THE RELATION OF AMERICAN DRAGONFLY-EATING BIRDS TO THEIR PREY

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INTRODUCTION

Twenty-two years ago (1926) the writer was given the privilege of examining the records of the U. S. Biological Survey (now Fish and Wildlife Service) on dragonflies as food of birds. For this opportunity I wish to thank Mr. Waldo L. McAtee who for many years was in charge of the extensive studies of the Biological Survey on bird foods.

Because the writer has not found time to review the Bureau's later collections and bring this paper down to date it is being published now as drafted then because of the great amount of data of that date summarized, data the conclusions from which later investigations have not invalidated. The problems are those of wide food tolerancies, and the necessary contact of bird with dragonfly. Birds eat what is available when pressed by hunger. This view must be held in mind by the reader: conclusions are suggestions: few are critically final.

Extent of the Problem

The present article turns out to be a review of the habits of the water and land birds of America north of Mexico, which concern their use or not of dragonflies as food. The A.(merican) O.(rnithologists') U.(nion) Checklist of North American Birds, Fourth Edition (1931) recognizes 468 named species and subspecies of land and sea birds. The data obtained by the examination of bird stomachs by the then United States Biological Survey showed in 1926 that 184 of the 468 species and subspecies used dragonflies at times. Muttkowski's (1910) Catalogue of the Odonata of North America lists 494 species of dragonflies for a slightly larger continental area, south to parallel 20° N. in Mexico. The present review thus covers a continental bird fauna in its contacts as predators operating against a continental dragonfly fauna. Our summary count shows 61,042 stomachs examined in the 184 species that were found to have eaten dragonflies and that the 184 species of birds (a total of 61,042 individual birds) had captured 2,652 nymphal or adult dragonflies. The reviewer did not copy records of stomachs of bird species that had no dragonfly records against them. This included nearly all sea birds and many land birds, a total of 284 named species and subspecies. Counting all stomachs of sea and land birds the figures suggest that the Survey had examined upwards of 75,000 stomachs by 1925. Cottam & Knappen (1939, p. 138) estimated 200,000 stomachs in the Survey's collection about half of which had been analyzed.

No such mass of expertly gathered data on the problem of predator *versus* prey appears in the literature of the fields of ecology or organic evolution. I wish to comment further: the mass of data has not been gathered by any one man but is that of a staff of some of the most expert ornithologists of recent times who up to 1925 had operated as a changing group over a period of more than forty years (Methods, McAtee 1912).

The accumulated data carries one unavoidable bias: the studies necessarily have been focused on economic species (Beal 1907, 1910), those of value to man and those suspected of being inimical to man's interests. It has been the privilege of a lifetime to review such a mass of expertly gathered data!

The organized study of bird food by the Biological Survey was begun in 1887 and up to 1925 when these notes were abstracted from their files the staff of the Survey had collected and examined the stomachs of many tens of thousands of birds (McAtee 1913). The early history and background of economic ornithology was covered by T. S. Palmer (1900) in one of the most important reviews written on an ornithological subject. At that time the Biological Survey had collected 32,000 bird stomachs. Material piled up faster that it could be numerically invoiced from year to year. Hence we have no published figure on the total of stomachs for 1925. In Palmer's (1900) review it was 32,000 by estimate. This was followed by 26 years of intensive collection and study to the date of this review (1926) (McAtee 1933).

As of interest we wish to call attention to the historic fact that John Ray was the first biologist to open bird stomachs for positive data on bird food (Raven 1942, 327). Also we cite one of the best Scotch papers (Florence 1912) for a comparison of food habits of related palaearctic (Scotch) and nearctic (North American) birds: and Collinge (1924-1927).

Nature of the Records

The Biological Survey records are a card index system arranged according to the A. O. U. Check List which index was begun in the middle eighties of the past century before ornithologists concurred in the recognition of the many subspecies listed in the recent check list. Many of the cards at the time (1926) these notes were abstracted dated from earlier A. O. U. Check Lists (Ed. I, 1886; Ed. II, 1895; Ed. III, 1910). As the birds of the earlier records had not been in many cases identified to a subspecies these records stand as made, usually to the species name only. McAtee has stated to the

writer that "subspecies determinations of birds are unimportant except that birds will eat different species of plants and animals in different floral and faunal areas. That the general nature of bird food is the same in all subspecies of any one bird species." Probably in the succeeding discussion records are listed under the eastern subspecies that at a later date would have been credited to the western or southern subspecies of the same bird. The greater part of the records are of birds shot in the eastern United States.

The Survey studies on the food of birds cover the United States with some records from Alaska, Cuba and Puerto Rico. This article is confined to the Bureau of Biological Survey records with minor additions from literature cited as an outside record in each instance (See Forbes 1882). The writer has followed the American Ornithologists' Union "Check List of North American Birds," Fourth Edition, 1931, in his use of both common and scientific names of birds.

Back of the records on cards is the original collection of the contents of the stomachs that are recorded. These are preserved in alcohol, each stomach contents with its record number.

The earlier work by the Survey was a mere recording of the various kinds of food found in each stomach with the number of items of each when such could be easily counted. In later studies attempts were made to give percentages of the various foods found (Judd 1901, McAtee 1912a, Stevenson 1933). This has been exceedingly difficult as some foods digest so much more rapidly than do others and because percentages are not easily comparable among greatly different kinds of food. In later studies much of the material has been identified to the species of animal or plant used as food. This has involved the assistance of specialists in the different branches of zoology and botany, particularly men familiar with seeds. In insects this means frequently the identification of a beetle from a fragment of elytral sculpturing, a butterfly from an antenna or a leg, a dragonfly from a mandible. Knowing the region from which the bird stomach came, it is surprising how many positive identifications can be made from characters other than those usually used in keys. The writer has done some of this work on fragments of Odonata where frequently only the indigestible mandibles remained. The jaws of Odonata quite often have very specific characters as has been shown recently by Taborsky (1927). For these reasons the present records pertaining to dragonflies as bird food occur roughly in several forms which are not always easily comparable. They may be listed merely as Odonata, sometimes as Anisoptera or Zygoptera or as odonate nymphs or again as Anisoptera nymph or Zygoptera nymph. It will probably be many years before this mass of material can be identified more precisely as it is a very time-consuming process and the present evidence is that such definite identification is hardly warranted. To a bird a dragonfly is either large or small, an adult or a nymph. Only one or two instances, as will be pointed out further on, appear to be more specific. Within the range of their food-habits birds eat whatever is most available (Henderson 1927:59; and personal statement from McAtee). No general attempt was made to identify dragonflies to species to see if brightly colored forms were used more often than dull species. (McAtee 1932.)

The general impression among students of bird foods is that feeding habits are much more plastic than they were supposed to be before the era when students of birds began to examine stomach contents. A few species such as the swifts and bluebirds which at times are killed off by late freezes after they have returned north apparently are less able to make such shifts in food (McAtee 1912b).

It must be remembered that only in studies of abundant economic species, the crow, the English sparrow and such, have stomachs been collected in any number throughout the year. Jenks (1859) made a year-round study of the food of the robin but such studies are few. Thus the greater part of the data, except in a year-round study, is suggestive merely. The Biological Survey had its authority from Congress which was interested in economic species and only in such while they operated in the United States for or against voters (McAtee 1926).

LITERATURE AND DOCUMENTATION

Literature is cited to cover the habits of birds which eat dragonflies and frequently items on close relatives for comparison which do not eat dragonflies as freely. The three most comprehensive works each of which is well indexed and documented are cited by volume only under each family of birds. These are Bent (1919-1946), fourteen volumes, Forbush (1925-1929), three volumes, and Henderson (1927). These quote the work on contents of stomachs down to 1929 and partially (Bent) to 1946. Under each species items from 1929-1947 are cited by the present author less completely. Other useful reviews are Barrows (1912), "Michigan Bird Life," and Warren (1888, 1890), "Birds of Pennsylvania," and McAtee (1913, 1933). Final reference to U.S.D.A. publications is given in "Index to Publications" U.S.D.A. (1932, 1935, 1937, 1943). The extensive literature by the experts of the U. S. Biological Survey (now Fish and Wildlife Service, Chicago 54, Illinois) covered by the preceding general works has formed the heart of the literature studied. The volumes cited give easy reference to this mass of literature plus references to the work of other students in various journals. McAtee (1926), "The role of vertebrates in the control of insect pests" is a good brief review of the general problem with a good bibliography. Strong (1939), a bibliography of birds, was found too "selected." Chapman (1932) is the best review of correlated habits, height and type of nest, ecological distribution, etc. A good European paper Sømme (1933) covers this subject of "Birds as enemies of dragonflies." Tavener (1934) is a good review of food habits of Canadian birds. Allen, Glover M. (1925) is a good general biology of birds.

EXTENT AND POSITION OF ODONATA IN THE ENVIRONMENT

It must be remembered that dragonflies live a dual existence. The greater part of life is spent as a fully aquatic animal in fresh water ponds and streams. Except for a few species which pass the winter in the egg stage (*Lestes* spp.) the nymphs of dragonflies are present in the water at all seasons. The greatest number of *individuals* in the water is probably in the fall when the majority of the eggs laid the previous summer have hatched. Then the ponds and streams are full of small nymphs among which are a smaller number of large nymphs. The nymphs are used as food all fall, winter and early spring by fish, aquatic birds and other aquatic animals. In small ponds that contain no fish dragonfly larvae become very conspicuous by early spring because of numbers and increased size. In waters containing fish they also become more conspicuous because of growth having taken place over winter. Thus in both types of dragonfly water-environment they appear to be a greater part of the total weight of animal life per unit of water in the late spring than at any other season. Late spring, just before the spring emergence, is the best season for collecting nymphs. During the late summer sizable dragonfly nymphs are comparatively scarce except those of fall emerging species. Unfortunately, few or no around-the-year population studies of odonate nymphs appear to have been made. The preceding remarks are the casual observations of a collector. Notice that this seasonal distribution of nymphs of size throws dragonfly nymphs into the "duck season" of spring and fall migrations. Nymphs are less abundant when birds nesting within the limits of the United States are rearing their young. This seasonal distribution of nymphs large enough to be eaten appears to pit the ducks, grebes, etc. directly against dragonflies while in the aquatic stage of life (Kennedy 1928, Knappen 1933, Lyon 1915).

The second part of a dragonfly's life is spent as a land insect on the wing. Though in no sense aquatic except that the majority of flying Odonata live largely on the flying adults of minute species of aquatic Diptera (Warren 1915) and except for a few species that enter the water in oviposition the dragonflies are usually thought of as being mildly aquatic as adults. However, they are aerial land insects as adults. They are on the wing from the first freshet of warm rain water in the spring until the first heavy frost in the fall. Few individuals are probably on the wing more than three weeks (Borror 1934). Unfortunately, Borror's study of adult *Argia moesta* Hagen gives our only data on the length of this phase of life. The majority of species emerge over a short period of time (2-4 weeks?), live on the wing the two to four (?) weeks of adult life and die, apparently of old age (Kennedy 1915). Thus the warm season sees a succession of dragonfly species on the wing among which are scattered a few all-season species. Species on the wing follow in succession as do the flowers of the woods and fields. It is this seasonal succession (Kennedy 1928, Walker 1915) of aerial forms which are available as food to land birds. *But* they have to be birds which for one reason or another are associated with the aquatic dragonfly habitat. Dragonflies as a rule do not stray far from the water. They oviposit in or close to the water and usually use minute Diptera as food. Immatures of the latter are usually aquatic or live as larvae in the very wet ground bordering ponds and streams.

Odonata are exposed to both water and land birds at another time of life. This is during the few hours when the nymphs crawl out of water, the back splits open, the adults emerge from the nymphal skin and sit around flabby and helpless until wings and skeleton harden. While the crawling out of the water and the stripping off of the nymphal exuvium may occupy less than an hour, hardening with full color comes slowly. Frequently almost the whole of daylight is occupied in this change before the dragonfly can fly speedily. During this helpless stage dragonflies are fed upon by aquatic birds, grebes, nesting ducks, herons, etc. and by land birds, those species that search beaches and hunt in emergent aquatic vegetation, such as the yellow-headed blackbirds, western robins, marsh wrens, etc.

It must be remembered that dragonflies, while they may appear abundant in narrow areas because of their intense activity, bright colors, and rather large size, are actually seldom abundant as compared with herbivorous insects. On small streams where a species seemed abundant the writer (1915) has appeared to have been able to catch the majority of flying individuals on a mile of stream in four or five days' collecting. The total number of individuals taken, which, with their continuous activity, gave the impression of great abundance, might be twenty-five or might, with some other species, be one hundred or even two hundred, but after the four or five days' collecting they had dwindled to stray individuals only. For a mile or two of habitat even two hundred is a very small population of insects. Along the banks of the same stream might be from one hundred to one thousand ant nests, each of which would house twenty to several thousand ants. The activity, bright colors and size make dragonflies appear many times more numerous than they really are.

Dragonflies are predatory insects and occupy the same niche in the insect world as that occupied by hawks and owls in the bird world. They are at the peak of a pyramid of numbers (Elton 1935). As adults they feed on midges which as dragonfly food are many more times as abundant as the predator dragonfly species. The midges as larvae feed on yet smaller aquatic organisms, but more abundant than the midge species. This lowest level of the animal part of the pyramid of numbers the apex of which forms the food of dragonfly adults feeds on algae, large Protozoa, and perhaps dead organic matter, a still more extensive body of food. Thus being at the apex of a pyramid of numbers Odonata cannot be

enough to furnish a continuous (in time) supply of food to some other predator (in the instance of our study, birds). Dragonflies are rather exceptional insects in the environment when compared with the hemipteroid orders, the beetles, the flies and the world of ants and other hymenopterous insects. Except for an occasional local swarm, an event so rare that, if observed, it is recorded in the literature, dragonflies are never as abundant as are herbivorous insects. These conditions prevent them from ever becoming the regular food of any species of bird at our latitude, with the possible exception of the larger swallows and martins and as food for nestlings; (Franklin's gull the yellow-headed blackbird, purple martin—see Judd (1901).

BIRDS WHICH ONLY ACCIDENTALLY OR NEVER EAT DRAGONFLIES

Of the seventy-five families of birds of the United States about forty families do not eat dragonflies. Many of these exceptions are obvious but others are less so, and some must eat dragonflies at times though the present records have no data in that regard.

All of the birds of the open sea and the rocky foreshores of the ocean, birds that feed largely on fish, Crustacea or marine worms have usually no records against them. Dragonflies are insects of fresh water and, as has been shown by Osburn (1906), nymphs of various fresh water species cannot stand a concentration of sea salts of more than 11% of that of the open sea. In warmer regions than Woods Hole, where Osburn conducted his experiments, are various species of brackish water dragonflies that appear to be able to stand a greater concentration. A few such were studied by Pearse (1932) in brackish pools on Dry Tortugas where salinity was as high as 67% of that of sea water. Nymphs of *Erythrodiplax berenice* Drury and *Ischnura ramburii* Selys appeared to stand this high salinity. However, there are very few species of brackish water Odonata and these are usually found about waters of much lower salinity. Sea birds on this account do not come into contact with dragonflies but live in a separate saline environment. This appears in the records of the Biological Survey.

The writer includes in this list of sea birds the following families: Gaviidae (Loons, some spp.); Diomedeidae (albatrosses); Procellariidae (shearwaters); Hydrobatidae (storm petrels); Phaëthontidae (tropic birds); Pelecanidae (Pelicans, some spp.); Sulidae (gannets and boobies); Phalacrocoracidae (Cormorants, some spp.); Fregatidae (man-o'war-birds); Phoenicopteridae (flamingos, some colonies); Haematopodidae (oyster-catcher); Stercorariidae (jaegers); Laridae (gulls, some spp.); Rynchopidae (skimmers); Alcidae (auks and murres).

This is an interesting series of families as nearly all of them are rated low in bird evolution. Probably in their earlier evolution they had relatives on inland waters but these were exterminated in the late Mesozoic or early Tertiary with the rise of small carnivorous mammals. These birds usually nest in colonies and on the ground or in cliffs where small carnivorous mammals could easily exterminate whole colonies if they could get to their nesting grounds. Now they are limited to isolated islands, outlying bars and beetling cliffs which types of surface occur more often along sea shores because of tidal currents and the greater waves of storms. Further, their young develop slowly so that the family has a long period when exposure to ground vermin would be disastrous. Their few relatives that are colonial, gulls, terns, herons, etc., and which still exist around fresh waters have managed to build their nests away from continuous ground which would give an approach to beasts of prey.

Variously related to the preceding group of sea birds is a series of fresh water families that have managed to occupy the larger bodies of inland waters and coastal bays, swamps and estuaries. These are the following: Gaviidae (loons, some spp.) nesting on the edge of lakes; Pelecanidae (pelicans, some spp.) nesting on islands in sounds and western salt lakes; Phalacrocoracidae (cormorants, some spp.) nesting in trees and on cliffs, living on coastal lakes and coastal islands; Anhingidae (darters) nesting in trees in swamps; Ciconiidae (wood ibis) nesting in trees; Threskiornithidae (true ibises) nesting on islands; the Cygninae (swans) and the Anserinae (geese, brants) of the Anatidae nesting in wet marshes or on islands.

With the exception of the geese and swans which are vegetarian, the flamingos which feed largely on mollusks, and the wood ibis, these are largely fish eaters. Their specialized food habits eliminate dragonflies from their diet. It is interesting that the ducks which use a mixed diet and some of which eat dragonfly nymphs have in their close relatives, the geese, a group of species so wholly vegetarian that they never eat dragonflies.

To this group of families should be added the Rallidae (rails, gallinules, coots). These live in the very midst of the best dragonfly habitats but with the exception of the coot there are no stomach records showing dragonflies as food. Thus the geese and rails, while living in a dragonfly environment, appear to make little use of dragonflies as food. They are two groups of birds that would have been expected to have used them more.

Our next series of families are land birds that for various reasons do not eat Odonata. The usual reason is food preference but in other cases the environment of bird and dragonfly may not coincide or the seasons of occurrence of the bird in the area of the United States may not coincide with the flight season of dragonflies as in the case of northern birds wintering in this area.

This series of land birds which do not eat dragonflies includes the following forms that feed on the ground; Cathartidae (vultures); Tetraonidae (grouse, ptarmigan, sage hen, etc.); Perdicidae (quails); Phasianidae (pheasants); Columbidae (pigeons, doves); Alaudidae (larks).

The three gallinaceous families, while notorious-

feeders on insects, are upland groups where dragonflies are seldom found. They live on large slow insects which type of food with the component of seeds and grains is associated with slow movement, poor monocular vision and relatively short necks. The doves and pigeons are herbivores and live largely on nuts, seeds and grains. The vultures are carrion eaters. The larks, while using a small amount of insects in the summer, are largely feeders on seeds and also occupy upland areas where dragonflies are not found. An exception in this series is the family Meleagridae (turkeys). Of nineteen stomachs examined one contained a dragonfly. The turkeys are feeders on insects as well as grains and seeds and in many regions, particularly in the south, are inhabitants of swamps where Odonata abound. In such places where taste, bird and dragonfly coincide they probably eat dragonfles more often than the Survey records show.

Among the birds of prey the Pandioninae (ospreys) and the Tytonidae (barn owls) have no records of using dragonflies as food. The first eat fish while the barn owls feed at night when dragonflies are not on the wing. The barn owl lives almost entirely on small mammals and is one of the most highly specialized owls. Being more highly owl-like it is more strictly nocturnal than the other American owls which occasionally catch dragonflies at dusk. In its time of flight it is further from the time of flight of the diurnal Odonata.

The eagles, Buteoninae, and other large hawks of the Accipitriidae do not use dragonflies. They are usually interested in larger prey.

Among the tree-inhabiting and perching birds a few families show no records of stomachs with dragonflies. These are the Trochilidae (hummingbirds) which live on minute insects and nectar; Motacillidae (wagtails, pipits) which feed on insects and seeds but feed on high open ground where dragonflies seldom occur; Certhiidae (creepers) and Sittidae (nuthatches) which search tree trunks for minute insects and the Sylviidae (kinglets, gnatcatchers) which live on minute insects. The kinglets winter in the States when dragonflies are not on the wing but the family is represented in the western states by four species of gnatcatchers, one of which, the blue-gray gnatcatcher, extends to the Atlantic coast, which do not eat Odonata perhaps because of their diminutive stature and very small beaks.

Thus birds that do not eat Odonata are checked by one or more of the following factors:

1. They have a special food preference that does not include dragonflies as for example the osprey, a fish eater; the flamingo, a mollusk eater (Chapman 1905); the vultures, carrion eaters.

2. They may have a habitat that does not include dragonflies as for example the sea birds, the quails, grouse, pipits, larks, which inhabit high dry areas and the nuthatches which seldom leave the trunks and limbs of the larger trees.

3. They may be mere winter visitors in the United States when dragonflies are not on the wing but probably do eat dragonflies on their nesting grounds as for example the northern blue bird and the bohemian wax-wing.

4. They may be so deeply nocturnal that their time of flight does not coincide with even the crepuscular Odonata, thus by time of day being out of the dragonfly habitat, as for possible example, the barn-owl.

5. They may be so large that they ignore insects as food though their smaller relatives use them plentifully as for instance the eagles.

6. They may be so small that they show a distinct preference for minute insects, as example the gnatcatchers and the humming birds.

7. While feeding on the ground they may be so slow in reaction time, so short-necked and with such poor vision, monocular, that dragonfly adults are too fast for them. Examples are rails and perhaps turkeys.

