protective function.

During other periods of the day territoriality is operative. This spacing serves to hold to a minimum the disturbance of underwater prey by the surface activity of grebes. At least two hundred feet of open water normally separates feeding individuals.

An additional physical factor influencing the grebe in its daily cycle is light intensity. The relatively late peak of activity at 8:30 a.m. is two hours retarded in comparison to other non-diving birds. The factor here is lack of underwater visibility. Although the grebes venture forth from the tules as early as 4:22 a.m., there is only intermittent diving until the angle of the light which strikes the water is high enough to allow penetration and permit the grebes to pursue underwater organisms. An observation which tends to confirm this conclusion is that of a grebe which was seen to dive continually close to the tules at 7:15 a.m., on June 23, 1947, but dived only on the west side of the lagoon in the direct rays of the morning sun. Other birds feeding toward the center of the lagoon did not approach the opposite east bank where the tules cast a shadow well out into the lake. This habit of avoiding shaded water during feeding periods has been noted on many occasions.

The abrupt cessation of diving in the evening suggests reduced underwater visibility.

After about 7:30 p.m. during June, July, and August, grebes may be seen swimming about slowly in the fading light but the actual feeding and diving stops when the light is insufficient to see the underwater prey.

In order to determine the exact minimal light intensity which permits activity, a standard light sensitive photo cell, Number 917A, was used with current supplied by a large dry battery and readings were made directly on a microvoltmeter. The extreme sensitivity of the equipment limited the measurement of morning readings to levels of two feet and three feet beneath the surface. It was determined that the murkiness of the water, owing to silt and algal content, caused the readings to be decreased by an exponential factor of one-seventh less for each foot in depth below the two- and three-foot levels. These microvoltmeter readings were converted into a standard General Electric light meter scale of foot-candles light intensity. The intensity readings at 8:30 a.m. on August 16, 1947, during a maximum activity period of the grebes show the following values at two to eight feet below the surface.

Table 2
Light Intensity Beneath Surface

| Time of readings | Depth of water | Light intensity in foot-candles |
|---|---|---|
| 8:30 a.m. | 2 | 0.61 |
| 8:30 a.m. | 3 | 0.087 |
| 8:30 a.m. | 4 | 0.0138 |
| 8:30 a.m. | 5 | 0.0021 |
| 8:30 a.m. | 6 | 0.00032 |
| 8:30 a.m. | 7 | 0.000043 |
| 8:30 a.m. | 8 | 0.0000058 |

As indicated by the table, the adult grebes capture aquatic organisms in light intensity readings ranging from 0.61 foot-candles to 0.00032 foot-candles at six feet beneath the surface, the usual maximum feeding depth in upper Clear Lake. These figures apply to the optimum active feeding period of the daily cycle. During the relatively inactive period at 2:00 p.m., the light intensity reaches its maximum of 3.00 foot-candles at two feet depth (figure 3).

On June 20, 1947, at 7:18 p.m., a bird dived slowly in open water some 28 minutes after the sun had left the sky. This individual was active in minimal light intensities of 0.023 foot-candles at two feet beneath the surface and 0.0000014 foot-candles at six feet deep, the maximum depth at this point. This diving activity does not represent normal feeding behavior, and no instances of successful food capture were observed in such adverse lighting conditions.

The occurrence of the morning peak of activity appears directly correlated with the period at which the sun's rays strike the water at a high angle. This condition permits effective underwater visibility at the six- to nine-foot levels. The adjustment of the iris in the eye of the grebe must be rapid to permit clear vision when ascending from the darkened deep water to the glaring brightness of the surface, involving a range of light intensities from 0.0000058 to a maximum of 158 foot-candles in direct sunlight.

In analyzing a further physical factor, that of temperature, as it affects the activity cycle of this species, it becomes apparent that weather bureau readings of air temperatures are not usable, as they are not recorded at the levels of grebe activity. Readings were taken, therefore, at the subsurface level of two feet during August, 1947, at Clear Lake, and air temperatures were taken from Fish and Game Commission readings at five feet above the surface. The more significant water temperature readings during