8. A few birds have bills so specialized for specific foods accompanied by tastes for diets which do not include insects that the shape of the bill prevents use of the bill for insects. Examples are the flamingo (Phoenicopteridae), a mollusk-eater, and the oystercatcher (Haematopodidae) with its chisel used on bivalves. Uusally the problem is not as simple as listed. In the skimmers (Rynchopidae) the bill is specialized but the skimmers in being wholly marine are already out of dragonfly environment.

BIRDS WHICH EAT DRAGONFLIES

EGGS OF ODONATA EATEN ONLY ACCIDENTALLY

Apparently dragonflies while in the egg stage are not regularly attacked by birds. Some plant-eating waterfowl may take such occasionally (the eggs of Zygoptera) while feeding on floating aquatic plants but few birds feed on floating plants, those large and tough enough to interest an ovipositing female dragonfly. Dragonfly eggs are oviposited in three or four ways. The Libellulidae and Gomphidae wash them off the vulvar parts by touching the abdomen to the surface of the water. The eggs usually float apart almost immediately and drop to the bottom. However, the Cordulidae lay eggs, as do toads and frogs, in masses of gelatinous envelope, usually gelatinous strings of eggs festooned over submerged vegetation. We have no records that birds eat these, but the facts have never been sought out. A few dragonflies with a large shovel-like ovipositer (Cordulagesteridae, and occasional species of Libellulidae) oviposit by thrusting eggs into mud or stream bottom. The majority of the Zygoptera oviposit endophytically, as also do the Aeshnidae. Here with a sharp, hard, needle-like ovipositor the eggs are placed deep into plant tissue, less often in crevices of mossy rock as laid by *Aeshna walkeri* Kennedy (1917).

The birds which take *insect* eggs as a regular part of the diet are largely the smaller tree-inhabiting land species, insectivorous forms that search the bark, twigs and leaves of forest shrubs and trees. Some such are titmice, wood warblers, vireos, nuthatches,

brown creeper, the smaller woodpeckers, etc. These egg hunters seldom enter the environment where dragonfly eggs are deposited. Only one North American dragonfly (*Archilestes californica* McL.) is known which oviposits in trees (willow; Kennedy 1915).

Birds Take Nymphs and Adults at a Disadvantage

The few species of birds that use dragonflies to any considerable extent as food take the dragonfly at a disadvantage. Several such types of advantage of bird predator over dragonfly as prey can be pointed out.

1. The bird may scoop the dragonfly nymph up with a shoveling bill as do the ducks when the nymph is burrowing in the mud, sand or trash at the bottom of a pond or stream. This is particularly a habit of feeding among the river ducks of which the Shoveller Duck is the outstanding example. This type of capture is especially destructive to dragonflies during the cooler parts of the year when the nymphs of many species of dragonflies drop to the bottom in a sluggish condition, a form of hibernation or semi-hibernation. The American avocet hunts with its upturned bill in somewhat the same manner.

2. Some species of birds take great numbers of dragonflies when nymphs crawl out of the water in the process of the emergence of the winged land adult from the skin of the aquatic nymph, which process has to be completed in the air. The dragonfly is at a great disadvantage at this time in two ways. First the nymph is not a land animal yet has to crawl some distance on land sometimes a hundred or more feet (Cordulinae). It is slow and awkward with no protection except perhaps a lack of bright color to the bird eye. Second, it is in a physiological condition which reduces its behavior, its reactions to dangers of the environment, to their lowest point in its life cycle beyond the egg stage. This low physiological condition continues for some hours until the wings are fully expanded, fully hardened and until after trial flights have been taken and the neuromuscular apparatus has turned up. It probably involves a meal or two before the imago is at top imaginal speed in its reactions to the dangers surrounding it. The species of birds that appear the heaviest feeders on Odonata at emergence are the martin, yellow-headed blackbird, the western robin, and Franklin gull (Gould 1871).

3. Birds that hunt in emergent vegetation, taking adult Zygoptera particularly, find the dragonfly at a disadvantage because of the slow flight of the latter necessary in dodging between the upright sedges, cattails, etc. Dragonflies are very slow in flight under such conditions. Here we were surprised to find that the rails did not get many Odonata. The American bittern, least bittern, and green heron excel in taking dragonflies in this type of disadvantage to the latter. The standing position of the immobile bittern with its bill pointed straight up could be a position useful in catching dragonflies flying over as well as a position of concealment, its usual interpretation.

4. Birds that fly as well or better than do dragonflies have dragonflies at a disadvantage not only in ability on the wing but because the bird has clearer eyesight. The dragonfly depends on mosaic vision (Exner 1891), which is dim with hazy outlines at best though it may define a moving object (enemy or prey) fairly well. The flying predator bird has the most highly developed eyes known in the animal kingdom and so must have a very fine vision. Such take many flying Odonata. Examples are the martins and the smaller falcons.

5. Dragonflies rest on tree trunks as well as on smaller plants when too cool for flight. This habit may account for Odonata found in woodpecker stomachs especially in yellow-bellied sapsucker stomachs. Also some dragonflies cease flight at 105° F. or higher when they rest as if too cold (Walker 1912).

6. Vast numbers of dragonflies are stranded as nymphs in ephemeral shallow pools each season. When found by birds they may account for the occasional bird stomach containing 10 to 30 nymphs in a series where other stomachs contained one or two.

Dragonflies as Food of Nestlings

Little manual stomach examination has been done on nestling birds. (The literature on observation by field glass has not been reviewed.) Discussion of the following cases will be found under the names of the species to which attention is directed here. The Franklin gull, a bird of northern mid-American marsh-bordered lakes, was found by Roberts to be feeding its nestlings on dragonfly nymphs. This gull is almost wholly insectivorous state McAtee and Beal (1924).

The purple martin has been found by Beal (1918) to feed its young on Odonata. See also Doolittle (1919). This bird prefers nest boxes near water. The yellow-headed blackbird which nests in the cattail swamps of the western states feeds its nestlings on teneral aquatic insects a high percentage of which are dragonflies. (See Fautin (1940) for a bibliography: see this article, northern crested flycatcher; Franklin's gull; western robin; marsh wrens. See Judd 1901).

Competition for Food between Birds and Dragonflies

Few birds compete directly with dragonflies for food which may be common to both. In the water, food common to both would include the smaller aquatic animals and on land largely the minute dipters (Campion 1914, 1921; Lyon 1915; Warren, Alfred, 1915). In the water, ducks take aquatic animals but usually those larger than would be attacked, except perhaps by the largest aeshnine numphs. On land there are few insectivorous birds which use small insects and which also fly regularly about streams. Some of the flycatchers live near streams and some of the smaller of these take many small insects. But the greater number of insectivorous birds that are small enough to be interested in the insects which are small enough (gnats) to interest the average dragonfly, are arboreal birds largely restricted to

timber. The possible competitors with flying Odonata for minute insects are such birds as humming birds, titmice, warblers, kinglets, vireos, some small flycatchers, etc. which seldom hunt near streams. (See early notes by Poulton 1906.)

THE UNITED STATES FISH AND WILDLIFE SERVICE'S DATA ON BIRD STOMACH CONTENTS. NOTES ON FOOD PREFERENCES AND HABITS WHICH CONTACT BIRD AND DRAGONFLY

FAMILY COLYMBIDAE (grebes)

The lowest order in the United States bird fauna (the members of which catch dragonflies) is the Order Colymbiformes which, in our area, includes the single family of the grebes. These are as thoroughly aquatic as any of our fresh-water birds and are remarkable for their great speed of muscular reaction.

With this speed of movement is associated a remarkable acuteness of vision. The retina of the eye is provided with a highly developed monocular (nasal) fovea which consists of the usual pit-like fovea but extending from it to the nasal edge of the retina is a fossa, probably an extension of the area of acute vision that gives the grebe the ability to see objects distinctly which lie to one side (monocular vision) but actually back of the grebe's position. Thus the grebe is very sensitively keyed to his environment by a remarkable range of acute vision. Apparently, the grebe does not have the acute binocular vision as do birds that on the wing strike prey, such as the owls, hawks, swallows, humming birds and others which usually have a well developed temporal fovea used binocularly. The foveae of the great crested grebe of Europe, *Podiceps cristatus* (Linnaeus), are figured (Fig. 121, p. 72) by Doctor Casey Wood (1917) on bird eyes. Compare Fig. 121 with the retina of doves and pigeons (Wood 1917, Figs. 118 and 119) which eat seeds, nuts and fruit, and whose retinas have no highly developed areas of acute vision.

The grebes are birds of swamps, ponds, and the edges of freshwater lakes. Nests are built on floating rafts of cattails in the outer edge of emergent vegetation which supports the densest population of dragonflies. The food of all species is about 100% animal substances including fish, worms, Crustacea, and insects. All species have a curious habit of eating their own feathers so that grebe stomachs usually contains balls of feathers. The following are monographic and apply to the species of grebes cited, Bent (1919), Forbush (1925), Henderson (1927), McAtee & Beal (1912, 1924), Munro (1941), Wetmore (1924).

Holboell Grebe, *Colymbus grisegena holboelli* (Reinhardt): 50 stomachs examined, one with several adult dragonflies. About 50% of the stomach contents, other than feathers, of the Holboell grebe is fish, often with crustaceans as high as 20%, the remainder being aquatic insects.

Horned Grebe, *Colymbus auritus* L.: 156 stomachs examined, 3 with libelluline nymphs and 3 with adult Odonata. In a third of the stomachs fish ran to about 35% and crustacea 7-10%.

Eared Grebe, *Colymbus nigricollis californicus* (Heermann): 35 stomachs examined, 6 with odonate nymphs and 1 with specimens of *Enallagma* sp., an adult Zygoptera. Less than 20% of the food of the eared grebe is rated as fish, the remainder being crustaceans, worms, and insects.

Pied-billed Grebe, *Podilymbus podiceps podiceps* (L.): 196 stomachs examined, 23 with Odonata. Of these 10 contained aeshnine nymphs, one a libelluline nymph, one a zygopterous nymph, 6 unplaced "odonate nymphs" and 4 adult dragonflies. The food of this bird averaged 24% fish, 27% crayfish with the remainder largely aquatic insects. According to Wetmore (1924) some of the stomachs contained adult Zygoptera up to 8-34% of the total food.

Antillean Grebe, *Podilymbus podiceps antillarum* Bangs: One Puerto Rican stomach contained 2 dragonflies and 25 crayfish (Wetmore 1916).

At the same low evolutionary level as the Order Colymbiformes (Grebes) are three other orders of aquatic fowl. One order, the Gaviiformes (Loons) are fresh water as well as salt water in habit and while living largely on small fish eat insects, crustacea, leeches, amphibians, etc. Probably loons at times take dragonfly nymphs though the Survey's records contain no such records. The other two orders, the Procellariiformes (albatrosses, shearwaters, petrels) are marine while the Pelicaniformes (pelicans, cormorants, darters, etc.) are salt water fowl generally with a few exceptions on salt lakes and estuaries. The darters, found in semitropical swamps, may at times take Odonata as insects are recorded in their stomachs. The other families of these orders are outside the fresh water environment of dragonflies.

The succeeding orders of birds tend towards a fresh water or land habitat and in the sixteen orders to follow only two, the Columbiformes (doves and pigeons) and the Trogoniformes (trogons), a tropical group, have no records whatever of having eaten Odonata. This brings us to the first family of this series of fresh water and land birds.

FAMILY ARDEIDAE (herons, egrets, bitterns)

In this series of families which compose the Order Ciconiiformes are the ibises, storks, bitterns, cranes and herons where we come into a series of birds which feed on a wide group of moving animals. With this preference for moving prey is the fact of their life about the shores of fresh waters where dragonflies are most abundant and the further factor that the majority of species are of that intermediate size among birds which is associated with the capture of dragonflies. The positive combination of food habit or preference, of living in a dragonfly environment and of size of bird in relation to food eaten shows at once in the large number of Odonata eaten by most members of the Order Ciconiiformes.

Casey Wood (1917) shows that the Ciconiiformes have besides the usual nasal fovea for monocular

vision a well developed temporal fovea or area of acute vision on the outer rim of the retina which indicates an acute binocular vision. This type of eye is found widely in birds that take moving prey. It permits accurate and speedy bill work. Further the long legs of this group permit wading in the shallow vegetation-filled waters where, because of vegetation, swimming is more difficult than in open water. Here dragonflies are the most abundant. The long neck in these birds gives range in striking prey. All the species of the Ardeidae probably eat dragonflies regularly, both in the nymphal and in the adult form.

However nine species of this family found within our area have no records of having eaten Odonata. The herons are a group of birds that live in the very midst of the most densely populated dragonfly habitat and eat any small, moving vertebrate, crustacean or large insect. Some species, notably the green heron, catch more adult Odonata than nymphs. The latter species lives along wooded streams where dragonflies fly more slowly on account of the vegetation than they do over more open water which may account for the greater proportion of adults in their food.

Birds of this family feed while standing on their feet. Compare their records with marsh-inhabiting Passeriformes of the same general insectivorous tastes but perhaps of a slightly smaller order of size such as the red-winged blackbirds. The heron-like birds have the distinct advantage of a long neck in obtaining active insects. As we shall see, the birds that feed standing and that have short necks use slow insects, Orthoptera, Coleoptera, Hemiptera, caterpillars, etc. (Bent 1927; Baynard 1912; Forbush 1925; Henderson 1927; Wetmore 1916).

Great Blue Heron, *Ardea herodias herodias* L.: 125 stomachs examined, 29 containing Odonata, 19 of which were adults and 12 of which were identified as adult Anisoptera. The usual articles of diet of this bird are fish, frogs and crayfish, but it takes almost any animal, including snakes, salamanders, mice, gophers and large insects including locusts.

(The American Egret, *Casmerodius albus egretta* (Gmelin) appears to use a diet of animals from the higher meadows and is a larger bird. This may explain the lack of Odonata in the stomachs examined by the Survey.)

Snowy Egret, *Egretta thula thula* (Molina): 20 stomachs examined, 5 of which contained dragonfly adults. Other published records indicate that it also eats nymphs. It is a bird of brackish waters and low, marshy meadows, feeding on crayfish, fish, and swimming aquatic insects.

Louisiana Heron, *Hydranassa tricolor ruficollis* (Gosse): 60 stomachs examined, 10 with dragonflies, 9 of which were adults: Food similar to the preceding egret but taking many top-minnows and grasshoppers.

Little Blue Heron, *Florida caerulea caerulea* (L.): 45 stomachs examined, 27 with dragonflies, 7 of which were adults. One stomach contained 18 and another 31 nymphs. Evidently dragonfly nymphs are a regular item of diet. This is a bird of more open waters than the next, the Green Heron, and the records show its food to be fish, frogs, crustaceans, and swimming insects.

Green Heron, *Butorides virescens virescens* (L.): 215 stomachs examined, 80 with dragonflies, 59 of which were adults and the majority of these Anisoptera. Several of the stomachs, 23 in all, contained 2 or more and 8 stomachs contained from 5 to 33 dragonflies. This is a bird, solitary in habit, living on small streams and in wooded swamps where it eats a diet of the usual heron type but of noticeably large forms including snakes, lizards and amphibians though it is the smallest heron, excepting the least bittern. However, it has a heavy short beak which may help it manage food large for the size of the bird. It catches more adult insects, including caddis flies, grasshoppers, etc., than do the other herons. (Bowdish 1903; Warburton 1948).

Black-crowned Night Heron, *Nycticorax nycticorax hoactli* (Gmelin): 100 stomachs examined, 12 with dragonflies of which 5 were adults. This heron eats fish usually but takes also amphibians, crayfish and miscellaneous aquatic insects.

Yellow-crowned Night Heron, *Nyctanassa violacea violacea* (L.): 110 stomachs examined, 1 with a dragonfly. This bird eats fish, crustaceans and worms. The two night herons are puzzles. Both are crepuscular as well as nocturnal. Bent considers the yellow-crowned more nearly diurnal but in 110 stomachs it has only 1 dragonfly. Habits are poorly known of either species. (Howell, A. H., 1924.)

American Bittern, *Botaurus lentiginosus* (Montagu): 125 stomachs examined, 29 containing dragonflies, 17 of which were adults. The speed of this bird in striking prey as it stands concealed amidst swarming dragonflies helps to account for these in its food. It eats also fish, frogs, crayfish, aquatic insects and marsh Orthoptera (Gabrielson 1914).

Least Bittern, *Ixobrychus exilis exilis* (Gmelin): 100 stomachs examined, 41 with dragonflies, 16 of which were adults. From the Survey records the food of this bird includes many small fish and submerged aquatic insects including Coricidae, Belastomidae, and Notonectidae. The records indicate that it catches Odonata twice as often as does its large relative, the American bittern. This is the same relationship of size of bird to size of food as will be noted in the ducks where the small ducks take dragonflies oftener than do the large ducks. We will see the same relationship in the hawks, owls and crows. Two possible explanations occur, one, that the larger birds are able to use larger animals as food and prefer to do so, the other that the larger birds more often occupy more open water including the sea and its bays while the smaller species live in the protection of vegetation about shallower waters where Odonata are abundant. Few published records of food of the least bittern; Sutton (1936).

FAMILY THRESKIORNITHIDAE (true ibises)

The ibises are birds of the fresh water marshes and wet prairies living on crayfish, small snakes, grasshoppers, and other large insects. The series of animals eaten by them suggests that they capture those which are slower and more easily taken than are adult Odonata and that, excepting crayfish which at times form a large item, and a few aquatic beetles, they live mostly on sedentary aerial marsh animals. If actually slow, this accounts for the few adult Odonata taken and their lack of interest in fully aquatic forms accounts for the lack of nymphs in their food.

Wood's (1917) study shows that the true ibises have only a nasal fovea hence only monocular vision. As compared with the herons which have both monocular and binocular vision they capture only nymphs and *may* take these only when stranded in drying pools (Bent 1927; Forbush 1925; Henderson 1927).

White-faced Glossy Ibis, *Plegadis guarauna* (L.): 15 stomachs examined, one stomach with 22 zygopterous nymphs and one with 2 nymphs. The single published record discloses a single stomach containing aquatic plants and one beetle.

There are no records against the Glossy Ibis as an eater of Odonata (Baynard 1913).

White Ibis, *Gaura alba* (L.) : 20 stomachs examined, one with an anisopterous nymph. Baynard's (1912) reports on food given young in nest lists crayfish as the largest item with cutworms, grasshoppers, and snakes.

(Rated as a subfamily of the true ibises are the spoonbills. The group is represented in the area of this study by the one species, the roseate spoonbill, *Ajaia ajaia* (L.). Little is known concerning its food. It lives in shallow fresh waters and feeds by emersing the bill and swinging it from side to side in search of food. By such indiscriminate feeding it probably takes dragonfly nymphs at times.)

(In the Order Ciconiiformes are two families against which there are no records of having eaten Odonata. The storks (Ciconiidae) are represented in our fauna by the wood ibis (*Mycteria americana* L.) which has only monocular vision (Wood 1917) and has food habits similar to those of the true ibises (Henderson 1927).)

(The flamingos (Phoenicopteridae), the other family, have been set out under our division of birds that do not eat Odonata because of their salt water habitat and taste for mollusks (Chapman 1905).)

The next order as rated in the A. O. U. Check List, 1931, is that of the Ansereformes which includes the geese, swans and ducks. This order tends towards more vegetable matter in the food which in the geese and swans becomes almost 100 per cent. As shown by Casey Wood (1917), the species of this order have only moderately acute monocular vision. All species have a nasal fovea and in some, the area of acute vision is extended on either side of the fovea in a narrow band. The taste for animal food on the part of the ducks and their use of the same environment as that used by odonate nymphs makes them active enemies of nymphal Odonata.

FAMILY ANATIDAE (ducks, geese, swans)

Excepting the sea ducks, the Anatidae live in the most abundantly populated dragonfly habitats. They are feeders on insects along with other animal and vegetable matter. They obtain their food by swimming or diving, so are constantly brought into contact with either nymphs or adults of dragonflies or both. Hence as a group, the ducks are consistently dragonfly eaters. But as in any large group of species, tastes and habits vary from species to species so that some prey oftener on dragonflies than do others. The group falls into two major series, (1) the geese, brants and swans and (2) the ducks (Munro 1940, 1943, 1944).

The ducks proper fall into three series: (1) the river ducks which live in a rich dragonfly environment and consume many such; (2) the sea ducks, the smaller species of which are the only ones which enter inland shallow waters and use dragonflies; and (3) the mergansers or fish ducks with toothed raptorial bills which variously occupy inland waters and in dragonfly waters use dragonfly nymphs as an item of food.

The River Ducks: In this series the bill is broad and is usually used to shovel mud from pond or stream bottom with bird up-ended or diving. The mud is sifted out through the fluted sides of the bill while morsels of food are retained. These catch burrowing nymphs and nymphs hibernating on the bottom (Bent 1923; Cottam 1939; Forbush 1925; Henderson 1927; Munro 1944).

Mallard Duck, *Anas platyrhynchos platyrhynchos* L.: 2,010 stomachs examined of which 197 contained remains of dragonflies. 126 records are of nymphs of which only 6 are zygopterous. Of the 71 stomachs with adults only 8 were zygopterous, but one stomach contained 7 and another 40 Enallagmas. Thus the mallard tends to use large dragonflies, whether nymphs or adults. The food of the mallard is 90% vegetable. The animal food of the mallard is about 10% of the whole, one-fourth of which is insects, one-half mollusks and the other fourth crustaceans and miscellaneous matter (McAtee 1918; Munro 1943, 1944).

Black Duck, *Anas rubripes tristis* Brewster: 645 stomachs examined, 25 with dragonflies of which only 5 were adults. The food of the black duck is about 75% vegetable, 12% mollusks, 8% crustaceans and 5% insects, fish and miscellaneous. Habits similar to those of the mallard but feeds more often on salt water where Odonata do not occur.

Southern Black Duck, Florida Duck, *Anas fulvigula fulvigula* Ridgway: 52 stomachs examined, 10 with Odonata of which only 4 were adults. While this duck rates as a brackish water duck it is resident on the Gulf Coast the year around and being in a con-

tinuous dragonfly habitat apparently catches these oftener than do the mallard and the black ducks, close relatives. Its food is 60% vegetable matter, mollusks 27%, insects 9%.

Gray Duck, Gadwall, *Chaulelasmus streperus* (L.): 410 stomachs examined, 5 containing Odonata of which only 2 were adults. The gadwall's food is 98% vegetable, insects ½% and mollusks 1.6%. The gadwall is a surface feeding duck but can dive in escape.

Baldpate, American Widgeon, *Mareca americana* (Gmelin): 270 stomachs examined, 2 with dragonflies of which one was an adult. The food is 96% vegetable matter, ½% insects and 6/25% mollusks. The baldpate is a surface feeder tending to the parasitic habit of stealing food from diving ducks. This habit raises the percentage of vegetable food.

Pintail Duck, *Dafila acuta tzisihoa* (Vieillot): 925 stomachs examined, 35 with dragonflies of which 28 were nymphs, 2 only of the latter being Zygoptera. The food is 87% vegetable, insects 2.8%, mollusks 5.8% and crustaceans 3.7%. This is probably the speediest and most active of the ducks but shows *no greater catch* of adult dragonflies than do the slower species. This super-duck which jumps into the air, not having to run on water to rise, and which has a circumpolar distribution tends to feed on shore lines where dragonfly larvae are few. It feeds just outside by a few feet of the winter habitat of odonate nymphs. Its great agility does not increase its intake of Odonata (Munro 1944).

Green-winged Teal, *Nettion carolinense* (Gmelin): 750 stomachs examined, 27 with dragonflies of which 18 records were of nymphs. The food of this species is 90% vegetable, insects, 4.5%, mollusks 4%. The 30% of adult Odonata are probably due to its habit of wading in shallow water during nesting season and to its well known speed in action: one of the speediest.

Blue-winged Teal, *Querquedula discors* (L.): 335 stomachs examined, 27 with Odonata, 6 of which contained adults. The food is 70% vegetable, insects 10%, mollusks 17%. The blue-winged teal comes south in late summer which accounts for adult dragonflies. It occupies marsh ponds, shallow waters and shore lines, has the speed of reaction found in the green-winged teal, which accounts for the greater number of Odonata.

Cinnamon Teal, *Querquedula cyanoptera* (Vieillot): 44 stomachs examined, 4 with dragonflies all of which were adults. This is a western species breeding in the densely populated dragonfly habitats about western ponds and marshes. Unfortunately, the published records are of eastern individuals strayed from their natural habitats, or may be misidentifications. Vegetable food, 80%, insects 10%, mollusks 8%.

Shoveller Duck, Spoon Bill Duck, *Spatula clypeata* (L.): 88 stomachs examined, 3 with Odonata of which 2 were nymphs. Vegetable matter 65%, mollusks 18%, insects, small fishes 3%. The shoveller duck is built to feed by sifting mud through its highly specialized bill so that its take of nymphs is purely accidental. However, McAtee (1922) states that much of its food is obviously taken without such sifting of the bottom mud.

Wood Duck, *Aix sponsa* (L.): 400 stomachs examined, 78 containing dragonflies, of which 56 were nymphs, the majority being Anisoptera. Of the total food, 90% is vegetable, insects 6.3%, spiders, mites and crustaceans 1%; no mollusks taken. McAtee's figures for the wood duck are, vegetable food 10%, dragonflies and nymphs 2.5%, bugs 1.56%, beetles 1.02%, Orthoptera .23%. He found that in 16 stomachs taken in March 1.75% of the food consisted of dragonflies the majority of which were nymphs, of 9 taken in April, 10.44% was dragonflies, mostly nymphs. This rise in the number of nymphs taken during the early spring was found also in the southern black duck and is accounted for by the fact that odonate larvae are then full grown and are awaiting for the late spring emergence. They are then large enough to be taken by a duck and their numbers have not been depleted by emergence. Warren (1888) records seeds including acorns and calls it "Summer Duck, Wood Duck, Acorn Duck."

This ends the series of river ducks all of which use dragonflies to some extent.

The Sea Ducks or Diving Ducks: The following are called sea ducks and live on more open and deeper waters where there are fewer opportunities to capture dragonflies. Of the 18 species of sea ducks 10 have no records of having used dragonflies as food. These are the eiders and other ducks of the sea coast and more open bays and estuaries, the majority of which are vigorous, active ducks that do not seek the protection of shallow, weedy waters. However, three of the smaller species of this group do not venture into open waters. They feed about in shallow waters, and rate high as eaters of dragonflies. These are the blue-bill, ring-necked and bufflehead ducks (Bent 1923, 1925; Cottam 1933, 1939—best bibliography; Forbush 1925; Henderson 1927).

Redhead Duck, *Nyroca americana* (Eyton): 360 stomachs examined, 10 with dragonflies only one of which was a nymph. No thorough analysis of the food of this duck has been published (1925). It is a heavy eater of vegetable matter but takes also fish, amphibians, mollusks, and a few insects.

Ring-necked Duck, *Nyroca collaris* (Donovan): 655 stomachs examined, 92 with Odonata, 84 of which were adults. This is another small Nyroca and according to Bent the greater part of its food is vegetable but it takes a scattering of insects. It is more of a fresh water duck than the other Nyrocas and thus comes more often into the dragonfly habitat.

Canvasback Duck, *Nyroca valisineria* (Wilson): 380 stomachs examined, 10 with dragonflies all of which were adults. A vegetarian duck but takes also a few snails, crustaceans and insects. This again is a large duck very similar to the redhead and eats a few such animals as amphibians, fishes, leeches, and mollusks. As the canvasback and the redhead tend to feed along the Altantic coast in brackish water

they come into contact with few dragonflies. When in fresh-water they feed largely on eel grass which grows in deep water where odonate larvae are probably scarce as they are constantly exposed to fish. Thus these ducks come into contact with few dragonflies even when feeding in inland waters.

American Scaup Duck, Greater Scaup Duck, *Nyroca marila* (L.): 752 stomachs examined, 10 with dragonflies, 8 of which were larvae. According to Bent in its summer home in fresh-water (the Arctic Coasts) it lives on small fishes, amphibians, mollusks, insects, and some vegetable food while in its winter habitat on the southern sea coasts it uses less animal food and more vegetable food. Within the coastal waters of the states it is essentially a salt-water and brackish-water duck.

Lesser Scaup, Blue-bill Duck, *Nyroca affinis* (Eyton): 1155 stomachs examined, 176 containing dragonflies. The records show that about 150 of the stomachs contained adults. This is a very active duck which winters during a long season that overlaps late fall and early spring dragonfly flight. This accounts for the greater proportion of adult dragonflies taken. It is also a smaller duck than the two preceding of the same genus, *N. marila* and *N. affinis*. It frequents fresh-water estuaries, sounds and inland waters where it comes into the dragonfly habitat. Because of its smaller size than that of the preceding it eats smaller animals such as insects and fewer mollusks and crustaceans (Cottam 1933).

American Golden-eye Duck, *Glaucionetta clangula americana* (Bonaparte): 175 stomachs examined, 6 with dragonflies, 3 of which were adults. The Survey records indicate that its food is largely crustaceans, mollusks, and insects with vegetable food in moderate amounts. Its short, strong bill would seem adapted to an animal diet. These ducks usually occur on large lakes and rivers where they dive for food. This takes them into deeper water than that in which dragonflies are usually found. Munro (1940) gives Odonata as 2.75% to 11% of the food of the Golden-eye. This rates it as one of the bad bird enemies.

Bufflehead Duck, Butter-ball, *Charitonetta albeola* (L.): 60 stomachs examined, 11 with dragonflies of which 9 were adults. This duck feeds mostly on animal matter, using vegetable matter sparingly. It feeds as does the Golden-eye in the more open fresh waters but from the limited data it takes a larger percentage of dragonflies than do any of the diving sea ducks. This may be associated with its small size as it is only 14-15 inches long, being one of the smaller of the group of sea ducks. Because of its smaller size it probably feeds closer to emergent vegetation in shallower water. In fact, Vernon Bailey states that it is even found at times in small creeks and ponds (Munro 1940).

(The Old Squaw, *Clangula hyemalis* (L.) is a deep water duck taken in Lake Michigan in nets 150 feet deep (Barrows 1912). The three species of Scoters *Melanitta* spp. and *Oidemia,* three species of Eiders *Somateria* and the Harlequin Duck *Histrionicus histrionicus* (L.) are salt water ducks that have no records against them of having eaten Odonata. They frequent open salt water out of the dragonfly environment. They are occasional on the Great Lakes. See Dewar (1915) on diving of British birds.)

Ruddy Duck, *Erismatura jamaicensis rubida* (Wilson): 55 stomachs examined, 4 with dragonflies. It is one of the smaller sea ducks, 13.5-16 inches long, but is most abundant in the marshes and brackish ponds of the western states. It falls in the group of about ten species of scoters, eiders and relatives which are true salt water ducks and seldom, if ever, eat Odonata. It is the smallest of the group and sticks to shallower inland waters which brings it into the dragonfly habitat. It is so small that gunners count four to make a pair in estimating bags. Cottam (1939) found most dragonfly nymphs (3.5% of food) in December.

The Mergansers or Fish Ducks: The mergansers have slender, toothed bills. They eat fish and other small active aquatic animals. The first, the hooded, frequents small shallow streams while the other two are frequenters of more open and deeper waters. As might be expected, the hooded merganser in shallow dragonfly water uses more dragonflies than do the others in deeper waters (Bent 1923; Forbush 1925; Henderson 1927).

Hooded Merganser, *Lophodytes cucullatus* (L.): 50 stomachs examined, 18 with dragonflies, of these 8 were adults and 10 anisopterous nymphs. This species is a frequenter of small streams where it breeds as far south as Tennessee and even Florida, hence it comes more often into contact with adult dragonflies than do the preceding mergansers of more open waters. The food of the hooded merganser is largely aquatic insects with an occasioral aquatic animal of other type.

American Merganser or Sheldrake, *Mergus merganser americanus* Cassin: 140 stomachs examined, 2 with adult aeshnids and one with an anisopterous nymph. This species is a fish eater and frequents open waters away from the denser populations of Odonata (Munro & Clemens 1932.)

Red-breasted Merganser, *Mergus serrator* L.: 175 stomachs examined, 6 with adult dragonflies and 4 with nymphs. This species also frequents open waters and is chiefly a fish eater though it includes crustaceans and aquatic insects.

The ducks, aquatic in habit, eat many nymphs as well as some adult dragonflies. The following series of birds, the Order Falconiformes, the hawks, kites and falcons with the exception of the red-shouldered hawk use only adult or flying dragonflies. Thus do kinds of locomotion which limit species to specific habitats effect the nature of the food taken.

The Order Falconiformes contains the most highly developed birds of the Class Aves, *if we think of birds as evolving towards individualism* rather than towards a social life. They are more bird-like in fine vision, ability on the wing and in the more highly

evolved nature of their food (flying insects, birds and mammals). Having evolved in an aerial environment vision has had to have high development as it is the prime distance sense. Birds in general appear to be eye-minded rather than odor- or nose-minded as are the mammals which are associated more closely with the ground and its protective dark holes, warrens and caves where odors have high value. Odor-mindedness is of value in the close contacts of the ground nest or cave, usually dark, where vision is at a discount. Odor-mindedness leads to social life with its numerous close contacts in illy lighted nests and caves. Thus the eye-minded birds of essentially aerial life tend towards individualism. This is in spite of the fact of the high development of the "family" in all higher vertebrates and particularly in the birds. The family behavior is the link between individualism and social life. Thus with this definite trend of bird evolution towards eye-mindedness and individualism the Falconiformes can be rated as structurally our most highly evolved birds in the non-social branch of bird evolution. The swallows and swifts combine fine flight, fine sight and social habits, but have the smaller size that follows social life. Termites are smaller than their ancestral roaches; ants are smaller than their ancestral digger wasps.

This evolutionary trend shows in the extraordinarily acute vision of hawks. They have a high development of both nasal and temporal foveae which gives them both acute monocular and acute binocular vision (Casey Wood 1917). Flight is developed until some, the kites, even mate on the wing and various forms, eagles, vultures, kites, remain on the wing for long hours in their daily flights. Without reduction of speed on the wing they are larger in size than the average bird which makes for greater individualistic abilities. The feet have evolved into raptorial organs which gives the eyes freer use while taking prey. Vision is no longer tied closely to the grasping bill.

Thus in this order we find forms that can match Odonata in speed and ability on the wing. The only factors which keep many of the Falconiformes from using more Odonata are the large size of the bird and the special tastes in some such as the ospreys and vultures. Apparently birds of this order which do eat Odonata take only adults of large species, mainly Aeshnidae which are frequently high, wide fliers. An exception as cited previously is the red-shouldered hawk which fishes at times and captures some odonate nymphs. See also the everglade kite, a mollusk eater (Fisher 1893; May 1935).

FAMILY ACCIPITRIIDAE (hawks, eagles, kites)

This family includes the largest of the raptorial birds. A review of the records following will show that only a few of the smaller species take dragonflies and only occasionally, one might say accidentally. Except the red-shouldered hawk which fishes at times and may take an occasional nymph, the Accipitriidae take only adult dragonflies. Compare the records of this family of the larger hawks with the next family of smaller hawks, the Falconidae, or falcons, where various species appear to catch adult dragonflies regularly.

Certain species and groups of species are out of the dragonfly habitat being upland birds, others are out by size and others by taste. The Harris hawk (*Parabuteo unicinctus harrisi* (Audubon)) of the mesquite regions of the southwest has no records of having taken Odonata. It lives in the dry uplands. The American rough-legged hawk (*Buteo lagopus johannis* (Gmelin)) and the ferruginous rough-legged hawk (*Buteo regalis* (Gray)) are out. The first is a feeder on mammals, the second a bird of the prairie. Three or four other semi-tropical hawks come into the southwest but the food of these has been little studied.

The gray sea eagle (*Haliaeetus albicilla* (L.)) of Greenland eats fish; while the bald eagle (*Haliaeetus leucocephalus* (L.)) eats fish, birds, and mammals; and the golden eagle (*Aquila chrysaetos canadensis* (L.)) confines its food to birds and mammals. The eagles are out of the dragonfly complex because of their greater size.

The ospreys (Pandioninae) eat fish (when not robbed of a meal by some eagle) and are out of the dragonfly environment by both size and taste.

The vultures (Cathartae) eat carrion and do not feed on material as small as insects. They are out of the dragonfly habitat both because of size and taste. (Bent 1937; Fisher 1893; Forbush 1927; Henderson 1927; May 1935; Sutton 1928).

Mississippi Kite, *Ictinia mississippiensis* (Wilson): 15 stomachs examined, one with an adult dragonfly. This species lives largely on flying insects.

(The other kites, swallow-tailed (*Elanoides forficatus forficatus* (L.), white-tailed (*Elanus leucurus majusculus* Bangs and Penard), and everglade (*Rostrahmus sociabilis plumbeus* Ridgway) have no records of stomachs containing dragonflies. The swallow-tailed eats snakes and frogs; the white-tailed a wide mixture of reptiles, frogs, mice and insects; the everglade many large snails, but the Mississippi kite lives largely on flying insects.)

Sharp-shinned Hawk, *Accipiter velox velox* (Wilson): 925 stomachs examined, 2 with adult dragonflies. This hawk lives largely on small birds and mice. Large insects are rarely taken though one of the stomachs listed contained 6 dragonflies. See the pigeon hawk, a falcon.

Cooper's Hawk, *Accipiter cooperi* (Bonaparte): 215 stomachs examined, 2 with adult dragonflies. This, again, preys on birds. In the Yakima Valley (Sunnyside, Wash., 1910-1914) the writer observed it many times on the wing in orchards chasing small birds at full speed under and between closely placed apple trees. Its quick turning ability at full speed on the wing is phenomenal (Johnson 1925). Only occasionally it takes mammals, reptiles, amphibians or insects (Sutton 1928).

(The related species, the Goshawk (*Astur atricapillus* (Wilson)) is a larger bird attacking poultry, game birds, and mammals and rarely takes an insect.)

Red-tailed Hawk, *Buteo borealis* (Gmelin): 510

stomachs examined, one with an adult dragonfly. This Buteo feeds largely on small mammals, reptiles, amphibians, and occasionally on insects and birds (May 1935; Snyder 1936; Sutton 1928).

Red-shouldered Hawk, *Buteo lineatus* (Gmelin): 325 stomachs examined, 6 with adult dragonflies. Three of the stomachs contained the large *Anax junius* (Drury), while one contained 3 nymphs. This hawk feeds on mice, 25%, poultry 2%, crayfish, small fish, and many large insects. Its taste for large insects *and* aquatic animals explains the catch of nymphs (May 1935).

Broad-winged Hawk, *Buteo platypterus* (Vieillot): 90 stomachs examined, one contained an adult dragonfly. This is the smallest of the Buteos and takes few birds and mammals but lives largely on flying insects, caterpillars, spiders, snakes, toads, and crayfish. It would be expected to take dragonflies oftener but it is a shorter winged and more sluggish species that feeds much on the ground (May 1935).

Swainson's Hawk, *Buteo swainsoni* Bonaparte: 30 stomachs examined, one with 2 adult dragonflies. This western Buteo has a diet similar to that of the preceding but takes fewer water animals as it is distributed over the dryer half of North America from Alaska to northern Mexico. Swainson's Hawk uses many grasshoppers in summer and fall (May 1935; McAtee 1935).

(Sennett's White-tailed Hawk, *Buteo albicaudata hypospodius* Gurney: 4 stomachs, one with 1 frog, 1 snake, contained Odonata nymph remains and aquatic insects "considered to be the food of the two vertebrates," Cottam & Knappen 1939.)

Marsh Hawk, *Circus hudsonius* (L.): 530 stomachs examined, 7 with adult dragonflies, one was an Anax. Another stomach contained two. The marsh hawk lives largely on small mammals but takes also frogs, lizards, snakes, insects, and small birds. As its name implies it lives in a dragonfly environment (Coale 1925; May, 1935).

FAMILY FALCONIDAE (falcons, caracaras)

The falcons, of which there are about ten species north of Mexico, are so skilled on the wing that the majority feed principally on birds, this being especially true of the larger forms. One, the sparrow hawk, feeds on Orthoptera, one, the Caracara (*Polyborus cheriway auduboni* Cassin), of the southwest, feeds on carrion, mice, rabbits, snakes, and fish. The three listed as taking Odonata are among the smaller species. Thus, as with the preceding family of hawks, the smaller species are the dragonfly eaters. (Lit. listed by Bent 1938; Forbush 1927; Henderson 1927; May 1935).

Aplomado Falcon, *Falco fusco-coerulescens septentrionalis* Todd; 3 stomachs examined, one with two adult dragonflies. This is a desert hawk of the southwest.

Pigeon Hawk, *Falco columbarius* L.: 700 stomachs examined, 421 with adult dragonflies, 102 containing one dragonfly each and the remainder (319) containing from 2 to 34 each. All of the species of dragonflies that were identified were Aeshninae, including *Aeshna canadensis,* Walker, *A. multicolor,* Hagen; *A. verticallis,* Hagen; *Anax junius,* (Drury); and *Epiaeachna heros* (Fabr.). 120 stomachs contained *Anax junius* the one all-season species. This falcon lives on birds, small mammals and insects. Obviously it takes large dragonflies in large numbers. The above records show 1,872 individual aeshnine dragonflies eaten by 421 pigeon hawks, an average of 4.5 each for the birds whose stomachs contained dragonflies of an average of more than two each (2.67) the average for all stomachs examined. As some of the records represent merely the indigestible chitinous jaws, legs, etc., which may have remained in the bird's stomach for a longer time than that necessary to digest the other parts, these records may represent more than one meal each, or even more than one day's feeding.

Further, a large series of these stomachs came from a hunting preserve on Fisher's Island near New York City where there had been complaint of the large number of pigeon hawks. The majority of the stomachs collected at this place were taken in the late summer and fall after the hawks had migrated along the coast from farther north. (McAtee, W. L., statement to the author.) At that season the fresher coastal marshes swarm with large aeshnine dragonflies. This is the region where they are so abundant that they frequently collect in large so-called "migrating swarms" of dragonflies. Evidently the pigeon hawks on their southward migration came into such a region supercharged with large dragonflies. (Osburn, R. C. 1916; Kennedy 1917, p. 622.) Thus the Fisher Island records probably have a large element of biological accident (Heape 1931).

Before proceeding with a further discussion, it might be well to admit that only about half of the dragonfly remains in this series of stomachs were examined critically but that all so examined contained aeshnine dragonflies.

The fact that no libelluline dragonflies were present is probably not that the hawks avoided them but the fact that the aeshnine dragonflies fly high and wide where they are easily taken by an active hawk while the libelluline dragonflies hug the surface of the water or seldom rise above the marsh vegetation where the hawks would be less liable to take them. Also in the late summer the libelluline dragonflies of the larger species comparable with aeshnines are fewer in number while the aeshnines are at the height of their season. Apparently these bird-eating hawks reacted to dragonflies with a wing spread equalling that of small birds and flying in the same air level.

The record of *Aeshna multicolor,* if correctly determined, came from the stomach of a western specimen as this hawk is distributed from coast to coast with three western subspecies.