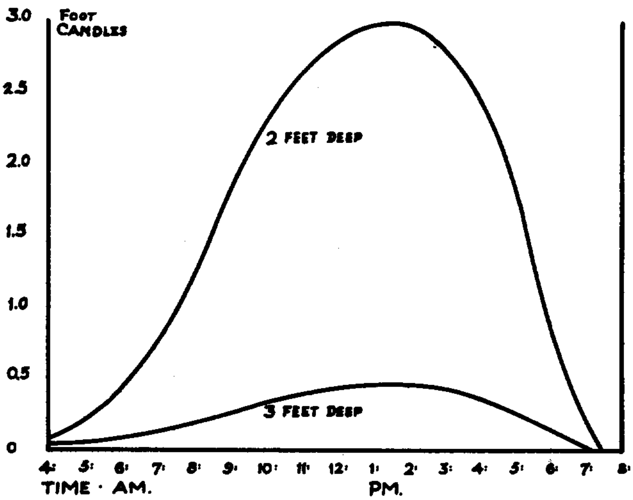


Fig. 3. Light intensity readings measured at 2 and 3 feet beneath surface of Clear Lake on August 16, 1947.

August, 1947, are given in figure 4; the hourly averages range from 20°C. or 68°F., to 27.7°C. or 82°F. These temperatures are unusually high for such a large body of water, but as the floor of the lake slopes very gradually toward the center, the margins may be no more than eight feet in depth for several hundred yards from shore. The lake is not drained or fed by running streams during most of the year; thus the water stands quite motionless, and little mixing occurs between the cool, deeper levels and the surface water which is warmed by the sun's radiation.

Figure 4 also illustrates the range of the more variable air temperatures from the minimum average hourly readings of 12.8°C. or 55°F. to 33.8°C. or 93°F. maximum.

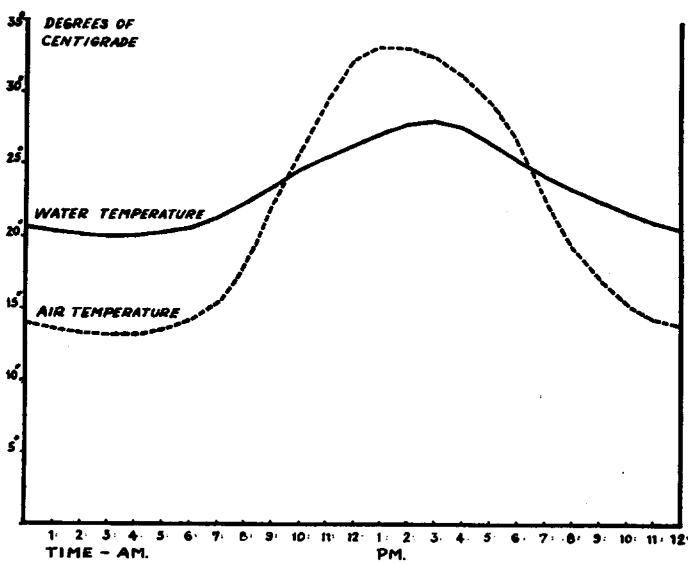


Fig. 4. Temperature averages for August, 1947, at Clear Lake.

The peak of air temperature precedes the peak of water temperature readings by more than one hour and the late afternoon decline in air temperature is much more rapid than that of the water. The influence of temperature on the daily activity cycle of the Western Grebe apparently is indirect. The rise in water temperature causes a corresponding decrease in the oxygen-holding capacity of the water. As the amount of available oxygen in solution decreases during the warm mid-day period, there is a decrease in activity of the fish and insect life. The decreased movement of the food source organisms apparently determines in part at least the decline in grebe activity during the warm part of the day from 10:30 a.m. to 4:30 p.m.

The necessity for a proper balance of these two physical factors, light intensity and underwater temperature, is apparent. During the hours of dawn and twilight, oxygen content of the water is high because the water is cool and the food organism activity is therefore great. This time of day does not permit optimum feeding activity, however, because the light intensity is very low, limiting underwater vision. The mid-day period illustrates the reverse situation with the light factor at a high level but the underwater temperature excessive for the best feeding conditions. The two peaks of daily activity cycle therefore indicate the periods when these two factors of light and temperature are in proper balance, thus allowing underwater feeding of maximum effectiveness.

## FOOD HABITS

In order to determine the foods used by the Western Grebe on the breeding grounds, contents of stomachs from collected specimens were analyzed. This technique made possible an examination of the relatively insoluble materials consumed during the previous feeding period. The time of collection was normally late afternoon, but in some instances was after the activity peak of the morning. Thus, the maximum opportunity for the stomach contents to represent the result of a normal feeding period was obtained.