Sparrow Hawk, *Falco sparverius* L.: 550 stomachs examined, 32 of which contained remains of adult dragonflies. Eighteen stomachs contained one each, the others two to six each. This falcon lives mainly

on grasshoppers and crickets and thus might be expected to take stray dragonflies. As a rule the sparrow hawk and its western forms are usually found in the open uplands away from dragonfly territory. The southern form (*Falco sparverius paulus* (Home & King)) of the Gulf Coast and Florida may be more closely associated with marshes and such odonate environment. (Breckenridge & Errington 1938.)

This brings us to the Order Galliformes, the "chicken-like" birds which in our area includes the guans (subtropical), grouse, quails, pheasants, and turkeys. As stated below, knowing the insect-eating proclivities of chickens and turkeys, we were surprised that the lowland species, turkeys, quails, etc., did not show dragonflies in their food more often. As a group these birds consume quantities of seeds and insects of the Orders Orthoptera and Coleoptera. On examining their records as reviewed by Henderson (1927, pp. 179-185) we see that they take rather slow insects. On further thought the Galliformes are slow in movement and Casey Wood (1917, pp. 68-70) shows that they have as poorly developed vision as any of our birds. There are no areas of acute vision (foveae) whatever. All have monocular vision. The common hen stares at the visitor with one eye, then turning her head around checks her first impression by staring with the other eye. This is a time-consuming process which would permit fast-moving insects to vacate the premises before any direct action would be forthcoming from the bird. The Galliformes feed while on the ground, are short-necked and usually occupy dry upland.

There are no records of dragonflies being taken by quails (Perdicidae) by grouse, partridges or ptarmigan (Tetraeonidae) or by pheasants (Phasianidae).

FAMILY MELEAGRIDIDAE (turkeys)

The following records, showing few or no Odonata taken by birds of the Order Galliformes was one of the puzzles in the investigation. Having raised turkeys we realized the absolute necessity of animal food in their diet. Wood-swamps are a usual habitat for turkeys from Arkansas to Florida. Perhaps turkeys are not hunted for study much during the dragonfly season when mosquitoes, deerflies, and horseflies are also prevalent. These were the last areas in the United States explored for Odonata and partly on account of biting insects. We would have supposed that quails collected in swamps during the dragonfly season would have left records but quails are usually on the drier ridges. (Bent 1932; Forbush 1927; Henderson 1927; Kozicky 1942).

Wild Turkey, *Meleagris gallopavo silvestris* Vieillot: 19 stomachs examined, 1 with two adult libellulid dragonflies. This is the only Biographical Survey record (up to 1925) of a dragonfly being taken by a gallinaceous bird. It is possible that turkey stomachs collected in the swamps of the southern states might show more Odonata. However, there, insect food is so abundant that the swift dragonflies may be passed for insects more easily taken. (See Kozinecky 1942).

The next order, the Order Gruiformes, or "crane-like" birds are not well represented by stomachs in the Biological Survey collection. This may account partly for the few records of their having eaten dragonflies as shown in the Survey's notes. The smaller species, the rails, gallinules and coots live exactly in the areas of densest dragonfly population. All eat a very mixed diet of vegetable matter and small animals. Wood (1917, pp. 71-73) shows that these birds have a fairly acute monocular vision. A distinct nasal (monocular) fovea is present and the area of acute vision is extended by a specialized, narrow band which extends across the retina (Wood, Fig. 120, the coot). The larger species, the cranes, tend to use a more upland environment.

FAMILY GRUIDAE (cranes)

Sandhill Crane, *Grus canadensis tabida* (Peters): 16 stomachs examined, 2 of which contained odonate nymphs, one stomach containing two. This crane eats a wide variety of foods including starchy vegetable products such as bulbs, roots, berries, and grains along with its animal food of reptiles, mice, frogs, toads, millipedes, insects, and molluscs. It is not confined to marsh foods. (Bent, Marsh Birds 1927; Forbush 1925; Henderson 1927).

FAMILY RALLIDAE (rails gallinules and coots)

It is a curious fact that no stomach of rails or gallinules contained dragonflies, either nymphs or adults. As a group they use a very mixed diet of vegetable and animal matter, the latter being mostly invertebrates, such as crustaceans, worms, and molluscs—all slower animals than insects. These birds occupy the same general habitat as the herons but miss the Odonata. However, they are much more secretive in habit and live oftener in the denser portions of the marsh vegetation where dragonflies occur less often. Professor D. J. Borror, while teaching nature study in a boy's camp some years ago, reports having watched a King Rail (*Rallus elegans elegans* Audubon) eat an adult dragonfly. Birds of this family have shorter necks than do the herons and may on this account be less able to take swiftly flying insects. Further, they have a broad taste for vegetable food and the work of Wood (1917) shows in general that vegetable feeders do not have as acute vision as do those birds that feed exclusively on moving animals. (Bent 1927, Marsh Birds; Forbush 1925; Henderson 1927).

Coot, *Fulica americana americana* Gmelin: 40 stomachs examined, 3 containing dragonfly nymphs. The coot is again mainly a vegetable feeder but takes slowly moving animals such as tadpoles, molluscs, crustaceans, etc.

Under the shore birds (Order Charadriiformes) we find two series of families. In the recent A.O.U. Check List the gulls, terns, auks, and murres have been united with the usual shore birds, the plovers, snipe, sandpipers and their close relatives.

The first family, Jacanidae is represented in our area by one Mexican species of Jacana on the Rio

Grande, with no records against it. We find next the aberrant oyster-catchers (Haematopodidae) which have chisel-shaped bills with which they pry open molluscs. These, because of taste for molluscs and the specialized bill, are out of contact with dragonflies. Further, they are usually found on salt water shores. The next series of families are the shore birds proper, the snipe, plover, sandpipers, avocet, stilts, and phalaropes.

As will be seen in the records to follow, the birds of this series live more or less in the dragonfly environment (along shores) but take surprisingly few Odonata. Wood's (1917, p. 79-80) studies show that these birds with a highly developed nasal fovea probably have fairly acute monocular vision. However, many are waders on the water line of the beach, in the edges of the breaking ripples where Odonata, either nymphs or imagoes are seldom found. Dragonflies as nymphs are in slightly deeper water (six inches to six feet) or as adults they fly over deeper water or over the adjacent land or marsh vegetation.

The nymphs, except when crawling out to emerge, avoid breaking waves. The flying adults distribute themselves on the wing according to three interests, that of food (both sexes), that of oviposition (females) and that of sexual desire (males). The food of dragonflies is mainly small Diptera. These usually avoid the wave line and fly over either the emergent vegetation of slightly deeper water or over the vegetation of adjacent low land. Thus dragonflies when feeding tend to be in one or the other place. In oviposition the female odonate usually washes the eggs off the tip of her abdomen (Gomphidae and Libellulidae) in water deep enough for the nymphs or inserts eggs (Zygoptera and Aeshnidae) in emergent vegetation which is usually in water deep enough for the larvae. The males in lust seek the females while ovipositing or while hunting food either of which type of flight tends to take them away from the wave line which is frequented by the smaller snipe, sandpipers, phalaropes, etc. We will connect this banded distinction of dragonflies with the records of the various species that do take Odonata as we come to the species of shore birds which appear to show such.

FAMILY CHARADRIIDAE (plovers)

Of the ten species of plovers listed from our area only four have records of having eaten dragonflies. The plovers are eaters of insects but tend to eat the slower types. They tend to be tide flat or upland birds rather than waders as are the snipe and sandpipers. (Bent 1929; Forbush 1925; Henderson 1927).

Killdeer, *Oxyechus vociferus vociferus* (L.): 260 stomachs examined, 10 with dragonflies, 5 of which were adults. The food of the killdeer is 97% animal matter, mostly worms and insects but as with the other plovers and the snipe, the insects are such things as cutworms, ground bettles, weevils, grasshoppers and other slowly moving forms. This plover feeds on wet flats and sand bars as well as on high dry pastures where it more often nests.

Antillean Killdeer, *Oxyechus vociferus rubidus* Riley: 20 stomachs from Puerto Rico, animal food 98.34%; Orthoptera 16.46%; Coleoptera 32.26%; fly larvae 19.53%; ants 3.92%; snails 19.02%; dragonflies 3.92% (Wetmore 1916).

Golden Plover, *Pluvialis dominica dominica* (Müller): 100 stomachs examined, 4 with dragonflies, all of which were nymphs. This is a bird of the barren grounds in the June breeding season and is the plover that makes the remarkable migratory flights from Nova Scotia across the Atlantic to the pampas of southern South America.

Black-bellied Plover, *Squatarola squatarola* (L.): 440 stomachs examined, 15 with dragonflies, 4 stomachs containing adults. One of these contained 41 Enallagma (Zygoptera) adults. One stomach had 6 nymphs, another 10. This plover is a bird of tide flats only rarely being found inland on fresh water. It breeds on the arctic tundra but spends the late summer on seashore flats. Thus only rarely would it come into the dragonfly habitat. It eats molluscs, worms, crabs, cutworms, grasshoppers, and other insects, also berries.

(Here we will call attention to a relative of the plovers which has taken more positively to the seashore during the winter when and where dragonflies are not present. This is the Surf-Bird (Subfamily Aphrizinae) the stomachs of which might show some Odonata if taken in their nesting grounds in the interior of mountainous southern Alaska.)

The Subfamily Arenariinae, represented in America by two species of Turnstones (Arenaria), has one record of Odonata as food (Knappen 1933, p. 452). Here, again, a relative of the plovers has become a sea-beach bird as a winter visitant. We do not know its food on its arctic breeding grounds. In the winter when Odonata are not on the wing these feed on shore animals, crustaceans, molluscs, etc., along the Atlantic and Pacific Coasts, and as recorded by Knappen eat the bodies of large Odonata (Epiaeshna) washed up on beaches. This is one of the earliest (May) spring dragonflies.

FAMILY SCOLOPACIDAE (snipes, sandpipers, woodcocks, curlews)

(Compare with remarks under the preceding family, the Charadriidae.)

Out of about thirty forms of Scolopacidae found in our area only sixteen have been found to eat Odonata yet the group as a whole, excepting the bartramian sandpiper with upland habits, live almost constantly in a densely populated dragonfly habitat. All eat much animal food of small size and all come within the limits of size for birds that eat Odonata regularly. In the first place the records for many species are incomplete and may show more when more stomachs have been examined. Secondly, many species feed actively and completely exposed at the edge of the water where fewer dragonflies occur than

farther out in the water (nymphs) or farther back in the shore vegetation (adults). (Remarks under Charadrüdae.) Their activity and complete exposure while feeding would tend to frighten away adult dragonflies and they would not catch nymphs except when these were crawling out to emerge. Third, they are not exclusively carnivorous but take considerable vegetable food. Wood's work (1917) on the eyes of birds shows that vegetable feeders have poorer eyesight than do strictly insectivorous and raptorial birds and that the retina of the birds of this and the plover families are not adapted for as acute vision as is found in many other birds that catch moving insects or other fast animals. However, in the two examples figured by Wood (1917) (Figure 114, greater yellow-legs and Figure 125, hudsonian curlew) there is an extended and well developed nasal fovea for good monocular vision.

The curious exceptions are the jack snipe and the two species of yellow-legs with perhaps the instance of the solitary sandpiper. Their eyes should be examined to see if they may not have the fovea better developed than is the case in their relatives. (Bent 1927 and 1929; Forbush 1925; Henderson 1927; Spawn 1942).

American Woodcock, *Philohela minor* (Gmelin): 130 stomachs examined, 1 with an adult dragonfly. The woodcock feeds largely by probing in soft ground for earthworms and burrowing larvae but stomach records show that it feeds also on aquatic and marsh insects such as click beetles, ground beetles, crickets, ants, etc. It takes also the seeds of marsh plants.

Wilson's Snipe, Jack Snipe, *Capella delicata* (Ord): 725 stomachs examined, 139 with dragonflies, 128 of which were nymphs. Apparently this species seldom takes adult Odonata. It feeds quite generally without probing. It takes seeds of marsh plants, snails, worms and many of the slower aquatic and marsh insects of considerable size.

Eskimo Curlew, *Phaeopus borealis* (Forster): 4 stomachs examined, 1 containing an adult dragonfly. This is a marsh and upland bird with plover habits. It is on the verge of extinction, (the last one seen, April 8, 1926, as reported in the A. O. U. List, 1931) but was an inhabitant of the Barren Grounds and a transient in the United States. (Cottam & Knappen 1939).

The curlews, the long-billed and hudsonian, are shore birds living on a very mixed diet of seeds, berries, crustaceans, molluscs, worms, spiders, and insects. All three species have long down-curving bills which may hinder them in catching active insects as is shown by the foods listed above. Thus the curlews are a group living in a dragonfly habitat but catching few of these.

Bartramian Sandpiper, Upland Plover, *Bartramia longicauda* (Bechstein): 200 stomachs examined, 1 of which contained an adult dragonfly. It is a sandpiper-like bird which lives in the uplands with plover habits. It feeds on grasshoppers, locusts, crickets, white grubs, and cutworms, slow insects.

Solitary Sandpiper, *Tringa solitaria* Wilson: 7 stomachs examined, 1 containing 2 nymphs. Wetmore (1916) reports two stomachs of birds taken in Puerto Rico the contents of which were nearly one-half dragonfly nymphs. A bird of woods pools, Barrows (1912). This remarkable bird needs study. It nests in woodland birds' abandoned nests. It catches insects on the wing and can stand on one leg while it stirs up aquatic insects waving its free foot in the water. With only 7 records the number of nymphs is startling. (Forbush & May 1939).

Willet, *Catoptrophorus semipalmatus* (Gmelin): 230 stomachs examined, 16 with dragonflies of which 6 contained adults, 1 with 3 and 1 with 14. Of the stomachs with nymphs 2 had 2 each, one 14 and one 18. This is a shore bird of sandpiper habits eating crustaceans, molluscs, marsh and aquatic insects, and a few small fish. As it is a bird of sea beaches as well as of fresh waters those collected on sea beaches would have had few Odonata. (Forbush & May 1939).

Greater Yellow-legs, *Totanus melanoleucus* (Gmelin): 702 stomachs examined, 153 with Odonata, only 27 of which were adults, mostly 1 each, but 1 stomach contained 39 and another 31 adults, while many stomachs (37) contained from 4 to 110 nymphs each. Eight stomachs had each over 30 nymphs. This bird is a giant sandpiper and its food contains amphipods, top minnows, swimming insects, and worms. See the next for comment. (Allen, G. M. 1925; Danforth 1926).

Lesser Yellow-legs, *Totanus flavipes* (Gmelin): 760 stomachs examined, 123 with dragonflies, 43 of which were adults. Four stomachs had 2 and two had 3 adults each. Sixteen stomachs had 2 nymphs each, five had 3 each, five 4 each, five 5 each, five 6 each, one 8, one 10, two 11, one 12, one 14, one 15, one 18, one 26, one 60 and one 120 nymphs, the last item all Zygoptera. Twenty-seven of the stomachs contained anisopterous nymphs. This species again has sandpiper habits and eats many fish and aquatic insects.

The two species of yellow-legs are surprises in the large number of dragonflies eaten by them. These are mostly nymphs with large numbers in many of the stomachs. Of adults the lesser yellow-legs appears to take more than twice as many as the greater. Roughly about 20% of the food of each species consists of dragonflies. Obviously they are in a different class from that of the other sandpipers. Their greater size may account for this. The sandpipers feed at the edge of the water where there are few dragonflies except when these emerge. Dragonflies seldom occur in the top six inches of the water and seldom fly in the six inches just above the water. The greater height of the yellow-legs may permit them to reach farther up in the air and deeper into the water. The greater number of adults taken by the lesser may indicate distinct food preferences. Doctor Edward S. Thomas, Curator of Natural History in the Ohio Archaeological Museum, an experienced student of birds, stated to the author that the

lesser is more active than the greater. (See Forbush & May 1939 for habits; Bent 1927; Allen, G. M. 1925; Howell 1924).

Knot, *Calidris canutus rufus* (Wilson): 215 stomachs examined, 2 with adult Anisoptera. With the Knot we come into a group of snipe and sandpipers with shorter and heavier bills, that apparently take adult dragonflies as easily as nymphs. The preceding long-billed species caught more nymphs than adults.

Pectorial Sandpiper, *Pisobia melanotos* (Vieillot): 104 stomachs examined, 3 stomachs with Odonata, each of which contained 3 adults. Food, various insects, worms, molluscs, and plants.

Baird's Sandpiper, *Pisobia bairdi* (Coues): 45 stomachs examined, 7 contained Odonata, only one stomach containing a nymph, while another contained 5 adults. Food consisting of seeds of marsh plants mixed with marsh insects.

Dowitcher, Red-breasted Snipe, *Limnodromus griseus griseus* (Gmelin): 200 stomachs examined, 89 with Odonata, 4 of which were adults and one stomach contained 3 adults. Two stomachs contained 3 nymphs each and one had 2. The dowitcher takes more aquatic plant seeds than usual among snipes and besides insects takes molluscs, small fishes, and crustaceans (Spawn 1942).

Long-billed Dowitcher, *Limnodromus griseus scolopaceus* (Say): 90 stomachs examined, 6 with dragonfly larvae. The general food of this species is similar to that of the dowitcher.

Stilt Sandpiper, *Micropalama himantopus* (Bonaparte): 15 stomachs examined, 3 with odonate nymphs. Its food contained many aquatic insects.

Marbled Godwit, *Limosa fedoa* (L.): 90 stomachs examined, 1 with an adult dragonfly. Food more aquatic than the preceding, crustaceans, aquatic insects, worms, leeches, snails, and some vegetable food.

FAMILY RECURVIROSTRIDAE (avocets and stilts)

These rather large, slender, snipe-like birds have long needlelike bills which in the avocets curve up very decidedly, less so in the stilts. In spite of the peculiar bill they catch many aquatic insects, including dragonfly nymphs and even small fish. In walking and wading with their long stilt-like legs they appear slow and awkward but in the use of sight and in the use of neck and bill they appear from food records to be able to take active prey swimming in or on the surface of the water. (Bent 1927; Forbush 1925; Henderson 1927; Wetmore 1925).

American Avocet, *Recurvitostra americana* (Gmelin): 55 stomachs examined, 3 containing dragonfly nymphs, one stomach with 3 nymphs. The American Avocet is a bird of the shores of inland waters where it feeds by moving its long, needle-shaped bill about over the bottom so that it finds much of its food by the sense of touch. This habit of feeding accounts for nymphs.

Black-necked Stilt, *Himantopus mexicanus* (Müller): 70 stomachs examined, 9 with dragonfly nymphs, one stomach containing 3. The food of this species includes crayfish, Coricidae, caddisfly larvae, small fish and some land insects such as grasshoppers. As observed by the writer on the marshes of the Yakima Valley, Wash., it is a slow, awkward bird and may be too slow to take adult Odonata easily. Another factor may enter but one on which we took no observations. On the mud shores a black-necked stilt is so tall and conspicuous adult dragonflies may recognize any slight movement and avoid capture. Among other shore birds this stilt is startlingly conspicuous to the human observer.

FAMILY PHALAROPODIDAE (phalaropes)

This is a family of curious birds intermediate in leg and foot structure between the rails and the snipes. They look like snipes, some have lobed feet like rails and they swim like ducks. (Personal observations on Wilson's phalarope in the Baker Valley, Ore., marshes.) The female is more brightly colored than the male and the latter broods the eggs. They swim and wade in shallow open waters.

This is another family of birds of the general size that eat Odonata. They live in the midst of a dragonfly environment (except the red phalarope in winter) and feed on an animal diet including insects. Why do they not use more dragonflies? The odd red phalarope is pelagic in our area, being found off the coast in winter and apparently does not come to land except in storms. Its food is mainly crustaceans. (Bent 1927; Forbush 1925; Henderson 1927; Wetmore 1925).

Wilson's Phalarope, *Steganopus tricolor* Vieillot: 105 stomachs examined, one with a dragonfly larva. This phalarope feeds on aquatic and terrestrial insects, snails, etc.

Northern Phalarope, *Lobipes lobatus* (L.): 150 stomachs examined, 3 with adult Odonata. The food of this species consists of aquatic worms, crustacea, insects, with a few seeds of marsh sedges.

FAMILY LARIDAE (gulls and terns)

The gulls in general are scavengers and feeders on small animals both land and marine, including the larger insects such as Orthoptera and Odonata. In this problem too little is known about the food fed to nestlings. The evidence cited in this article is mostly from adult stomachs. See Franklin Gull below where dragonflies (larvae) are fed the young. The terns tend to eat small, live fishes more often than do the gulls, perhaps because of greater agility on the wing. The eyes in this family have good monocular vision, a nasal fovea, but only gull eyes were studied by Wood (1917). The ability of the terns to strike fish from the air as a falcon strikes suggests better vision than that in the scavenger gulls.

The gulls and terns are marine birds usually nesting on the ground or on floating vegetation in marshes. They nest in colonies and have young that mature slowly so that colonies survive only on inviolate nesting sites. Thus the nesting site, the swallow-like ability on the wing and

a taste for large insects set the limits on their use of dragonflies as food. The nesting site appears to be the main limit as the eggs and young have to be protected from ground vermin by water. The scavenger gulls appear to use dragonflies less often than the raptorial terns. (Bent 1921, 1947; Forbush 1925; Henderson 1927.)

Ring-billed Gull, *Larus delewarensis* Ord: 50 stomachs examined of which 4 contained adult Odonata. This species feeds much on insects, small rodents, etc., only 29 of the stomachs containing small fish.

Franklin's Gull, *Larus pipixcan* Wagler: 125 stomachs examined, 8 with remains of dragonflies. McAtee records one stomach with 327 odonate nymphs while Roberts records another stomach taken in the nesting season with 321 nymphs. Judd (1901) quotes Roberts (1900): "The parent birds were feeding their young by regurgitating into them the nymphs of dragonflies." This gull nests on the fresh-water ponds of southern central Canada, the Dakotas, and Minnesota and is almost wholly insectivorous being the most beneficial of the gulls. Its diet is largely insects of some size such as Orthoptera, caterpillars, aquatic bugs, grubs, etc., which it hunts over the dryer fields as well as over marshes. (Beal 1912b).

Common Tern, *Sterna hirundo hirundo* L.: 116 stomachs examined. Food, besides fish, moths 2%, other insects including Odonata, Orthoptera, ants, Coleoptera, etc., 1.5% (McAtee & Beal 1924).

Arctic Tern, *Sterna paradisaea* Brünnich: 45 stomachs examined, 5 containing dragonfly nymphs, 30 contained small fish, 8 had crustaceans but the bulk of the food is marsh and aquatic insects. This species breeds in inland waters as well as on the northern coasts.

Black Tern, *Chilidonias nigra surinamensis* (Gmelin): 280 stomachs examined, 42 contained adult dragonflies. This is the common species in the inland marshes of the northern states. Here it has the flight of a giant swallow and is almost wholly insectivorous. McAtee and Beal (1924) give dragonflies as 20% of its food, mayflies 13%; grasshoppers 12%, and small fishes 19%.

Two other terns nest on fresh-waters in the interior, the Caspian *Hydroprogne caspia imperator* (Coues) and the least tern *Sterna antillarum antillarum* (Lesson). Both are fish eaters. The six or more other species in North America are marine birds.

FAMILY ALCIDAE (guillemots, auks, murres, puffins)

While we have listed the Alcidae among the sea birds that do not eat Odonata one record stands against one species. The group as a whole feed almost entirely on sea fishes and crustaceans. (Bent 1919).

Black Guillemot, *Cepphus grylle grylle* (L.): 15 stomachs examined, 1 with an adult dragonfly. This is a salt-water bird that feeds on small fish, isopods, amphipods, and marine worms. The dragonfly, probably a windblown individual, may have been picked up on a beach while the bird was searching for crustaceans and worms.

(Classed in the Order Charadriiformes with the Laridae are the families Stercorariidae (Jaegers) and Rynchopidae (Skimmers). These are strictly marine birds which do not normally enter a dragonfly habitat in fresh- or brackish-waters. Together with the preceding family, the Alcidae, we have classed these in our first division of birds, those which do not eat Odonata.)

This closes the series of water and shore birds in our fauna, a series which in many ways is primitive as bird evolution goes and which feed largely or wholly on animal matter (exception, the geese). As a whole they are more closely associated with the habitat of the aquatic Odonata, particularly the nymphs of dragonflies than are the next series of Orders, the more strictly land birds.

(There are no records of dragonflies taken by pigeons or doves, Order Columbiformes, all of which are fruit and seed eaters and which we have already classed with the series of families that do not eat Odonata.) (See Chard, 1937).

No records stand against the parrots, Order Psittaciformes, represented at one time by the now extinct Carolina and Louisiana paroquets. Perhaps we could include here the skeletons of the Mexican military macaw found in numbers near Flagstaff, Arizona about pueblo ruins on the Wupatki National Monument. ("Nat. Hist.," 1948, 57: 41.) Parrots in general are vegetarians, largely fruit eaters.

FAMILY CUCULIDAE (cuckoos, anis, road-runners)

The anis and road-runners, Order Cuculiformes, eat an extraordinarily diverse mixture of small animal life but there are no observations or records of their having used dragonflies as food. The road-runners are usually found in very dry habitats where Odonata seldom occur. The anis are lowland birds of pastures and farming areas where they frequently follow cattle as do cow-birds. They occur on the southern edge of our area.

Both northern cuckoos are shy birds that remain much of the time in the foliage of trees though the nest is often low. Dragonflies prefer the surface of lower vegetation-stands and open places. No data has been found on Maynard's cuckoo of the mangrove swamps of the southern tip of Florida. (Beal & Judd 1898; Bent 1940; Forbush 1927; Henderson 1927).

Yellow-billed Cuckoo, *Coccyzus americanus americanus* (L.): 340 stomachs examined, 10 of which contained adult dragonflies, 1 stomach containing 2 and another 8. From the last record we may infer that they catch Odonata if plentiful and easily taken, but otherwise usually feed on arboreal insects. Both the yellow-billed and black-billed cuckoos are birds of the dense tree tops where dragonflies seldom occur. (Beal, McAtee & Kalmbach 1941).

Black-billed Cuckoo, *Coccyzus erythropthalmus* (Wilson): 160 stomachs examined, 8 of which contained adult dragonflies. Both cuckoos are almost wholly insectivorous. The black-billed cuckoo hunts over low, wet areas more often than does the yellow-

billed (Forbush & May 1939) which is an arboreal bird. The scant data indicates about twice as many dragonflies are eaten by the black-billed.

The next, the Order Strigiformes, contains the owls which in general are nocturnal. However, not all owls are wholly nocturnal and not all Odonata are wholly diurnal. Thus, as far as flight time is concerned, some species from each group can contact species of the other group. The majority of owls are of the order of size of birds that catch Odonata and all are flesh eaters.

FAMILY TYTONIDAE (barn owls)

The Family Tytonidae, or barn owls, of which we have one species *Tyto alba paratincola* (Bonaparte) in our area, apparently never eat dragonflies. A great amount of data has been obtained on the food of this owl by the collection about nests and roosting places of the pellets of indigestible parts that are regurgitated. The student of bird-foods collects and analyzes these. This applies also to the next family, the horned owls. The barn owl lives almost exclusively on small mammals. (See Lantz 1906; Fisher 1896.) It is the most highly specialized of our native owls in that it is the most deeply nocturnal of owls. This latter character puts its activities so far into the night that it must seldom come into contact with even those species of Odonata (Aeshninae spp.) that tend to be crepuscular. Its lack of interest in insects as food in general also separates it from the dragonfly complex. (Bent 1938; Forbush 1927; Henderson 1927.)

FAMILY STRIGIDAE (horned owls)

Of the fifty-six varieties of owls in our region only two have records of having eaten dragonflies. In general dragonflies are very diurnal, flying usually only in direct sunshine. Owls are generally nocturnal though various forms hunt on dark days, in twilight, etc. The records are of the less specialized family, the Strigidae, many of which can hunt in intermediate light. The owls appear to take dragonflies less often than do hawks of the same order of size. The larger owls use mice as a large part of their diet. (Bent 1938; Forbush 1927; Henderson 1927).

Screech Owl, *Otus asio naevius* (Gmelin): 440 stomachs examined, 3 contained adult dragonflies. The screech owl in its ten or so forms uses a great variety of food including small mammals, birds, reptiles, crustaceans, and insects. (Allen, A. A. 1924; Clabaugh 1926; Lantz 1906).

Pigmy Owl, *Glaucidium gnoma* Wagl.: 50 stomachs examined, 1 contained an adult *Aeshna palmata* Hagen. This is a diurnal owl that lives largely on insects but can eat small birds. It is a woods owl and thus misses most of the dragonflies except such as *Aeshna palmata* that frequently flies in beats in open glades of woods bordering on streams. The six subspecies of pigmy owl listed in the A. O. U. Check List are lumped in this instance. (Johnson 1903).

The Order Caprimulgiformes (Goatsuckers) in our area contains 17 named forms, including the chuck-will's widow, whip-poor-wills, one pauraque (lower Rio Grande), and nine subspecies of nighthawks. Only three of the goatsuckers (Caprimulgidae) have dragonflies charged aaginst them.

FAMILY CAPRIMULGIDAE (goatsuckers)

The goatsuckers are nocturnal birds but all will fly on cloudy days. The nighthawk has the habit of flying before and after summer storms, and has the swallow habit of flying over water which may account for the dragonflies in its food. The nighthawk has taken to nesting in cities on high tar-gravel roofs from where it flies widely over wooded suburbs. All records are for adult dragonflies.

The goatsuckers are large flying insect traps. Because of their large size they take larger insects than do the swallows; further, they are crepuscular and nocturnal when more large insects fly to greater heights than do insects generally in daylight hours. The crepuscular nighthawks which fly in the dusk before storms and at twilight take many flying ants, many species of which swarm on sultry evenings.

The food listed against various species suggests that some, at least, feed on the ground. The whip-poor-wills regularly patrol bare knolls in their breeding areas as can be told from their night calls from such areas. In general their contacts with dragonflies are with those normally diurnal species which also tend to fly into the twilight. (Bent 1940; Forbush 1927; Henderson 1927).

Chuck-will's-Widow, *Antrostomus carolinensis* (Gmelin): 40 stomachs examined, 4 contained adult dragonflies, 1 being the very large *Epiaeschna heros* (Fabr.) which frequently flies into the dusk as do several species of Aeshninae. This is the largest of the North American goatsuckers and occasionally eats small birds though usually taking large insects on the wing, such as moths and night-flying beetles. (Beal, McAtee & Kalmbach 1941; Bowdish 1902, 1903).

Nighthawk, *Chordeiles minor minor* (Forster): 315 stomachs examined, 22 containing adult dragonflies. One contained 13 individuals of the rare *Ischnura prognata* Hagen, a zygopter. Fourteen stomachs contained other Zygoptera and 8 contained Anisoptera. (Beal 1903).

Texas Nighthawk, *Chordeiles acutipennis texensis* Lawrence: 20 stomachs examined, 1 contained an adult dragonfly. The food of this species consists of miscellaneous flying insects, especially beetles and moths. (No published records of *texensis*).

The Order Micropodiiformes (the small footed birds) includes the swifts and hummingbirds.

With the possible exception of some hummingbirds such as our very nectarofagous ruby-throated hummingbird, *Archilochus colubris* (L.), both swifts and hummingbirds are insectivorous, the swifts scooping insects during a steady winging flight, the hummingbirds operating from high perches more as do flycatchers. The swifts are of an order of size large

enough to take small dragonflies. The hummingbirds are generally so small that they normally use much smaller insects.

FAMILY MICROPODIDAE (swifts)

Only one swift is abundant enough that a series of stomachs has been collected. Probably all four swifts in our area take small Odonata at times though the black swift *Nephoecetes niger borealis* (Kennerly) and the white-throated swift *Aeronautes saxatalis saxatalis* (Woodhouse) nest and fly at such great elevations that they may seldom contact Odonata. The swifts, again, are flying insect traps but normally use insects smaller than the smallest Odonata. (Bent 1940; Forbush 1927; Henderson 1927).

Chimney Swift, *Chaetura pelagica* (L.): 150 stomachs examined, 7 with adult Odonata, 2 of which were Anisoptera and 5 Zygoptera. This bird is wholly insectivorous and the records show that it sometimes takes insects as large as locusts.

(The Hummingbirds, Family Trochilidae, are largely insectivorous though they feed on nectar in season but are so diminutive that they do not take insects much larger than gnats and minute parasitic Hymenoptera. Apparently the species of this family are below the size necessary to take Odonata easily.) (Bent 1940; Forbush 1927; Henderson 1927; Lucas 1893).

(The American Trogons, Family Trogonidae, Order Trogonoformes, of which one species extends into southern Arizona, live on fruits and insects including large forms such as grasshoppers.) (Henderson 1927, p. 208).

The Order Coraciiformes is largely a tropical group which includes the many kingfishers, motmots, rollers, bee-eaters and hornbills. Only the belted kingfisher interests us.

FAMILY ALCEDINIDAE (kingfishers)

This very specialized family is represented in our area by the eastern and western forms of the belted kingfisher, and casually on the Mexican border by two tropical species. The belted kingfisher is a noisy, frank but interesting land bird which, while it swims little manages to live comfortably off of swimming fish and other moving aquatic animals. (Bent 1940; Bowdish 1902-1903; Forbush 1927; Henderson 1927).

Belted Kingfisher, *Megaceryle alcyon alcyon* (L.): 330 stomachs examined, 33 with dragonfly nymphs, 1 to a stomach except 2 that contained 2 nymphs each. The food of the kingfisher is mainly live fish but it contains also 16% crayfish, 4% batrachians, and 3% insects. It takes only moving, swimming animals. By food habits the kingfisher is a diving water-fowl. (See Part III. Taxonomy of kingfisher.)

The Order Piciformes includes the woodpeckers, toucans, jacamars and barbets, the latter three tropical. This in structure and habits is one of the most highly specialized groups of birds.

FAMILY PICIDAE (woodpeckers)

The 1931 A. O. U. Check List records sixty species and subspecies in our area. Only three forms have Biological Survey records showing the use of dragonflies as food. Woodpeckers live on insects, fruits and seeds but have such highly specialized habits in feeding either on the trunks of trees or on the ground that they seldom encounter Odonata. (Beal 1911; Bent 1939; Forbush 1927; Gardner 1927; Henderson 1927; Lucas 1895).

Northern Flicker, *Colaptes auratus luteus* Bangs: 700 stomachs examined, 2 contained adult dragonflies. This species feeds frequently in open fields on the ground on the larger field species of ants where it could easily pick up wind-blown dragonflies or those strayed away from neighboring streams and slowed down by cool weather. (Knowlton & Stains 1943).

Yellow-bellied Sapsucker, *Sphyrapicus varius varius* (L.): 325 stomachs examined, 2 contained adult dragonflies.

This species cuts rows of holes into the bark of thin-barked trees. It eats the cambium (10% to 20% of stomach contents) brushes out the sweet sap with its short hair-tipped tongue (Lucas 1895), and catches the insects attracted to these traps baited with sap. This damage to valuable trees, mainly orchards, has been estimated at over one million dollars annually. (Beal 1913). This very specialized habit of feeding keeps its attention applied largely to areas free of dragonflies. However, birch trees which usually grow near water are attacked by it. The dragonflies taken were probably chilled and roosting on tree trunks in cool weather. Because of this "sap-sucking" habit the yellow-bellied sapsucker has had more than its share of persecution by orchardists and an unusual amount of scientific publicity.

Downy Woodpecker, *Dryobates pubescens medianus* (Swainson): 750 stomachs examined, 1 with an adult dragonfly. In the genus Dryobates the tongue is long and is used in probing insect galleries in tree trunks for wood boring larvae. A dragonfly would be the accidental take of one chilled and resting on a tree trunk. This woodpecker and related innocent species have been carefully checked along with the sapsuckers in Biological Survey studies hence the number of published studies.

THE PASSERIFORMES

With the Order Passeriformes or perching birds we complete this study. Ornithologists place this as the highest and latest order in evolution of bird life. They are fartherest in structure and habits from ancestral dinosaur types. (See remarks under Order Falconiformes on the evolutionary position of the hawks, eagles and falcons, and the remarks on the primitive habits of the kingfisher under Part III.) Apparently birds evolved from aquatic or semi-aquatic dinosaurs that inhabited the sea shore and the Mesozoic lakes and streams. The land birds appear to have arisen in a dragonfly environment and then in later evolution to have evolved out of such an environment onto higher and drier land.

The perching birds in general are land and tree forms. Usually they are highly insectivorous. Some are almost wholly so and nearly all raise their young

on an insect diet, even to those forms that are seed and fruit feeders as adults.

No bird-food study made so far indicates that any species of insectivorous perching bird lives exclusively on any one kind of insect, even any one order of insects. The insectivorous forms take all insects up to the largest usable size, in the case of the larger bird species all sizes down to those too minute for the size of the bird. Thus they eat adult dragonflies, if such stray into higher ground and whenever the bird lives over or near the water. A few stream-bank scavengers get dragonfly nymphs as these crawl from the water to emerge. The insect-egg-eating birds occur in this order, the small twig and tree-trunk searchers such as nuthatches, creepers, titmice, warblers, vireos, etc. Dragonfly eggs are not taken by these egg-eaters because dragonfly eggs are either dropped into the water or are placed with the use of an ovipositor beneath protective surfaces.

FAMILY TYRANNIDAE (tyrant flycatchers)

Seventeen of the thirty-five forms of tyrant flycatchers found north of Mexico are recorded as taking dragonflies occasionally. Only three or four take them with any regularity. This is in spite of the fact that many of the species of this family have the habit of nesting near water and all are very insectivorous. Their food in general shows that they prefer Hymenoptera and Diptera with some of the smaller Coleoptera and Hemipteroidea. Some of the tropical Tyrannidae as told the author by E. B. Williamson, deceased, formerly banker of Bluffton, Indiana, and Col. F. C. Fraser, I.M.S., Bournemouth, England, both experienced dragonfly collectors in tropical lands, are much more specifically dragonfly eaters. (Beal 1912a; Bent 1942; Forbush 1927; Henderson 1927).

Eastern Kingbird, *Tyrannus tyrannus* (L.): 700 stomachs examined, 39 with adult dragonflies. Those identified are the small anisopter, *Leucorrhinia intacta* (Hagen) and the zygopters, *Agrion* sp. and *Argia* sp. Food, 10% fruit, 90% insects, over half of which are Coleoptera and Hymenoptera. In the western United States the kingbird nests in trees along streams and probably there catches more Odonata. Because of the reputation of the kingbird for catching honey bees it has been studied extensively by the Biological Survey. Its other common name is bee bird. The Biological Survey publications up to 1911 on the food of the kingbird are listed by McAtee 1913. (Knappen 1933).

Arkansas Kingbird, *Tyrannus verticalis* Say: 145 stomachs examined, 3 with adult dragonflies. This is a western desert bird nesting in the forks of large trees along streams but since man's arrival it nests on telephone poles, hay derricks, etc., miles from original streams. (Beal 1912).

Cassin's Kingbird, *Tyrannus vociferans* Swainson: 45 stomachs examined, one with an adult dragonfly. (Beal 1910).

Scissor-tailed Flycatcher, *Muscivora forficata* (Gmelin): 130 stomachs examined, one only with an adult dragonfly. This is a bird of the open southwestern prairies and mesquite plains where dragonflies are few in number, Orthoptera constitutes 46% of its food. (Beal, McAtee & Kalmbach 1941).

Northern Crested Flycatcher, *Myiarchus crinitus boreus* Bangs: 265 stomachs examined, 23 with adult Odonata. Mr. E. B. Williamson reported by letter to the writer that this species is one of the worst offenders in its catching of Odonata.

The northern crested flycatcher has a record of one stomach out of ten with dragonflies. But E. B. Williamson, dragonfly specialist, watched a pair with a nest in a hole of a tree on the banks of the Wabash River, three blocks from his home at Bluffton, Indiana. Before they built the nest large Macromia dragonflies were abundant on that stretch of the Wabash. In three or four years the Macromias became rare. The flycatchers caught them persistently. He attributed the scarcity of Macromias to the one pair of northern crested flycatchers. This specialized taste does not show in the Biological Survey records. The crested flycatcher nests widely. As a boy we found a nest with its characteristic snake skin in a hollow black walnut, where probably few Odonata ever occurred one mile from the nearest water.

Collectors of dragonflies in the tropics report species of Tyrannidae that at least individually are persistent catchers of dragonflies. These observations made by experienced field men do not agree with stomach records based on long series of stomachs of any one species. Several cases appear in the records where one stomach is gorged with dragonflies while the others of the same species of bird may have one or a few or more. We believe that individual birds develop a taste for one type of prey and may individually become addicts to that one kind of insect. Wolves and other mammalian carnivora are known to become individual specialists on special prey. We even observe special tastes developed around the breakfast table at home.

Ash-throated Flycatcher, *Myiarchus cinerascens* (Lawrence): 90 stomachs examined, 6 with adult dragonflies. This is a desert bird that frequently breeds several miles away from water.

Eastern Phoebe, *Sayornis phoebe* (Latham): 365 stomachs examined, 11 with adult dragonflies. Three of these contained Zygoptera while 8 contained Anisoptera, one stomach having the remains of 12 of the latter. For an insectivorous bird of its size and with the habit of nesting over water, the Phoebe catches relatively few dragonflies. It is well classed as a fly (Diptera) catcher.

Black Phoebe, *Sayornis nigricans nigricans* (Swainson): 340 stomachs examined, 67 with adult dragonflies. This species uses more mud in the construction of its nest than do the preceding, the nests of which are largely of moss, trash, feathers, etc. As this is a bird of the dry southwest its nest material may indicate that it is more closely associated with streams even than the preceding which may account for the fact that it eats 3-5 times as many dragonflies as either of the others. The stomach contents show

that the Black Phoebe is "one of the most exclusively insectivorous of the family" of tyrant flycatchers.

Say's Phoebe, *Sayornis saya saya* (Bonaparte): 130 stomachs examined, 7 with adult dragonflies. This is a bird of the western plains and mountains but has the same habit as the Eastern Phoebe of nesting near water.

Yellow-bellied Flycatcher, *Empidonax flaviventris* (Baird and Baird): 105 stomachs examined, 2 with adult dragonflies. This is a bird of bogs and woods swamps living in a dragonfly environment but using comparatively few as food.

Alder Flycatcher, *Empidonax trailli trailli* (Audubon): 155 stomachs examined, 9 with adult dragonflies. This is a northern bird nesting near water and is small in size. This is distinctly a stream loving bird but prefers Hymenoptera and other small insects.

Least Flycatcher, *Empidonax minimus* (Baird & Baird): 170 stomachs examined, 4 with adult dragonflies. This is the smallest of the flycatchers of our area except the buff-breasted flycatcher of northwestern Mexico. It is smaller than a chipping sparrow and is one of the smallest birds that eats dragonflies, comparing in size with the smaller swallows, the wrens and the warblers.

Wright's Flycatcher, *Empidonax wrighti* Baird: 20 stomachs examined, one with an adult dragonfly. This is a bird of the Great Basin desert and is usually found near streams. (No published data.)

Western Flycatcher, *Empixonax difficilis difficilis* Baird: 162 stomachs examined, one only with one adult dragonfly. This is a western bird of the small size of the wood pewee and nests near water. Obviously it prefers other insects than Odonata. The records show about 40% Hymenoptera and 30% Diptera.