Six adult individuals were examined each month during the four-month period from June through September. The results of all collections are tabulated in table 3. At this season, the birds were present in large numbers in the Clear Lake area. Collections in May included only three.

In analyzing the contents of the stomach, all material from the esophageal tract was forced into the stomach, the stomach removed, and the contents washed to extract silt and mud. The remaining mass, including feathers and traces of food materials, was then separated under 24× magnification, so that all insect exoskeletal parts, fish scales and vertebrae could be recovered for identification. The mass of stomach contents varied from 60 to 88 millimeters in diameter, depending on the overall size of the grebe.

An earlier study by Wetmore (U. S. Dept. Agr. Bull. No. 1196, 1924) reported the Western Grebe to be entirely piscivorous. The individuals then analyzed, however, were taken from widely distributed points along the Pacific coast, a majority of them from salt-water habitats.

The present study, on the fresh-water breeding grounds, indicates that the diet of the Western Grebe is not wholly fish. During the entire period under study, there were more findings of insects than fish, numerically. The occurrences of insects totaled 146, while those of fish totaled only 91 individuals. These numerical data obscure the true picture of actual bulk of the two food types. Insects constituted an estimated 17 per cent of the total food volume, whereas the smaller number of fish fragments contributed 81 per cent. Two grebes showed no trace of fish vertebrae or scales in the stomach contents, while considerable insect material was present. The mandibles and head parts of 29 predacious diving beetles of the family Dytiscidae were found in the stomach of an individual taken in June, insect material constituting the entire diet of this grebe.

Further evidence of deviation from an entirely piscivorous diet is the occurrence of the uneroded shells of two small limpets, resembling immature *Acmaea mitra*. These gastropods were found in a grebe taken on June 16, 1947; the shells may have been exposed to the digestive juices of the bird for two weeks and possibly longer. The salt water distribution of limpets indicates that these shells were carried in the grebe's stomach from the Pacific Ocean in the inland migration of April or May.

Table 3

Analysis of Stomach Contents of Twenty-seven Western Grebes

| Classification of material | Number of occurrences | Per cent of occurrences | Per cent of total volume |
|---|---|---|---|
| Nematoda | | | |
| Ascaradina | | | |
| *Ascaris* sp. (alimentary parasites) | 122 | 61 | 3 |
| Mollusca | | | |
| Gastropoda | | | |
| *Acmaea* sp. (small limpets) | 2 | 3 | 1 |
| Arthropoda | | | |
| Orthoptera (mouth parts only) | 9 | 4 | 2 |
| Ephemerida (May fly larvae) | 4 | 3 | Trace |
| Hemiptera | | | |
| Corixidae | | | |
| *Sigara* sp. (water boatmen) | 41 | 54 | 2 |
| Diptera | | | |
| Chironomidae (larval forms) | 5 | 11 | 1 |
| Coleoptera | | | |
| Carabidae | | | |
| *Bembidion* sp. (ground beetles) | 4 | 3 | Trace |
| Dytiscidae (predacious diving beetles) | 32 | 11 | 2 |
| Hydrophyllidae (water scavengers) | 1 | 2 | Trace |
| Dryopidae (aquatic beetles) | 7 | 11 | Trace |
| Unidentified Coleoptera | 43 | 34 | 2 |
| Pisces (Chordata) | | | |
| Siluridae | | | |
| *Ictalurus catus* (common catfish) | 3 | 11 | 4 |
| Centrarchidae | | | |
| *Archoplites interruptus* (perch) | 5 | 19 | 6 |
| *Lepomis macrochirus* (bluegill) | 67 | 92 | 71 |
| Unidentified fish fragments | 13 | 31 | Trace |
| Plant material unidentified | 28 | 27 | 4 |
| Small white stones (1-5 mm. diameter) | 99 | 37 | 6 |
| Feathers occurred in all stomachs | | | |

A large number of nematode parasites of the genus *Ascaris* were recovered from the feather masses of the grebe stomachs. These roundworms were all free in the alimentary tract; none appeared attached to the walls of the stomach. An individual grebe taken in June, 1947, was found to contain 34 nematode worms in the feather mass of the stomach. Current studies being conducted by the California Fish and Game Commission indicate that this same parasite occurs in the alimentary tract of the common catfish, *Ictalurus catus,* but an analysis of the host-parasite relationship remains to be made.