Eastern Wood Pewee, *Myiochanes virens* (L.): 365 stomachs examined, 14 with adult Odonata, one stomach containing 5. This is a bird of the open glades of the eastern deciduous forest. According to Forbush (1927) the wood pewee has been known to catch small trout from hatchery ponds.

Western Wood Pewee, *Myiochanes richardsoni richardsoni* (Swainson): 165 stomachs examined, 19 with adult dragonflies. Deciduous woods are preferred by flycatchers. In the West these tend to be along streams which may account for the western wood pewee's large take of Odonata.

Olive-sided Flycatcher, *Nuttalornis mesoleucus* (Lichenstein): 60 stomachs examined, 6 with adult dragonflies: a bird of the northern coniferous forest, a tree-top bird when feeding.

(We pass over the larks, Alaudidae, the skylark which has been introduced, and the sixteen subspecies of the native *Otocoris alpestris* (L.) or horned lark. These are birds of high dry areas that nest on the ground and feed on the dry ground. Either habit is seldom associated with catching dragonflies when it is found in other birds. There are no records against them.)

FAMILY HIRUNDINIDAE (swallows, martins)

The swallows have been investigated extensively by the Biological Survey perhaps partly because they are so obviously beneficial in their food habits and thus made good evidence for the protection of the smaller birds, partly perhaps because around barns the barn swallow at times litters well-kept premises with unsightly nests.

Swallows tend to fly over or near water, live on insects exclusively and are large enough to take the smaller dragonflies. However, the evidence from stomach examination suggests that they are on the borderline in size. The smaller swallows do not take dragonflies as regularly as do the larger martins which appear to be among the outstanding eaters of small Odonata. The martin boxes of the country-home are more often regularly successful in attracting nesting pairs where there is a considerable stream or body of water near.

The evidence is that the martins are enemies of dragonflies. Apparently they hunt for them. Perhaps the larger size of the martins as compared with the other swallows gives them an advantage over the smaller swallows in taking insects as large as dragonflies. What the limits are that protect dragonflies by keeping the populations of martins low is difficult to say, but social animals are usually preyed upon heavily by disease, parasites and predators. Further, the highly specialized nesting sites of the martins, while protecting them from predators, limit the population of martins by the scarcity of nesting sites. (Beal 1918; Bent 1942; Forbush 1929; Henderson 1927).

Tree Swallow, *Iridoprocne bicolor* (Vieillot): 330 stomachs examined, 32 with adult Odonata. The tree swallow is most abundant along the Atlantic coast and usually nests near water. Barrows (1912, p. 550) records it catching early spring stoneflies with the temperature 2-3 degrees above freezing.

Bank Swallow, *Riparia riparia riparia* (L.): 415 stomachs examined, 33 with adult dragonflies. This is the sand swallow of Europe with habits identical with those of this American group. From the records, the bank swallow appears to catch Odonata twice as often as does the rough-winged swallow. The bank swallow, before the advent of railroad engineers with their cliff-producing cuts, found its clay-bank nesting sites almost entirely in banks over or near water and it still flies almost entirely over or near water. On the other hand, the rough-winged swallow seldom makes its own holes but nests in any crevice or cranny that is convenient and so probably does not feed as often over water. See notes on the martin.

Rough-winged Swallow, *Stelgidopteryx ruficollis serripennis* (Audubon): 135 stomachs examined, 4 with Odonata. This species nests in vertical banks in any convenient hole.

Barn Swallow, *Hirundo erythrogaster* Boddaert: 467 stomachs examined, 35 with adult dragonflies. As with the cliff swallow this bird has adapted its

nesting to the structures of man but it appears to take dragonflies oftener than does the cliff swallow.

Northern Cliff Swallow, *Petrochelidon albifrons albifrons* (Rafinesque): 380 stomachs examined, 12 with adult dragonflies. Before the advent of white man this swallow built its mud jugs under overhanging cliffs and banks. In the eastern states it has adapted itself to the protection of overhanging eaves though in the western states it still uses cliffs. This change in the east has taken it away from streams. Its food is mainly insects of which small beetles are the largest item.

Purple Martin, *Progne subis subis* (L.): 210 stomachs examined, 65 with adult dragonflies. From these records the purple martin eats twice as many dragonflies as does any other species of the swallow family. Beal (1918) says of them, "dragonflies appear to be a favorite food of the martin. They were eaten every month except February and were contained in 65 stomachs, of which 7 held nothing else. Many were of the larger species, seemingly rather large morsels for the bird." The total for the season is 15.1% of the food, a percentage unusually large for Odonata and indicating that the martin hunts especially for them. The bank swallow is the only other species that eats enough dragonflies to warrant a separate record. Aquatic in their larval stage, dragonflies naturally stay about water or wet places, and as martins are likely to nest at a distance from water, to get them the birds must go to the haunts of the insects. Doolittle (1919) observed fifteen pairs of Martins feeding their young for some time entirely on dragonflies. (Widmann 1884).

Cuban Martin, *Progne cryptoleuca* Baird: 3 stomachs examined, each with one dragonfly. (No published records of food of Cuban martin found.)

Caribbean Martin, *Progne dominicensis* (Gmelin): Wetmore (1916) on the basis of 12 stomachs taken in Puerto Rico found 8.09% of the food to be dragonflies.

FAMILY CORVIDAE (crows, ravens, magpies, jays, nutcrackers, pinon jays.)

This family contains the brains of our North American bird fauna. The brain is so large that the skin has to be split up the neck to clean the head in making a skin of any of the species. After having watched American Magpies and the California Jay operate in accomplishing a fat living in a semidesert country one has great respect for their intelligence. Crows and blue jays are also almost as wise. Instances of behavior can be cited that suggest the presence of a very playful instinct and a sense of humor.

However, all the species tend to be rovers. They are on the hunt for the occasional bountiful dinner, whether fruit, grain, flesh of larger animals or insects. This roving habit brings Odonata into their diet only casually. In general the birds that prey most on dragonflies are those that remain closely associated with a dragonfly environment.

Because the crows, magpies and some of the jays are at times more harmful to farmers and fruit growers than they are beneficial, several of the species have been extensively studied by the Biological Survey and other agencies. The literature on such is extensive. (McAtee 1913).

There are no Biological Survey records of dragonflies taken by the white-necked raven, *Corvus cryptoleucus* Couch, of the southwestern states, of the Clarke nutcracker, *Nucifraga columbiana* (Wilson) nor of the pinon jay, *Cyanocephalus cyanocephalus* (Wied.). However, few stomachs of these have been taken. (Bent 1946; Bull. 141; Forbush 1927; Henderson 1927; Kalmbach 1927).

Northern Blue Jay, *Cyanocitta cristata cristata* (L.): 680 stomachs examined, 5 with adult dragonflies, one with a nymph. The blue jay is a bird of the woods, a heavy eater of acorns, beech nuts, and other large seeds, and thus does not often contact dragonflies.

The fifteen or so other northern and western true jays are also birds of the woods where dragonflies are seldom met with. Probably any jay would eat a dragonfly if the two met. In general the jays use smaller foods but have the omnivorous habits of the magpies and crows.

American Magpie, *Pica pica hudsonia* (Sabine): 560 stomachs examined, 18 with remains of Odonata, 7 of these containing anisopterous adults, one with 2 and another with 3 while 2 contained zygopterous adults. Six stomachs contained nymphs, one with 100 anisopterous nymphs and another with 35 zygopterous nymphs. From the large numbers found in some of the stomachs the magpie must make it a point to eat as many as are available when they are found. They are not picked up accidentally as with many birds.

The magpie has the crow habit of cruising about over an enormous area but usually in pairs or family flocks. When it does find food in its wanderings it stops and cleans up the local supply and returns on the next day to check. It is omnivorous but eats many insects in season. (Kalmbach 1927)

Yellow-billed Magpie, *Pica nuttalli* (Audubon): 25 stomachs examined, 3 with adult Anisoptera but one of these contained 12 and another 13 dragonflies. This is a bird of the Californian foothills of the Sierra where it nests along streams and uses the inner bark of cottonwoods as a feature of its nest. It may have the western robin habit of hanging about water and catching dragonflies as they emerge in numbers. (Kalmbach 1927).

American Raven, *Corvus corax sinuatus* Wagler: 20 stomachs examined, 2 with Odonata, one with an anisopter the other with a zygopter. The raven is a carrion eater feeding more often on dead fish than anything else but eats any kind of animal food. It is too large and slow to catch many really active Odonata.

American Crow, *Corvus brachyrhynchos* Brehm: Over 2,000 stomachs examined, only 19 of which contained Odonata. Four contained adult Anisoptera, 5 contained adult Zygoptera, one with 5 individuals

and another with 16. Seven contained anisopterous nymphs, one stomach containing 40. Evidently crows eat dragonflies freely when they are easily taken but are too slow and large to get many adults. (Gardner 1926; Hering 1936; Kalmbach 1940).

Fish Crow, *Corvus ossifragus* Couch: One observation by Miss Phoebe Knappen (1933) of the Biological Survey. The fish crows were eating dead Odonata on the beach. It is a bird of the coasts of the southeastern states.

FAMILY PARIDAE (titmice, chickadees)

In our area the species of this family tend to be winter visitants as the majority of the forms breed from the northern tier of states north or in the west on the crests of the higher mountains. They search the trunks, limbs and twigs of trees for small insects. When dragonflies are found on trees they are either on the outer leaves in the sunshine or are chilled or sleeping on the trunk.

The food of the Paridae is very much like that of the nuthatches, if anything, containing more vegetable matter in the form of buds and seeds. The feeding habits are similar except that the Paridae usually search small branches as well as trunks. The taking of Odonata is purely accidental. (Bent 1946; Forbush 1929; Henderson 1927).

Black-capped Chickadee, *Penthestes atricapillus atricapillus* (L.): 660 stomachs examined, 2 with adult dragonflies.

The black-capped chickadee is the only species of the twenty or more forms of this family which has records of having eaten Odonata.

(The A. O. U. List next records three families, the nuthatches (Sittidae), the creepers (Certhiidae) and the Pacific Coast family, the wren-tits (Chamaeidae) none of which have any records of having used dragonflies for food. These are mostly small birds on the borderline of being smaller than the birds that may use dragonflies as food. The nuthatches and creepers are tree-trunk birds. Only rarely are dragonflies, and then in a chilled condition, found on tree trunks.)

FAMILY CINCLIDAE (dippers, water ouzels)

Dipper, Water Ouzel, *Cinclus mexicanus unicolor* Bonaparte: 60 stomachs examined, 1 with a dragonfly. This curious bird feeds on larvae of water insects, small fish, crayfish and on insects floating on the surface of the streams it inhabits.

One of the thrills of dragonfly hunting in the west was given by the ouzels or dippers on the mountain streams. These slate gray thrush-like birds were generally found in pairs in the shadowy gorges where, bobbing like sandpipers, they skipped from rock to rock or ran along the stream edge in their hunt for insects or other aquatic animals. They are said to have the remarkable ability of walking and swimming under the water. The writer has observed several pairs in the Coast Ranges of California but has not seen any so aquatic. The mossy nest was usually on a nearby wet cliff, or even under a water fall.

In western streams there are few dragonflies in the swifter parts preferred by ouzels and such as are found in such swift waters are cordulegasters, gomphines or aeshnines all of which are large even among the Anisoptera or larger dragonflies. The smaller dragonflies, Zygoptera, with the exception of some argias, are found in abundance on the lower, slower portions of the mountain streams which are not frequented by ouzels. The stomach examinations show that they feed on the larvae of Trichoptera, Neuroptera, Ephemerida and on small insects floating on the water. Thus, while they live in a dragonfly habitat of a kind, they are adapted by size to smaller insects than the usual large, swift dragonflies that live in this very special habitat. (Henderson 1927).

FAMILY TROGLODYTIDAE (wrens)

Records show that the wrens are almost wholly insectivorous in their food habits. They show also that these very nervous and active birds usually catch slow insects, Orthoptera, Coleoptera, Hemiptera, caterpillars, and ants. By other birds fast insects are more often taken on the wing so the wrens which seldom thus catch insects, capture only the slower forms. The dragonflies recorded may have been taken in early or late hours when chilled and settled on vegetation. Thus only seven of the twenty or more forms of wrens in our area have records of having taken dragonflies. Two of these are marsh birds nesting in emergent vegetation in the very midst of the greatest dragonfly population and though insectivorous one shows only 3% of stomachs with Odonata and the other 5%. The wren's habit of feeding while perched appears to be the explanation of the lack of dragonflies. (Beal, McAtee & Kalmbach 1941; Forbush 1929; Henderson 1927).

House Wren, *Troglodytes aedon* Vieillot: 390 stomachs examined; 1 with an adult dragonfly. See Henderson (1927) for many references to the obnoxious feeding and fighting habits of the house wren.

Eastern Winter Wren, *Nannus hiemalis hiemalis* (Vieillot): 230 stomachs examined, 3 with Odonata, one of which was a larva: a swamp thicket bird but probably too small to care for even many small Zygoptera. (Barrows 1912 pp. 675-677 for habits.)

Bewick's Wren, *Thryomanes bewicki bewicki* (Audubon): 250 stomachs examined, 2 with adult Odonata.

Carolina Wren, *Thryothorus ludovicianus ludovicianus* (Latham): 415 stomachs examined, 2 with adult dragonflies.

Long-billed Marsh Wren, *Telmatodytes palustris palustris* (Wilson): 415 stomachs examined, 13 with adult Odonata. Ground and tree insects mostly. (Knappen 1933, p. 452.)

Short-billed Marsh Wren, *Cistothorus stellaris* (Naumann): 100 stomachs examined, 5 with adult dragonflies. (Little published data on stomach contents: Howell 1924).

Common Rock Wren, *Salpinctes obsoletus obsoletus* (Say): 60 stomachs examined, 1 with an adult dragonfly. Knowlton and Harmston 1942 found 3

Odonata in 88 stomachs and give a detailed list of the very miscellaneous insects used by this bird.

FAMILY MIMIDAE (mockingbirds, catbird, thrashers)

Birds of this family are highly insectivorous eating the larger and slower forms of insects which they capture while the bird is on its feet. They are also very fond of berries and other small fruits, which constitute over 50% of their food. Dragonfly catches appear to be accidental and are probably sleeping or chilled specimens hanging under trees and bushes. The mocking bird is one of similar behavior in the southern states but is more a tree than a bush inhabitant. (Beal 1915b; Forbush 1929; Henderson 1927).

Mockingbird, *Mimus polyglottos polyglottos* (L): 500 stomachs examined, one with a dragonfly. (Knappen 1933).

Catbird, *Dumetella carolinensis* (L.): 690 stomachs examined, 9 with adult dragonflies, one stomach containing 12. The catbird is more of a bush bird than the mocking bird which may bring it more often in touch with dragonflies along bushy streams. (Gabrielson 1913).

Besides the eastern brown thrasher there are recognized nine western thrashers about the food of which less is known. See Kennedy (1911, 1912). While the thrashers are highly insectivorous they are birds of the thickets of high open land where they contact few dragonflies.

Brown Thrasher, *Toxostoma rufum* (L.): 660 stomachs examined, 2 with adult dragonflies: a bird of open forest on ridges as compared with the catbird in bushes frequently in lower areas. (Gabrielson 1912).

FAMILY TURDIDAE (solitaire, thrushes, robins, bluebirds)

The thrushes and robins are ground feeders except for some fruit taken at times. They catch a very mixed lot of ground animals including many larvae and worms of various kinds. Except for an occasional opportunity of taking dragonflies emerging, as cited below, they probably catch few insects of this order. Ordinarily dragonflies are accidental catches.

The blue bird appears to catch somewhat more active insects which may account for the greater number of Odonata. Also it feeds more often in low trees and bushes where dragonflies may be roosting in early morning. In February and March, 1895, it was nearly exterminated by a late cold spell but has recovered its numbers (Barrows 1912). As a boy the writer gathered dead bluebirds and chimney swifts in the family cow pasture in Spencer County, southwestern Indiana. (Beal 1915a; 1915b; 1915c; Forbush 1929; Henderson 1927).

American Robin, *Turdus migratorius* L.: 1230 stomachs examined, 5 with adult dragonflies. (Beal 1915a; Howell 1942; Jenks 1859).

The Western Robin (*Turdus migratorius propinquus* Ridgw.) at times as observed on Donner Lake, California, is a distinct enemy of dragonflies. On the shores of Donner Lake a flock of robins patrolled the beach and caught many emerging gomphine dragonflies of the species *Ophiogomphus morrisoni* Selys. They caught the tenerals as these crawled across the beach from the edge of the water where they had emerged from the larval skins. Apparently the robins were taking little else. (Kennedy 1917; A. C. Howell 1942).

Olive-backed Thrush, *Hylocichla ustulata swainsoni* (Tschudi): 403 stomachs examined, 2 with adult Odonata, one with a larva.

Gray-cheeked Thrush, *Hylocichla minima aliciae* (Baird): 111 stomachs examined, one with an adult dragonfly; as with other thrushes a ground feeder on insects and other invertebrates: breeds in northern Alaska and Canada.

Eastern Bluebird, *Sialia sialis sialis* (L.): 855 stomachs examined, 4 with adult dragonflies: a bird of orchards and open bushy areas. Any dragonflies eaten are strays. (Beal, McAtee & Kalmbach 1941; McAtee & Kalmbach 1927).

Townsend's Solitaire, *Myadestes townsendi* (Audubon): 41 stomachs examined, one with a dragonfly. This is a bird of the highest mountain ranges living at boreal elevations where few dragonflies occur on the cold snow-water streams. According to Florence Merriam Bailey (1902), they may breed in the high transition zone, even into the high mountains of northern Mexico, but in central California at 7,900 feet.

(We next come to the Sylviidae, true warblers, gnatcatchers and kinglets and the Motacillidae, wagtails and pipits, two native families which are in most species too small to be tempted by insects as large as dragonflies. Usually they are birds of the foliage and smaller branches of the tree tops. They are birds of north of the Canadian border during the breeding season for which reason their summer diet has not been studied by the Biological Survey.)

FAMILY BOMBYCILLIDAE (waxwings)

The waxwings are interesting because in the season between periods of rearing young they are very gregarious and may be viewed as being semi-social. During the breeding season they lead a more nearly family-life, each pair of parents with interest in its own nest. It is at this time when with more nearly solitary habits and the necessity of insect food for their young that dragonflies may enter the waxwings diet, incidental to the taking of any easily available insects. Social tendencies (such as occur in waxwings during the migratory and winter seasons) in birds which *do not live* on the water will tend to keep individual socii away from the water, will help hold them on the land areas with their fellow land-socii. Also the social season is the off season for dragonflies.

(There are no records of the bohemian waxwing (*Bombycilla garrula pallidiceps* Reichenow) having eaten dragonflies. It breeds from lower central Canada north and may take occasional Odonata when feeding its young. (Forbush 1929; Henderson 1927)).

Cedar Waxwing, *Bombycilla cedrorum* Vieillot: 225 stomachs examined, 3 with adult dragonflies. In this series of stomachs one contained a stonefly and 5 contained mayflies. This species is mainly an eater of wild fruits and in the winter an eater of frozen fruits but it feeds its nestlings on insects largely. (Beal 1902).

(The silky Flycatchers (Ptilogonatidae) are a family of one species in the valleys of southern California and Mexico. We found no record of their having eaten dragonflies.)

FAMILY LANIIDAE (shrikes)

It is interesting to compare the shrikes with the sparrow hawks, and other small falcons. The two groups are in the same order of size, the same order of density of population, the same geographic distribution, the same general taste for prey of the size of mice, grasshoppers and the larger dragonflies. The small hawks take a considerable number of large dragonflies. The shrikes take few. The hawks take Odonata when the latter are on the wing in open places where large dragonflies prefer to fly. The shrike more often is a hunter in the undergrowth and brush where dragonflies seldom occur. The northern shrike, *Lanius borealis borealis* Vieillot, nests far to the north and does not meet adult Odonata during its winters in the States. (Beal & Judd 1898; Forbush 1929; Henderson 1927).

White-rumped Shrike, *Lanius ludovicianus excubitorides* Swainson: 303 stomachs examined, 3 with adult dragonflies. This is a general feeder on small land animals, mice, small birds, lizards, insects, etc. From the records most of the insects eaten are conspicuous and large, such as crickets, locust, caterpillars and ground beetles. (Beal & McAtee 1922; Knowlton & Haimston 1944; Tate 1925.)

California Shrike, *Lanius ludovicianus gambeli* Ridgway, a western form of the white-rumped shrike, the Survey records for which are included in *excubitorides* in the above. It is noticeably associated in the field with the sparrow hawk (Beal 1907), yet in hunting over similar ground the sparrow hawk takes many more Odonata. (Bryant 1914b).

FAMILY STURNIDAE (starlings and mynahs)

Because of the success in the United States of the immigrant starling we would not expect it to be a feeder on dragonflies. Such are too scarce an item on nature's bounteous table for a successful mass population development. Stomach studies show that the starling had 2749 chances out of a total of 2750 of not getting noticed in this article. Having been born with the stainless steel spoon of success in its mouth it entered our list on that one chance in 2750. The one dragonfly recorded against it may be interpreted as evidence of the starling's great adaptability.

We need not fear the extermination or serious reduction of Odonata by successful immigrant birds. Such come from Eurasia where, because of the greater size of the continental area, bird-evolution is one geological age ahead of bird-evolution in North America. (See Taverner 1935 on shape of continents and bird evolution.) Such successful species are advanced evolutionary types. They are gregarious almost to a social life. They have a broad and catholic taste which gives access to a great variety of foods permitting them to live well on that which is most abundant locally. Dragonflies are too small an item to receive the attention of such a species. See remarks on the social factor under the waxwings and the martins.

Starling, *Sturnus vulgaris vulgaris* L.: 2,750 stomachs examined, one with one anisopterous adult. (Bready 1929; Judd 1931; Lindsey 1939; Kalmbach 1931).

FAMILY VIREONIDAE (vireos)

The vireos are small shrikes, or perhaps the shrikes are large vireos. The difference in habits between the two families is largely due to the difference in size between a vireo and a shrike. The large shrikes are bushwhackers that include small vertebrates (birds, mice, lizards) in their diet of fairly large insects. The small vireos are more generally tree species where they search the foliage and smaller branches for any insects whatsover. Caterpillars, large bugs and small beetles are the main items in their diet. Because they take many ladybird beetles and parasitic Hymenoptera the value of the vireos to the agriculturist has been questioned. It is a group the Survey has studied rather thoroughly. From the records following, dragonflies are accidents in the vireo diet, probably an occasional chilled individual roosting in the foliage of a tree.

The nine other recognized forms of vireo in our area (not listed as dragonfly eaters) have no records of having taken Odonata, partly because their ranges are limited and less is known concerning them. Obviously the family as a whole prefer caterpillars and Hemiptera but are predators on many kinds of insects which they catch in bushes and tree tops. (Chapin 1925; Forbush 1929; Henderson 1927; McAtee 1907).

White-eyed Vireo, *Vireo griseus griseus* (Boddaert): 245 stomachs examined, 10 with dragonflies, 6 of which were Zygoptera. The white-eyed vireo lives about water more than do the other species. Its food is 88% animal of which 20% is caterpillars, 20% Hemiptera, 7% Hymenoptera, 4% Diptera, 3.5% Arachnida. Barrows (1912, p. 575) points out that the nesting area of bushes in swampy areas is similar to that of the yellow-breasted chat. Habits are curiously alike. Our data is on only 25 stomachs of the chat but those have the same proportion of Odonata as this vireo.

Hutton's Vireo, *Vireo huttoni huttoni* Cassin: 75 stomachs examined, one with a dragonfly. The food of the bird is 98% animal of which 8% is coccinellid beetles, 12% caterpillars, 46% Hemiptera, 6% Hymenoptera, 3% Diptera, 2% Arachnida.

Bell's Vireo, *Vireo belli belli* Audubon: 60 stomachs examined, one with a dragonfly. The food of the

Bell's vireo is 99% animal of which 15% is caterpillars, 34% Hemiptera, 15% beetles.

Yellow-throated Vireo, *Vireo flavifrons* Vieillot: 155 stomachs examined, 5 with dragonflies, 4 of which were Anisoptera. The food of this species is 98% animal of which 23% is caterpillars, 19% other Lepidoptera, 23% Hemiptera, 5% Hymenoptera, 7% Diptera and 2% Arachnida. In nesting the yellow-throated vireo prefers heavy hardwood timber but also oaks in wet ground (Barrows, 1912, p. 572). The dragonflies suggest wet areas.

Blue-headed Vireo, *Vireo solitarius solitarius* (Wilson): 325 stomachs examined, 9 with dragonflies. The food of the red-eyed vireo 85% is animal of which 23% is caterpillars, 30% Hemiptera, 7% Hymenoptera, 4% Diptera, 2.63% Arachnida. Hunting areas and nest sites similar to those of the yellow-throated vireo but nests nearer the ground.

Red-eyed Vireo, *Vireo olivaceus* (L.): 660 stomachs examined, 14 with adult dragonflies. Of the food of the red-eyed vireo 85% is animal of which 32% is caterpillars, 11% Hymenoptera, 4.5% Diptera and 4% Arachnida. A widely spread woods bird with fewer Odonata to its credit, it is repeatedly credited as our most beneficial vireo.

Warbling Vireo, *Vireo gilvus* (Vieillot): 350 stomachs examined, one with a dragonfly. The food of this species is 94% animal of which 35% is caterpillars, 17% Hemiptera, 6% Hymenoptera, 9% Diptera and 2% Arachnida: A tree bird with a low take of dragonflies.

FAMILY COMPSOTHLYPIDAE (wood warblers)

From the records following below less than 10% of the species of the wood warblers have been found to catch Odonata. Warblers are in general small birds of the tree tops though a few, such as the yellow-breasted chat and Maryland yellow-throat, live low in thickets (Chapman 1937, Height of nests). While highly insectivorous the majority do not meet many small dragonflies in the dense foliage of tree tops. Such meetings are accidents and account for the occasional dragonfly taken. Except for the yellow-breasted chat the majority of the warblers are smaller than the usual dragonfly eating bird. (Chapman 1937; Forbush 1929; Henderson 1927; McAtee 1907.)

Black and White Warbler, *Mniotilta varia* (L.): 21 stomachs examined, 2 with dragonflies. This species takes more Odonata than other warblers. It hunts more often over the bark of trunk and large limbs where cold-bound dragonflies often rest.

Yellow Warbler, *Dendroica aestiva aestiva* (Gmelin): 120 stomachs examined, 3 with dragonflies. Food of caterpillars, beetles, miscellaneous minute insects with 6% spiders. (Brigglestone 1913).

Audubon's Warbler, *Dendroica auduboni auduboni* (Townshend): 390 stomachs examined, one with a dragonfly; a western mountain species.

Black-throated Gray Warbler, *Dendroica nigrescens* (Townshend): 11 stomachs examined by the Survey, one with a dragonfly. A western species. (No references on food.)

Maryland Yellow-throat, *Geothlypsis trichas trichas* (L.): 125 stomachs examined, one with a dragonfly larva. This species is partial to thickets along streams and the larva had probably crawled up to emerge. This is a surprise record. The Maryland yellow-throat is an abundant bird in humid bushy areas, a southern blackberry-thicket bird. Its tastes and size probably enter in: it avoids large hard Hemiptera but uses soft caterpillars.

Yellow-breasted Chat, *Icteria virens virens* (L.): 25 stomachs examined, one dragonfly, an Anisopter. As the chat is a giant among warblers it might easily catch an Anisopter which had strayed into the bushes. See note on white-eyed vireo.

FAMILY PLOCEIDAE (weaver finches)

The English sparrow, long placed in the Family Fringillidae with our less aggressive North American sparrows has recently been shown through a study of its anatomy by Peter P. Sushkin (1927) to belong to the family of weaver finches which are birds of a more generalized behavior, greater vigor and aggressiveness, more social development and greater reproductive ability. As with other successful immigrant birds, such as the starling, the English sparrow comes from Eurasia where because of the great area it has been able to reach an evolutionary level about one geological age in advance of the majority of native North American birds. As with the starling it makes use of any abundant local supply of food. As with the starling this habit of life tends to tie it to man's works in agriculture, and in storage and transportation of agricultural products as man is the greatest producer of foods used by the English sparrow. The tie-up with man and his food production tends to hold the English sparrow away from dragonfly environments which are usually untouched areas yet in a relatively primitive condition. See remarks on the martin and the starling for the other factors in this problem. (Barrows 1889).

English Sparrow, *Passer domesticus domesticus* (L.): 1,500 stomachs examined, 4 with adult dragonflies. The English sparrow has been one of the birds very much studied by the Survey. For the extensive literature we refer the reader to Henderson (1927).

FAMILY ICTERIDAE (blackbirds, orioles, bobolink, meadow larks)

Of the twenty or more forms of blackbirds and meadowlarks found north of Mexico only two are regular eaters of dragonflies and then only in the nesting season. These are the yellow-headed blackbird and the thick-billed redwing. The others, as shown in the following notes, take dragonflies only accidentally as would any land insectivorous bird. Much depends on the nesting site as it is then that they are most insectivorous. Those that nest entirely away from the water catch dragonflies only occasionally.

The seven forms of oreoles found in our area are tree birds and have no records of having eaten dragonflies. (Beal 1900: Forbush 1927; Henderson 1927).

Bobolink, *Dolichonyx oryzivorus* (L.): 315 stomachs examined 3, with adult dragonflies. Beal's (1898) report shows 90% of insect food for the bob-o-link in June and 5% in September. Out of the nesting season the food is mainly seeds and grain. This bird nests in meadows in the higher of which few dragonflies are found. In the lower marshy meadows that are dry in the late fall, dragonflies are usually on the wing in late summer and fall after the nesting of the bob-o-link is over.

Meadowlark, *Sturnella magna* (L.): 1,400 stomachs examined, one with an adult dragonfly. This is strictly a dry meadow or prairie bird. The meadowlark does not take insects on the wing and is slow on its feet so that dragonfly catches are gastronomic accidents in its life. Probably our list of birds would be doubled, if for each species of American bird as many stomachs had been examined as have been for the meadow lark. Its food, of which 74% is animal matter, is largely composed of the larger, slower ground insects. It has special economic value in the large item of grasshoppers, and other Orthoptera in its diet. One Mormon cricket campaign at Adrian, Washington, in 1919 (Burrill 1920) was abandoned because the meadowlarks flocked in and did the necessary work of cleaning up the crickets.

Thus the meadowlark, while an eater of insects as large or larger than dragonflies, favors high, dry ground where Odonata seldom stray. Also they are slower in action than the successful catchers of dragonflies. (Bryant 1914; Knowlton & Maddock 1943).

The blackbirds are heavy grain eaters in the more southern fields of irrigated rice, milo, barley, etc. Here they raid low areas in great flocks in late summer, and at such times are near or in a dragonfly environment. Their take is above that of birds which catch Odonata accidentally. The tricolored, brewer, redwing, thick-billed and yellow-headed were the worst offenders. The yellow-headed breeding in cattails over water, is one of the three species of birds most interested in Odonata as food for the young. They are the species most closely associated with a fresh-water marsh environment.

Yellow-headed Blackbird, *Xanthocephalus xanthocephalus* (Bonaparte): 262 stomachs examined, 67 with remains of dragonflies. Two contained Odonata nymphs.

All blackbirds except the bronzed grackle love low wet ground. Few Odonata appear in the records against them except in the case of the yellow-headed blackbird which nests in emergent cattails. They use teneral Odonata. All species feed standing and use slow insects. Probably all have the poor vision of short-necked ground-feeding birds.

The following is from the writer's observations among the cattail-bordered ponds of the Yakima Valley, Washington. The yellow-headed blackbirds nest over the water in the cattails and feed their young almost exclusively on aquatic insects, taking these as they emerge from the water in vast numbers coincident with the nesting season of the birds. They confine their foraging to the emergent vegetation of the ponds and marshes and practically live on aquatic insects at this season. After the young can fly they forage more widely over the surrounding higher ground. The dragonfly nymphs found in their stomachs were probably taken as they crawled up to emerge. (Fautin 1940, 1941).

Several birds were shot and their stomachs on examination contained wads of dragonfly wings, mostly partially expanded zygopterous wings. This bird thus nests in the cattails over the water and rears its young at the peak of dragonfly emergence. The desert days are always bright so that dragonflies can be depended on to emerge daily in large numbers. It is one of the few birds in our area that the writer feels is a direct and important enemy of dragonflies, at least during the season of emergence. The others are the western robin, the purple martin, and Franklin's gull. Beal (1900) credits nestlings of the yellow-headed blackbird with 43% of dragonflies in their food.

It would be interesting to map the nesting areas of this species and see if there is any correlation between nesting area and abundance of Odonata in the cattails. Western ponds vary greatly in the number of Odonata produced. Those with insect eating fish produce noticeably fewer than do the more temporary ponds which become dry enough each fall to keep the fish population low.

Eastern Red-wing, *Agelaius phoeniceus phoeniceus* (L.): 1,000 stomachs examined, 30 with dragonflies, 22 of which contained adults. As the red-wing tends to be a marsh bird, the nymphs were probably taken while crawling out to emerge. (Allen, A. A. 1914; Knappen 1933).

Thick-billed Red-wing, *Agelaius phoeniceus fortis* Ridgway: Beal (1900) records the thick-billed redwing as giving its young dragonflies to the amount of 9.84% of the total food.

Tricolored Red-wing, *Agelaius phoeniceus tricolor* (Audubon) (?): A redwing at Sunnyside, Washington, in the lower Yakima Valley which in F. M. Bailey's "Handbook of Birds of the Western United States" did not key out satisfactorily to either the bicolored red-wing or the tricolored redwing was observed on the writer's dragonfly collecting trips. It was studied about the same Yakima Valley ponds as noted for the yellow-headed blackbird but no evidence was gathered that they were feeding their young on a noticeable number of dragonflies. Several were shot but these were feeding on land insects, caterpillars, moths, beetles, etc., and were observed feeding the same to their nestlings. (Bryant 1914).

Rusty Blackbird, *Euphagus carolinus* (Muller):

130 stomachs examined, one with an adult and one with a nymph. According to Brimley (1919) these feed in marshes in the spring. The rusty blackbirds "are never so happy as when their feet are wet," Barrows (1912, p. 454). They frequent the shallows of pools and streams; water beetles are a large item of food which contains more animal matter than that of other blackbirds (53%). Why few Odonata?

Brewer Blackbird, *Euphagus cyanocephalus* (Wagler): 725 stomachs examined, 19 with adult dragonflies. As this bird nests in low bushes and usually about water it is surprising that it does not take Odonata oftener. Beal (1910, p. 61) credits it with many caterpillars in its diet.

Boat-tailed Grackle, *Cassidix mexicanus major* (Vieillot): 250 stomachs examined, 5 with adult dragonflies. According to Beal (1900) it is a heavy feeder on grasshoppers, wild fruits and grains but Brimley states that in North Carolina it is a coast bird feeding on shrimps, crabs, etc., washed up on beaches and is rarely found as much as six miles inland. Brimley, *et al.* (1919) was a careful observer as noted by the writer on joint collecting trips around Raleigh, N. C. (Beal, McAtee & Kalmbach 1941).

Bronzed Grackle, *Quiscalus quiscula aeneus* Ridgway: 2,600 stomachs examined, 3 with Odonata, 2 of the stomachs containing nymphs. This is a bird that usually nests in the tops of the tallest trees of heavy woods and feeds in high open land. It apparently does not come into the dragonfly habitat to any extent. See notes under yellow-headed blackbird. (Beal 1894).

Eastern Cowbird, *Molothrus ater ater* (Boddaert): 700 stomachs examined, one with an adult anisopterous dragonfly. This is an upland bird that has the habit of riding on the backs of cattle and of feeding on the insects the cattle flush. It does not feed its own nestlings. (Beal 1900).

(The orioles had no records of dragonflies eaten by them. Our eastern species, the Baltimore and orchard orioles, are birds of tall trees above the zone of usual dragonfly flight. Bullock's oriole which nests in trees along desert streams in the West should be expected to pick up Odonata occasionally.)

FAMILY THRAUPIDAE (tanagers)

The five forms of tanagers are insect and fruit eaters but live in high trees, an area little used by dragonflies. (Forbush 1929; Henderson 1927).

Western Tanager, *Piranga ludoviciana* (Wilson): 54 stomachs examined, one with a dragonfly.

Scarlet Tanager, *Piranga erythoromelas* Vieillot: 330 stomachs examined, 3 with adult Odonata.

FAMILY FRINGILLIDAE (finches, sparrows, grossbeaks, crossbills, etc.)

The few records of this family of over one hundred and twenty forms found north of Mexico indicate how little the family as a whole is concerned with the eating of dragonflies. While all are essentially seed-eaters, the majority feed their nestlings on insects. It apears to be a group of species of the proper size of body, neither too large nor too small, and to be highly insectivorous during the nesting season. However, at other times they are seed eaters and as is the case with other herbivorous birds are less speedy in general reactions and probably seldom take food on the wing. This dullness of both senses and muscular reactions associated with herbivorous habits, perhaps because there is little chance of plant food escaping, may be the factor that allows swift insects to pass by untouched. Records show that they tend to eat the slower insects, Coleoptera, Orthoptera, and Lepidoptera, of the later usually caterpillars and pupae. (Forbush 1929; Henderson 1927; McAtee 1908).

Redbird, Eastern Cardinal, *Richmondena cardinalis cardinalis* (L.): 550 stomachs examined, 3 with dragonflies. As the redbird is one of the largest of the finches it might have been expected to have taken dragonflies oftener. In the author's backyard the redbird is noticeably a slow bird. (McAtee 1908).

Vesper Sparrow, *Pooecetes gramineus* (Gmelin): 260 stomachs examined, one with a dragonfly.

Slate-colored Junco, *Junco hyemalis hyemalis* (L.): 560 stomachs examined, 2 with dragonflies.

Brewer's Sparrow, *Spizella breweri breweri* Cassin: 65 stomachs examined, one with dragonfly. A western desert sparrow.

Song Sparrow, *Melospiza melodia* (Wilson): 750 stomachs examined, 3 with dragonflies. This species of all sparrows would be expected to take dragonflies oftenest as it has the habit of nesting close to or along streams. It is the best evidence of how few Odonata are eaten by birds of this family as it is the species most regularly in a dragonfly environment. (Haldeman 1913).

TAXONOMIC INDEX TO DRAGONFLY-EATING BIRDS, NUMBER OF STOMACHS PER SPECIES AND NUMBER OF STOMACHS WITH DRAGONFLIES

The following lists show that the use of dragonflies by birds is a primitive habit. The heavy consumers of dragonflies are in the first half of the list, about 80 species, which excepting the hawks are mostly associated with water. Nearly all nymph eating birds fall in the group, the grebes, herons, ducks and shore birds. In the higher half of the list only the belted kingfisher and the western robin prefer nymphs to adults, but the belted kingfisher by present classification is a modern bird which has evolved in reverse and has become a diving waterfowl with the habits and tastes of more primitive birds. Can evolution go into reverse among vigorous predators as well as among feeble parasites, if the taxonomists have interpreted the evolutionary data correctly? (*Vide postea*).

The present ornithological classification of the hawks and falcons places them in the lower half of the list, but their habits of feeding on the wing limit

their take to adult dragonflies except the red-shouldered hawk which tends to be a scavenger on the ground where it captures an occasional nymph.

Nearly all of the species in the more primitive half of the list retain the reptilian habit of nesting on the ground with a few exceptions which nest in trees such as the herons, wood duck, solitary sandpiper, and the hawks (excepting the marsh hawk which nests on the ground).

The latter half of the list, roughly from the cuckoos to include the Passeriformes, use only adult dragonflies, and use these very seldom. Probably all catches in the higher half are from accidental contacts except the martins, the two marsh wrens and two blackbirds (yellow-headed and perhaps the thick-billed). These apparently choose dragonflies when available particularly when feeding young. They use adults only, so are physiologically in the upper half of the bird series.

We wish to call the attention of ornithological taxonomists to the odd and exceptional placement of the belted kingfisher among the birds of the higher series. (See the following list.) The kingfisher has probably been placed so on his osseous anatomy. If so only one item of his physiology agrees with his placement anatomically.

He lives in holes in vertical clay and loess banks which in the verticalness of the bank are peculiar to swallows in the upper series of birds. Puffins and some murres dig holes in the ground as do Florida and western ground owls but holes in more horizontal surfaces, a somewhat different behavior. As a bird of the lower series of primitive habits he is a fish-eating diving water-fowl. In nesting he avoids broad-leaved trees of geologically recent forests and the prairies of even more recent times. The kingfisher is so perfectly attuned to his aquatic, fish-eating habits that he must have had a geologically long period back of his present repertoire of habits to have permitted their development to present perfection. His dragonfly-nymph eating habits are strictly those of waterfowl of the more primitive lower series. His voice is that of the lower series and so probably the structure of his syrinx. His colors and dense plumage are in the lower series. Even two toes are syndactyl (webbed?). Is it possible that the kingfisher is another misplaced "English Sparrow" where habits were for so long ignored?

On the side of the dragonflies, if Darwinian evolution would operate precisely and eliminate the present "living primitive" birds, the dragonflies would prosper as far as modern birds are concerned. They survived the cold weather of the Permian, the small, toothless, probably warm-blooded, bird-like pterosaurs of the Cretaceous and are at present out-evolving modern birds, the birds of broad leaved forest trees and dry grass lands. (But the dragonflies still have their worst enemies, fresh-water fish.)