The insect material found in the stomach contents presents the problem of distinguishing between those insects which were captured directly by the grebe and those fragments which were contained in the stomachs of captured fish. The arbitrary means of distinction was on the basis of size of the insect involved. Certain very small tenebrionids, nocturnal beetles of only four to six millimeters in length, were excluded from the report of insect findings because of their minute size. The traces of grasshopper mouth parts represent insects nearly as large as many of the smaller fishes taken by the grebes and therefore presumably were captured directly by the avian predator. At no time in the period of observation were feeding grebes observed to take insects from the surface of the water. Capture of floating insects may have been accomplished by an underwater approach as the grebe comes to the surface. Rarely was the insect material sufficiently intact to permit more than family identification due to the grinding action of the walls of the bird's stomach and the erosion by digestive juices.

Three species of fish were identified in the stomach contents, the common catfish, the Sacramento River perch, and the bluegill perch. Of these three, the bluegill constituted 71 per cent of all the food materials ingested, on the basis of volume. The fish taken by the grebe vary in size from 27 millimeters to 88 millimeters in length, all in the second year of growth. This species, the bluegill perch, is a wide-ranging shoreline fish, found in water from 3 to 19 feet in depth. The factors which contribute to make the bluegill perch the primary food source of the grebe are the abundance of this fish in the grebe breeding areas, its light color, its great dorsoventral depth and its wide distribution in all parts of the lake. The largest object taken by the grebes was a bluegill 88 millimeters in length and 34 millimeters in depth. This is remarkable in view of the narrow buccal orifice of the grebe.

The other species of fish, the Sacramento River perch and the common catfish, were found uncommonly in the stomach analyses. The catfish is ecologically significant, however, as an indicator of bottom feeding by the grebes. The difficulty of capturing the catfish and the Sacramento perch is probably due to the very dark dorsal and lateral aspects of these two species.

The best structural features for identifying the fragmentary fish material were the midline lateral scales. Without these scales and without the body outline and pattern of fins, no identification beyond class was made.

In addition to the food materials specified, other materials of less certain function were revealed in the stomach analyses. Plant material appeared in 31 per cent of all stomachs examined, the plant tissues resembling aquatic roots or underwater stems. This plant material was found in small quantities throughout each monthly collection period.

Non-digestible materials in the nature of small stones were found in 37 per cent of the grebes. These pebbles may serve as grinding elements, aiding in the food breakdown process. A large number of flattened egg cases, 2 to 3 millimeters in diameter, were present in more than half of the stomachs. These remain unidentified. They were either pure white or light brown. A knotted piece of strong braided twine, 122 millimeters in length and resembling a piece of fishing cord, was found in one stomach.

The feather mat which occurs in the stomach of the Western Grebe was found in all analyses. A generally accepted view is that its function is to protect the stomach walls from being punctured by sharp bones during the grinding action of the walls. In addition the feathers prevent undigested sharp bones from passing on into the lower alimentary tract before they have been softened by digestive action (see Wetmore, *op. cit.*). Undigested fish usually are situated on the periphery of the feather mat. In this position the feather mass serves to keep the recently taken materials close to the secretory surfaces of the stomach walls, thus speeding up digestion. The sharp bones and hard undigestible materials were regularly found to be within the center of the stomach mass. This central position protects the stomach walls and facilitates the straining function. The undigested bones move to the protected center of the stomach by the gradual encumbrance of the exposed bones with feathers as the digestion of the soft parts progresses. When the lateral or dorsal spines of the vertebral column become exposed by this erosion, feathers may be observed tangled about the projecting bones, and when the musculature is entirely digested, the skeletal structures are obscured by the entwined protective feathers. The regular churning action of the stomach walls moves this solid mass of tangled feathers and bones to the inner part of the feather mass and new undigested material takes the peripheral position in the stomach.

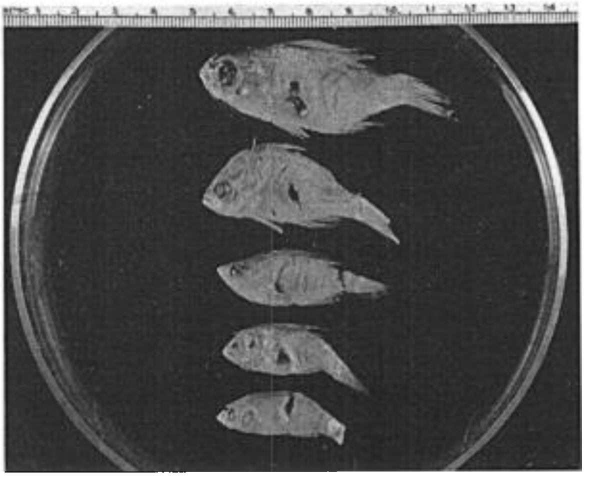

Fig. 5. Bluegill perch from stomach of an adult male Western Grebe, taken at 5:50 p.m., 6 miles northeast of Lakeport, California.