The taxonomists' listing of "primitive" and "modern" birds is deceptive in our arguments because, if arranged on a Lamarckian "phylogenetic tree," the present-day so-called primitive birds would occupy

Page	Bird	Total No. of stomachs	Stomachs with Odonata	With Nymphs	With Adults
Grebes					
111	Holboell Grebe	50	1	..	1
111	Horned Grebe	156	6	3	3
111	Eared Grebe	35	6	6	..
111	Pied-bld. Grebe	196	23	24	1
111	Antillean Grebe	1	1	2	..
Herons					
112	Gt. Blue Heron	125	29	10	19
112	Snowy Egert	20	5	..	5
112	La. Heron	60	10	1	9
112	Little Blue Heron	45	27	38	7
112	Green Heron	215	80	21	59
112	Bl. crown N. Heron	100	12	7	5
112	Yel. crown N. Heron	110	1	..	1
112	Amer. Bittern	125	29	12	17
112	Least Bittern	100	41	25	16
113	W.-faced Gl. Ibis	15	2	2	..
113	White Ibis	20	1	1	..
River Ducks					
113	Mallard Duck	2,010	197	126	71
113	Black Duck	645	25	20	5
113	S. Bl. Duck	52	10	6	4
114	Gadwall	410	5	3	2
114	Baldpate	270	2	1	1
114	Pintail	925	35	28	7
114	Gr. wgd. Teal	750	27	9	18
114	Bl. wgd. Teal	335	27	21	6
114	Cinnamon Teal	44	4	..	4
114	Shoveller Duck	88	3	2	1
114	Wood Duck	400	78	22	56
Sea Ducks					
114	Redhead	360	10	1	9
114	Ring-necked	655	92	8	84
114	Canvasback	380	10	8	2
115	Amer. Scaup	752	10	8	2
115	Lesser Scaup	1,155	176	26?	150?
115	Amer. Gold'-eye	175	8	5	3
115	Bufflehead	60	11	2	9
115	Ruddy Duck	55	4	?	?
Fish Ducks					
115	Hooded Mergans	50	18	10	8
115	Amer. Mergans	140	3	3	..
115	Red-br. Mergans	175	10	4	6
Hawks					
116	Miss. Kite	15	1	..	1
116	Sharp-shin. Hwk	925	2	..	2
116	Cooper's Hawk	215	2	..	2
116	Red-tailed Hwk	510	1	..	1
117	Red-shouldered Hwk	325	7	1	6
117	Broad-winged Hwk	90	1	..	1
117	Swainson's Hwk	30	2	..	2
117	Marsh Hawk	530	7	..	7
Falcons					
117	Aplomado Falcon	3	1	..	1
117	Pigeon Hawk	700	421	..	421
117	Sparrow Hawk	550	32	..	32
Turkeys					
118	Turkey	19	1	..	1
Cranes					
118	Sandhill Crane	16	2	2	..
Coots					
118	Coot	40	3	3	..
Shore Birds					
119	Killdeer	260	10	5	5
119	Antill. Killdeer	20	Odonata 3.92 %		
119	Golden Plover	100	4	4	..
119	Black-bellied Pl.	440	15	11	4
120	Woodcock	130	1	..	1
120	Wilson's Snipe	725	139	128	1
120	Eskimo Curlew	4	1	..	1
120	Bartramian Sandp.	200	1	..	1
120	Solitary Sandp.	7	1	1	1

Page	Bird	Total No. of stomachs	Stomachs with Odonata	With Nymphs	With Adults
120	Willet	230	16	10	6
120	Great. Yel. Legs	702	153	126	27
120	Lesser Yel. Legs	760	123	80	43
121	Knot	215	2	..	2
121	Pectoral Sandp.	104	3	..	3
121	Baird's Sandp.	45	7	1	6
121	Dowitcher	200	89	85	4
121	Long-billed Dowitcher	90	6	6	..
121	Stilt Sandpiper	15	3	3	..
121	Marbled Godwit	90	1	..	1
Stilts					
121	Amer. Avocet	55	3	3	..
121	Black-necked Stilt	70	9	9	..
Phalaropes					
121	Wilson's Phalarope	105	1	1	..
121	Northern Phalarope	150	3	..	3
Gulls, Terns					
122	Ring-billed Gull	50	4	..	4
122	Franklin's Gull	125	8	(other records nymphs)	
122	Bonaparte's Gull	140	1	..	1
122	Gull-billed Tern	7	3	..	3
122	Forster's Tern	60	2	2	..
122	Common Tern	116	a few	?	?
122	Arctic Tern	45	5	5	..
122	Black Tern	280	42	..	42
122	Black Guillemot	15	1	..	1
Cuckoos					
122	Yel.-bill. Cuckoo	350	10	..	10
122	Black-bill. Cuckoo	160	8	..	8
Owls					
123	Screech Owl	440	3	..	3
123	Pigmy Owl	50	1	..	1
Night Hawks					
123	Chuck-Will's-Widow	40	4	..	4
123	Nighthawk	315	22	..	22
123	Tex. Nighthawk	20	1	..	1
Swifts					
124	Chimney Swift	150	7	..	7
Kingfisher					
124	Belted Kingfisher	330	33	33	..
Woodpeckers					
124	Northern Flicker	700	2	..	2
124	Yel.-bellied Sapsucker	325	2	..	2
124	Downy Woodpecker	750	1	..	1
Flycatchers					
125	Kingbird	700	39	..	39
125	Ark. Kingbird	145	3	..	3
125	Cassins Kingbird	45	1	..	1
125	Scissor-tail Flyc.	130	1	..	1
125	N. crested Flyc.	265	26	..	26
125	Ash-throated Flyc.	90	6	..	6
125	East. Phoebe	365	11	..	11
125	Black Phoebe	340	67	..	67
126	Say's Phoebe	130	7	..	7
126	Yel.-bellied Flyc.	105	2	..	2
126	Alder Flyc.	155	9	..	9
126	Least Flycatcher	170	4	..	4
126	Wright's Flyc.	20	1	..	1
126	Western Flyc.	162	1	..	1
126	East. Wood Pewee	365	14	..	14
126	West. Wood Pewee	165	19	..	19
126	Olive-sided Flyc.	60	6	..	6
Swallows					
126	Tree Swallow	330	32	..	32
126	Bank Swallow	415	33	..	33
126	Rough-wgd. Swallow	135	4	..	4
126	Barn Swallow	135	4	..	4
127	N. Cliff Swallow	380	12	..	12
127	Purple Martin	210	65	..	65
127	Cuban Martin	3	3	..	3
127	Caribbean Martin	12	(8% of food drgfs.)		

Page	Bird	Total No. of stomachs	Stomachs with Odonata	With Nymphs	With Adults
Jays, Crows					
127	N. Blue Jay	680	6	1	5
127	Amer. Magpie	560	18	..	18
127	Yel.-billed Magpie	25	3	..	3
127	Amer. Raven	20	2	..	2
127	Amer. Crow	2,000	19	7	12
Chickadees					
128	Black-cap. Chickadee	660	2	..	2
Dippers					
128	Water Ouzel	60	1	..	1
Wrens					
128	House Wren	390	1	..	1
128	East. Winter Wren	230	3	1	2
128	Bewick's Wren	250	2	..	2
128	Carolina Wren	415	2	..	2
128	Long-billed Marsh Wren	415	13	..	13
128	Short-billed Marsh Wren	100	5	..	5
128	Com. Rock Wren	60	1	..	1
Mockers					
129	Mocking Bird	500	1	..	1
129	Catbird	690	9	..	9
129	Brown Thrasher	660	2	..	2
Thrushes					
129	Amer. Robin	1,230	5	..	5
129	Olive-backed Thrush	403	3	1	2
129	Gray-checked Thrush	111	1	..	1
129	East. Bluebird	855	4	..	4
129	Townsend's Solitaire	41	1	..	1
Waxwings					
130	Cedar Waxwing	225	3	..	3
Shrikes					
130	White-rumped Shrike	303	3	..	3
Starlings					
130	Starling	2,750	1	..	1
Vireos					
130	White-eyed Vireo	245	10	..	10
130	Hutton's Vireo	75	11	..	1
130	Bell's Vireo	60	1	..	1
131	Yel.-throated Vireo	155	5	..	5
131	Blue-headed Vireo	325	9	..	9
131	Red-eyed Vireo	660	14	..	14
131	Warbling Vireo	350	1	..	1
Wood Warblers					
131	Black and White Warbler	21	2	..	2
131	Yellow Warbler	120	3	..	3
131	Audubon's Warbler	390	1	..	1
131	Black-throated Gray Warbler	11	1	..	1
131	Maryland Yellow-throat	125	1	1	..
131	Yellow-breasted Chat	25	1	..	1
Weaver Finches					
131	English Sparrow	1,500	4	..	4
Blackbirds					
132	Bobolink	315	3	..	3
132	Meadowlark	115	1	..	1
132	Yel.-headed Blackbird	262	67	2	65
132	Eastern Red-wing	1,000	30	8	22
132	Thick-billed Red-wing (Beal.-Food of young 9.8% Odonata)				
132	Rusty Blackbird	130	2	1	1
133	Brewer Blackbird	725	19	..	19
133	Boat-tailed Grackle	250	5	..	5
133	Bronzed Grackle	2,600	3	2	1
133	Eastern Cowbird	700	1	..	1
Tanagers					
133	Western Tanager	54	1	..	1
133	Scarlet Tanager	330	3	..	3
133	Redbird	550	3	..	3
133	Vesper Sparrow	260	1	..	1
133	Slate-colored Junco	560	2	..	2
133	Brewer's Sparrow	65	1	..	1
133	Song Sparrow	750	3	..	3

tips of branches which would give them as much evolutionary modernness as is ascribed to perching birds which may be modern only in their more recent origin and adaptation to the protection of modern broad-leaved forests and the even more recent grasslands.

This brings us back to the arguments without much data: Why have "primitive forms" been preserved to the present when associated with an aquatic environment? Why do not evolutionists give more weight to the evolution of physiology in present forms where data are available. The writer feels certain that physiological evolution leads and is followed by anatomical adaptations. He has vivid evidence which he will present elsewhere.

SUMMARY: THE PROBLEM OF PREDATION IN THE GREATER PROBLEM OF DARWINIAN SURVIVAL OF SPECIES

As estimated we have reviewed the data obtained from probably 100,000 to 200,000 bird stomachs by the group of trained U. S. Biological Survey ornithologists. It has been a review of the activities of a continental bird fauna against a continental dragonfly fauna. It presents in broad aspect the problem of the Darwinian survival of a continental dragonfly fauna in the face of the assaults of a continental bird fauna.

Our general conclusion is that no species of dragonfly faces extermination by any species of bird or by any group of species of birds. For years in work on Odonata the writer has watched for evidence of the causes of the gradual evolutionary changes in odonate faunas and has become convinced that they are not a matter of predation by another animal group. (Gould 1871; McAtee 1912b, 1926, 1932).

The critical point in the problem of predator *versus* prey is that the predator has to meet the prey in the latter's own environment. In our specific example of the general problem, the bird has to meet the dragonfly as an egg or as a nymph in the water, or as an imago in the air. Because of this treble possible meeting of predator and prey our problem is the more vivid in analysis. Repetition by three environmental forms of meeting emphasizes the necessity of meeting. (Forbes 1882; Heape 1931).

We can narrow the problem by defining the much narrower environment of dragonflies as compared with the nearly continental spread of the bird fauna. With the exception of a few brackish water species of our coasts and inland salt waters as studied by Osburn (1916) and Pearse (1932) the dragonfly nymphs are confined to fresh water. (A few tropical species live in moist woods-loam or mud.) This restriction to fresh water confines North American dragonflies to streams, lakes, marshes, bogs, and swamps. The female dragonfly has to lay her eggs in fresh water or close enough to it (immediately adjacent) that the nymph can hatch from the egg in the water or on hatching can drop into water (Kennedy 1915, Archilestes). This necessity in the life history ties the winged adults to fresh waters. The males by sex habits remain with the females. Both are adapted in feeding to the numerous minute Diptera and other small flying insects whose larvae live in water or wet soil. Thus the birds which prey on dragonflies must of necessity be associated with fresh water or within dragonfly flight-distance of fresh water.

Poorly developed territorial rights may figure into the picture. In the birds they center roughly about a nesting site surrounded by a food-producing area. In dragonflies the territory is somewhat similarly defined. The female haunts an area pleasing to her as an egg-laying site and as with birds a site surrounded by a food-producing area. The same individual dragonflies will be found patrolling the same pond or stream-pool day after day. In the birds individual territories are sharply fought for and defined. In dragonflies territories are group concerns, more as in colonial birds. In birds territory is defined on physiological factors such as the bird's attachment to the nesting site plus a food producing area. In dragonflies territory is less sharply defined and that on ecological conditions such as local areas suitable for oviposition in a food-producing area. We cite only Nice (1937, 1943) from the literature on territorial rights in birds. The nearest study to the problem in dragonflies is the paper on *Argia moesta* by Borror (1934).

The dragonfly-fresh-water factor narrows the predation problem by the elimination of several extensive groups of birds. All marine or saltwater birds do not prey on Odonata. They are usually fish-eaters. (Our definition of group is physiological and only roughly taxonomic as there are exceptions. One type of exceptions are the birds which occasionally pick up wind-blown dragonflies strayed from a normal habitat). A great group are the birds of plains, prairies and other areas between streams and lakes. Another group is strictly arboreal, while we find a mixed group of birds some of which are too small or too large to be interested in large insects, added to which are a few with special tastes. With 468 named forms of birds in the faunal area (A.O.U. Check List, Ed. IV) 284 forms have no records of having preyed on dragonflies. This leaves 184 bird forms that have records as predators on Odonata. The estimate is involved with at least four disconcerting factors. (1) Dragonflies which have strayed from the fresh-water dragonfly habitat; (2) the practice of many non-insectivorous birds of feeding insects to nestlings and thus probably at such season eating more insects themselves; (3) the weight on economic species; and (4) a less tangible factor that stomachs may not have been collected as ardently in southern horse-fly and chigger areas and in northern black fly and mosquito areas. Under the last the meagre record for southern swamp turkeys showed up first. The last cannot be construed as a criticism as the field problem was vast beyond the efforts of a limited staff. More stomachs in any area were of

more scientific importance than a thinly spread coverage.

Of the 184 bird forms (species, subspecies) which by stomach records had eaten one or more dragonflies per species-record, only 35 birds showed records with 10% of the stomachs per species containing one or more dragonflies each. Sixteen species with less than 20 stomachs examined per species were not counted in the estimate for fear the data were too meagre. But 12 of these had 10% of the stomachs with dragonflies. If we add the two 10% groups we have 47 birds the stomachs of which showed 10 per cent of stomachs with dragonflies. Compared with the total fauna of 468 birds only 47 showed any noticeable predator-pressure in our predator *versus* prey problem. The assumptions in this problem need a word. We took as a minimum twenty stomachs per species because such a small amount of data appeared to be only a general qualitative sample in the known irregular distribution of most bird species. We feel that our figures on 20 stomachs per species as a minimum limit is reasonable and too few stomachs for any final evidence per species. Any mathematical treatment beyond the few preceding becomes very uncertain because we have first to introduce the judgments of the men who supposedly collected at mathematical random and then secondly add our own judgment, to the judgment of the collector without having seen the collector at work. Birds and dragonflies are not planted in rows to be inventoried in checkerboarded plots.

By Elton's (1935) analysis of pyramids of numbers the predator-prey problem in this case is one of the predator (the bird) on the peak of a pyramid of insects, feeding on another predator (the dragonfly) which itself is on a pyramid of smaller insects. That is simple in analysis but on closer inspection becomes deceiving when we examine the predator-prey problem in terms of possible and probable contacts between the two. The probability of necessary contact between the two fades out to where Darwinian survival probably favors the prey. (Gabrielson 1941).

For the predator to exterminate or even to reduce the prey the predation has to be continuous enough to keep up a continuous attrition or depletion of the numbers of the prey. Our evidence shows no bird species attacking dragonflies exclusively, an ideal pyramid peak, if found. One approach to the predator-prey problem is by way of the pyramid of numbers concept which we will examine as applied to the specific bird-dragonfly problem. We find at once several factors which involve the specific bird-dragonfly problem. (1) Nearly all the birds involved north of Mexico are migratory. The dragonflies are attacked by northern birds in the winter and by southern birds in the summer. This is a pyramid peak shift. (2) Many small birds during the breeding season feed their young on insects though they may be seed-eaters at other times and not then interested in dragonflies. This food shift reduces the usefulness of the pyramid concept as a unit of ecological analysis. (3) A third difficulty arises in the triple life of the dragonfly prey, as eggs and nymphs in a water environment the year around but in warm months as adults in an aerial environment. These involvements raise the problem to three very outstanding variables with each of which are innumerable minor variables. Thus the symbol of a stable triangular pyramid hardly diagrams a system of three cycles, (1) the migratory shift; (2) the food shift; and (3) the dragonfly shift from water to air. Its basic instability for a precisely drawn pyramid makes the pyramid deceptive. It reminds one of the astronomer's simple problem of three bodies moving freely in space, a problem as yet with no exact formula for the position of the Moon at any moment in relation to the Earth and Sun. The human mind craves constants but in biology deals with variables. (Errington 1946).

We have no certain suggestion for a diagram to clear this impasse for even the one problem of birds *versus* dragonflies. We have come to believe that, if a usable symbolic diagram is finally discovered it will have to be cyclic and may be found in the field of cycloid systems in spherical geometry, certainly not in plane geometry. Then develop the diagram to the hundred species of insects one species of bird may eat! Then follow the bird on a summer of hard work in the Subarctic and on a winter vacation to South America. The pyramid of numbers symbol is useful but has a deceptive appearance of stability. By label and theoretical structure it is composed of predators and prey. In reality it is functional and composed of cyclic functions. In the experienced hands of Elton as conceived for pure aggregates of fish-eating birds the pyramid of numbers is a useful concept. For other complexes of predator and prey it has to be used with discretion. Elton himself used it so.

This complex of two types of predators each operating in patterns of two or more seasonal behaviors which could puzzle good mathematicians has just been stated in its basic elements. We despair of breaking it down into the level of pyramids of numbers used by Elton (1935). The deadly evidence from examination of stomach contents, beyond which there is no rebuttal evidence, shows pyramids so scrambled in factors of time and material that it becomes exceedingly difficult to use pyramid concepts and symbols in its analysis. As shown by McAtee, Henderson and the Biological Survey's own data the bird at the peak of its usual pyramid slips down to lesser peaks when actually hungry on the greater peak. The pyramid concept is useful this far.

We do not wish to disparage ecology. Gradually that science is accumulating good diagrams and symbols and is slowly shifting from a descriptive form to one of energies and energy relationships.

More and more we have visualized the problem of bird *versus* dragonfly as one that swings around the contact of bird and dragonfly. The contact between predator and prey is the critical point in space and time for both elements, the bird and the dragonfly.

In a general system of energies a transfer of energy (dragonfly to bird) takes place at the point of contact. At the same general time and place a change of energy takes place (dragonfly energies into bird energies).

The contact is fairly stable in locality as far as the prey is concerned. In our case of bird *versus* dragonfly, the predator occupies a very unstable position in the matter of contact. Except at brief aggregation for migration (see Tavener 1935 on migratory aggregation and this article "Pigeon hawk (*Falco columbarins*)" the bird predator cannot attack the prey *en masse*).

(1) During breeding season bird families are separated and scattered by territorial rights except for some species which recognize common feeding areas. By the desire for privacy during the breeding season birds are more thinly scattered than at other times. This tends to draw stream and marsh loving birds away from the usually narrow shore and stream habitats of the dragonfly prey.

(2) Colonial birds tend to nest in small densely populated areas which, if dragonfly eaters, have colonies so widely scattered the bird predator tends to leave areas unattacked in between colonies. This is true of the yellow-headed blackbird in western tulle marshes, of martins limited to man-made bird houses and probably of the colonies of Franklin gulls in the north.

(3) The usual scattering is by ecological discontinuities. Dragonflies are very attached, each species, to a particular type of bottom, of density of vegetation, speed of water-flow and maximum and minimum temperatures. On the same lake system Ophiogomphus lives on sand bottom abundantly studded with cobble stones, Gomphus on mud bottom while Progomphus is usually limited to pure sand bottom in moving but not rough waters. (Straits of Macinac, Burt and Douglas Lakes, Mich.) These choices by the female while ovipositing are probably made by the female on surface characters of the water, wind drifts, and emergent and riparian vegetation. She does not examine the bottom and probably has no memory of it from nymphal days. But it gives a very local and discontinuous distribution of each species of dragonfly. If attacked by fly-catchers each species of which has a preferred type of outlook branch or limb, such choice outlooks may be so scarce that whole areas of proper dragonfly bottom may have no covering fly-catcher. The breeding waterfowl of the Canadian lakes and streams are equally particular about the type of shore-vegetation cover they choose for their nests and young brood. Food is abundant and secondary to protection for the predator in a competitive field. Our answer for the survival of dragonflies in a world of predator birds lies in the complexities of microecology. The bird predator cannot be particular about its home and its location and at the same time harvest the crop of dragonfly-prey. Contacts of predator-bird and prey-dragonfly become disjointed in space and time. The contact is the basic essential in Darwinian survival. In our present minor problem it does not operate to finality.

Another general factor enters the problem of survival of the prey-dragonfly. To survive down through evolutionary time the predator is usually a species that has to some extent food tastes broader than such as would make it obligate to dragonflies. Such tastes in the types of birds which do use dragonflies usually spread out beyond that for dragonflies to other insects which could be classed with Odonata physiologically rather than taxonomically. All bottom nymphs are food for those feeding on odonate nymphs. Many species of flying insects are common food for birds which eat adult Odonata. In the aquatic birds food tastes spread even farther into crustacea, fish, molluscs. In the flying birds the raptores may use mammals and other birds. This relationship of predator to prey is just the opposite of that of an obligate parasite to its one host.

This outside field of food other than that of Odonata makes for a plastic relationship between predator-bird and prey-dragonfly. It saves the bird at any scarcity of dragonflies and saves the dragonflies by the greater number of smaller insects drawing the fire of the predator-bird. (We badly need a physico-mathematical treatment of relative size in the predator-prey relationship and with it the same study of the parasite-host problem of relative size.)

We have written enough to give our general impressions (conclusions?) while sorting the great mass of data assembled by the experts of the U. S. Biological Survey to say that there is little evidence that any species of North American bird stands much of a chance of exterminating any species of North American dragonfly. The two faunas will wing their way together down through evolutionary time. Many contacts of predator-bird with prey-dragonfly will be made but none critical by species-healthy birds on species-healthy dragonflies.

Less than a half dozen species of birds appear to have a keen interest in dragonflies, the Franklin gull, the lesser yellow legs, the purple martin, the yellow-headed blackbird, the belted kingfisher and two marsh wrens. Except the lesser yellow legs on which we have no nesting data all use dragonflies heavily to feed nestlings.

We have come to believe that in the evolution of dragonflies down through the ages continental or even world changes in climate are at least partially responsible for the geological succession of dragonfly faunas. Coupled with this is the accumulating evidence that succeeding new species are produced by the several types of chromosome and gene change with what the geneticists term gene flow in populations. Dragonflies live in a keenly competitive world but for some illy defined reasons have a wide margin for survival.

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