The Western Grebe does not regurgitate undigested bones, scales and chitinous parts. These sharp objects have been found in many states of erosion by digestive action. Vertebral segments often were found discolored and spineless in the very center of the feather mass. The presence of the limpet shells and small stones also indicates that material not readily digested remains in the grebe stomach until it is softened or eroded.

The actual food-capturing mechanism of this predator is indicated by indirect evidence only. The observation of May 27, 1947, demonstrated how the grebe dives and progresses underwater. On this occasion the observer was able to follow the movements of the grebe as it moved a distance of thirty feet. The grebe swam only three feet beneath the surface, with its head drawn back slightly, wings held at the sides, and the legs stroking together. This was an exploratory dive, however, as are over 96 per cent of all dives. The evidence shown in figure 5 provides further information as to how grebes capture prey. The fish in the stomach of this male bird were recently taken and all clearly showed a small hole passing completely through the fish. The consistent appearance of this aperture, its location near the center of the body of the fish, and the similarity between the size of these openings and the diameter of the bill of the grebe, suggest that the sharp bill of the bird may serve as a rapier in piercing the fish.

An observation of June 28, 1947, shows that the fish may be moved into the mouth before surfacing. On this date a single isolated bird was under observation for a continuous period from 6:40 a.m. to 11:50 a.m. Early in the morning, at 8:05 a.m., the grebe emerged from a dive holding its head at an abnormally high angle. Gradually, after some effort, the head assumed its normal position horizontal to the water, and a swelling appeared high in the neck, causing an unnatural curvature in the neck. This swelling slowly moved downward in the esophagus until the neck again appeared natural in size and curvature, at which time the grebe dived. During this morning observation this swallowing behavior was seen only two times, being repeated again at 10:16 a.m. when another object large enough to be observed through 8× glasses was passed down the esophagus.

These field data also give evidence of the number of fish captured during a normal morning feeding period. The grebe just described would apparently take only four fish during the daily feeding cycle if the observed rate of food capture represents the normal situation. The fish shown in figure 5 are all eroded only slightly and evidently were taken the same day. The stomach contents of the grebe described above as catching two fish during the entire morning feeding period, revealed fragments of five fish present; three of the five were much eroded by digestive action and may not have been taken the same day.

Wetmore (*op. cit.*) reported as many as nine fingerling smelt present at one time in a Western Grebe stomach; these would compare closely in total volume with the maximum figure of seven of the broad-bodied perch of Clear Lake found in one grebe. Using the figure of 3.2 grams as the average weight of the perch taken, the maximum weight consumed in one day's feeding therefore would be 22.4 grams of fish. This small amount of food taken daily equals only 1.8 per cent of the body weight of the adult grebe. This is a low rate of food intake relative to the consumption rate of some other predators which may eat more than 50 per cent of their body weight daily.

Several of the species of fish in Clear Lake are important as game fishes. The large-mouthed black bass (*Micropterus salmoides*) is the most important of these species, although the perch and catfish are also taken as game fishes. Worthy of attention is the fact that no individuals of the black bass were recovered from the stomachs of the Western Grebes. This game fish occurs regularly in the same ecological area with the grebes, but the fact that it is not taken by the birds may be due to its slimmer body form and greater speed, as compared to the bluegill perch. The Western Grebe has been illegally killed by the sportsmen of the area on the claim that the birds were "eating all the young bass." The birds could more reasonably be accused of lessening the perch population of the lake, but the relatively few grebes consume only a small fraction of the young perch. They probably have no effect on the size of the adult population of this type of fish.

During the period of study from late April through September of 1947, the types of foods taken by the Western Grebe varied in proportion. Figure 6 illustrates the changes occurring in the per cent of total volume consumed during each month on the breeding grounds. The maximum insect consumption occurs in May, making up 32 per cent of the total diet during this month when the insect populations are at a peak. As the summer progresses the aquatic insect populations decrease so that toward the end of the breeding season the insect material contributes less than 8 per cent of the total volume. The fish taken make up the bulk of the diet throughout the entire period. In May, 64 per cent of the food volume is fish; this figure increases steadily through the season until in September, just before the fall migration to the marine habitat, 86 per cent of the entire diet is made up of fish. The plant material, which remains a fractional part of the diet throughout the period, may not represent a basic food source and occurs only as accidentally consumed material.

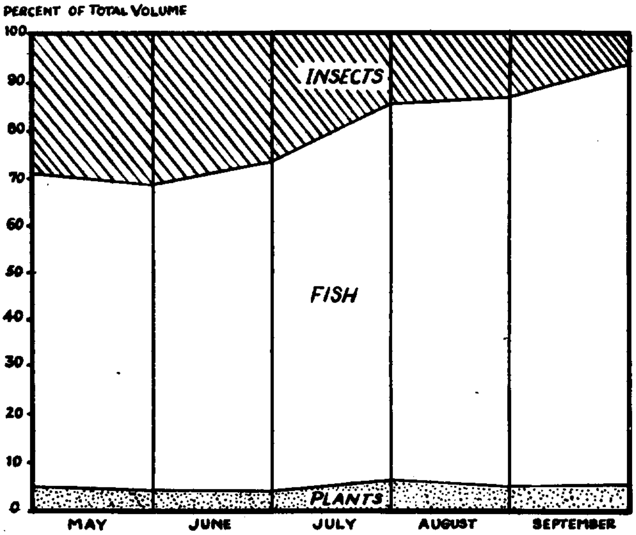


Fig. 6. Seasonal changes in food taken by Western Grebes at Clear Lake.

SUMMARY

The patterns of diving behavior of the Western Grebe (*Aechmophorus occidentalis*) are designated as the feeding dive, the springing dive, the alarm dive, the surface dive, and the courtship dive.

The courtship behavior was observed throughout the entire five-month period from May to September, 1947, at Clear Lake, California, continuing after the appearance of young.

The daily activity cycle was analyzed through hourly records of the dive-pause ratio. Activity reaches a peak between 8:30 a.m. and 9:00 a.m., at which time a maximal ratio of 2.73 occurs. The arithmetical averages for the 1700 dives of the Western Grebe recorded show 30.4 seconds beneath the surface (dive) and 21.3 seconds above the surface (pause).

The time-depth rule of Dewar is not corroborated by the diving behavior of this grebe. The longest of all subsurface dives recorded was one lasting 63 seconds. This individual was diving in water 5½ feet deep.

Flocking activity was observed only during the early afternoon hours. At that time, grebes were relatively inactive and gathered in groups of ten or twelve far out on the lake, where they preened and rested.

Of the physical factors influencing the activity cycle of this species, wind, light intensity, and water temperature were examined in some detail. Light intensity is critical in underwater predation, as grebes do not begin feeding in general until light values exceed 0.00032 foot-candles at 6-foot depths.

The water temperatures at Clear Lake reach 27.7°C. (82°F.) two feet beneath the surface during the middle of the day, especially between 1:00 and 3:30 p.m.; the amount of dissolved oxygen in this warm water is then decreased and activity of prey is retarded. Subsidence of hunting by grebes in mid-day may be correlated with reduced activity of prey animals.

The investigation of the food habits of this species revealed a diet consisting of fish (81 per cent), insects (17 per cent), and plant material (secondary traces). These find-

ings do not confirm the claim of earlier workers of an entirely piscivorous diet of the Western Grebe. Seasonal variation in food occurs, with insects ranging from 32 per cent of volume in May to 8 per cent in September. There is compensating variation in the per cent of fish.

The fish species constituting the majority of the grebe's diet was the bluegill perch, *Lepomis macrochirus,* which occurred in 71 per cent by volume.

The feather mass which completely fills the stomachs of all Western Grebes appears to function to protect the inner lining of the stomach from the sharp bones of fish; it also prevents undigested bones from passing into the lower alimentary tract.

The maximum weight of fish consumed in a single day is 22.4 grams, which represents only 1.8 per cent of the body weight of an adult grebe.

The influence of this avian predator on the game fish of Clear Lake is negligible because of the very small number of relatively unimportant game fishes consumed. The claim that this grebe is reducing the numbers of black bass (*Micropterus salmoides*) is entirely unfounded in view of the stomach analyses.

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