

FEEDING BEHAVIOR OF NORTH AMERICAN HERONS

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ALTHOUGH the literature on heron behavior is vast and long standing, the ethology of North American herons was not systematized until the work of Meyerriecks (1960a). Feeding behavior was a minor part of his study of four species of herons, and he included feeding behavior in a comparative behavior chart covering all North American herons except bitterns. This summary pointed out the current state of knowledge and stimulated and guided more recent work on heron feeding behavior.

The most complete descriptive review of heron feeding behavior is a popular paper by Meyerriecks (1962a). Feeding behaviors have also been described in various scattered papers, but a number of known behaviors have never been concisely described, including some noted by Meyerriecks (1960a). His comparative behavior chart listed 11 feeding behaviors and one head position, but unfortunately provided no references to document the occurrence of the behaviors listed. The purpose of the present paper is to supply brief descriptions of the feeding behaviors recorded for North American herons and to document their occurrence in various species insofar as is presently known. The results are based on a review of the literature supplemented by several years of intermittent study of heron feeding behavior in southern Florida. This paper is not meant as a detailed analysis of the homology, derivation, or relative importance of various behaviors, nor are minor behavioral variations definitively distinguished from more fundamental postures. Its function is to systematize and describe behaviors currently recognized in the field as a necessary aid to further study. Many behaviors described here are complex mixtures of basic postures and movements, which will require much additional analysis to understand.

The paper covers 12 species of herons found in North America north of Mexico: Least Bittern (*Ixobrychus exilis*), American Bittern (*Botaurus lentiginosus*), Yellow-crowned Night-Heron (*Nyctanassa violacea*), Black-crowned Night-Heron (*Nycticorax nycticorax*), Cattle Egret (*Bubulcus ibis*), Green Heron (*Butorides virescens*), Little Blue Heron (*Florida caerulea*), Louisiana Heron (*Hydranassa tricolor*), Reddish Egret (*Dichromanassa rufescens*), Snowy Egret (*Egretta thula*), Great Egret (*Casmerodius albus*), and Great Blue Heron (*Ardea herodias*).

DESCRIPTION OF FEEDING BEHAVIORS

Heron feeding behaviors are described below. Where applicable the name of a behavior is immediately followed by a reference to the source

of the name. Names recognized in this classification are italicized. The behaviors are broadly divisible for present purposes into three categories: stand or stalk, disturb and chase, and aerial and deep water feeding.

STAND OR STALK FEEDING

In *stand and wait* (Meyerriecks 1960a: 8) a heron stands motionless in water or on land waiting for prey to approach. There are two basic postures. In upright posture the body is held erect, head and neck are fully extended angled away from the body. In crouched posture, the body is held horizontal to the perch or the water, legs are bent, and the head and neck are partially retracted. *Upright stand and wait* is epitomized by the Great Blue Heron while *crouched stand and wait* characterizes the Green Heron. Intermediate postures may also be used.

Several variations of stand and wait behavior are recognizable. In bill vibrating (Kushlan 1973a), a heron in crouched posture stands with bill tip submerged in water and rapidly opens and closes its bill creating a disturbance that attracts prey. This behavior is probably what Buckley and Buckley (1968) called tongue flicking. In *baiting* (Lovell 1958), a heron feeding by stand and wait places bait in the water to attract prey to its feeding location. Lovell described the Green Heron as persistently returning bait to a position under its feeding perch. In *standing flycatching*, a heron using stand and wait behavior catches flying insects. In *gleaning*, a heron picks prey from objects above the ground or water.

In *walk slowly* (Meyerriecks 1960a: 8), a heron moves slowly, stalking prey. Walking becomes slower as the heron examines items or areas of interest, and just before striking the heron may walk so slowly that this behavior merges with stand and wait. Alternately herons feeding by stand and wait may periodically walk very slowly for several steps and then resume stand and wait. Merging of the two behaviors is best seen in species such as the Great Blue Heron and American Bittern. Meyerriecks (1960a) called this behavior wade or walk slowly but as wading and walking are behaviorally identical and such compound terminology is awkward to use, it seems best to call this behavior simply walk slowly. As in stand and wait, walk slowly has two basic postures, *upright* and *crouched*. Meyerriecks (1960a: 89) called these postures erect and low. The behavioral variations have been called upright stalk and low stalk by Recher and Recher (1972). There is much to recommend using the term stalking but Meyerriecks' well-accepted and widely used term walking slowly should have priority.

DISTURB AND CHASE FEEDING

In *walk quickly*, a heron walks through shallow water or fields catching prey disturbed by its movements. This behavior differs from walk slowly in that the heron flushes rather than stalks prey and the posture is not so rigid (see Jenni 1969). In *running* (Jenni 1969), a heron moves quickly after a specific prey item or runs from place to place disturbing prey. It stabs or lunges while in motion or after an abrupt stop. The behavior is characteristic of actively feeding herons such as the Louisiana Heron and Reddish Egret. Both *upright running* and *crouched running* may occur.

In *hopping*, a heron jumps into the air and flies a short distance to a potential prey item and often stabs simultaneously with landing. This behavior is also characteristic of actively feeding herons. Meyerriecks (1960b) distinguished a variation of this behavior called *leapfrog feeding* in which birds repeatedly fly to forward positions in a feeding flock. Blaker (1969) called this variation roller feeding. Meyerriecks thought that its function was to disturb prey. Siegfried (1971) disagreed, suggesting that it helped birds maintain contact in the high grass where it commonly occurs. The latter seems more reasonable. Hopping to another location would also be the best way to get out of a poor feeding spot, such as at the rear of a moving flock. A behavior reported by Bagg and Eliot (1937) may, in lieu of further observations, be considered another variation of hopping. They reported that a Great Egret jumped straight up out of the water, landed stiff legged in the same location, and then examined the disturbance for prey.

There are several recognizable variations in the use of wings during disturb and chase foraging. In *wing flicking* (Meyerriecks 1960a: 89), a heron walking slowly in an upright posture suddenly extends and retracts wings in a flicking action usually repeated several times. It often stops after flicking, looks around, and then resumes walking. In *open-wing feeding* (Meyerriecks 1960a: 108), a heron running, walking slowly, or standing extends completely one or both wings and then retracts them. Meyerriecks (1962a) described a variation called pirouetting in which the Louisiana Heron turns slowly while alternately raising and lowering each wing. In *underwing feeding* (Meyerriecks 1960a: 109), a heron extends wings completely while walking and holding them extended places its head under its wing and stabs at prey. In *canopy feeding* (Meyerriecks 1960a: 108), a heron running with wings extended stops, looks into water, and brings its wings forward forming a canopy above its head. It may hold this pose for several minutes. This behavior is well known in a more extreme form in the African Black Heron (*Egretta ardesiaca*) (Delacour 1946).

There are also several recognizable variations in the use of feet during disturb and chase foraging. In *foot stirring* (Meyerriecks 1959), a heron extends one leg forward and vibrates its leg and foot, or it vibrates its foot while wading forward normally. This motion stirs the area around its foot, thereby disturbing or attracting prey. Foot stirring can occur in mud, vegetation, mid-water, or, as Meyerriecks (1966) reported for the Snowy Egret, on land. In *foot raking* (Meyerriecks 1969, 1971), a standing heron extends one leg forward and rakes the substrate with its toes, or it rakes with its feet while walking forward. This behavior has also been called foot scraping by Meyerriecks (1959, 1966). In *foot probing* (Meyerriecks 1971), a heron extends one leg forward and slowly probes substrate, vegetation, or litter. In *foot paddling* (Meyerriecks 1959), a heron rapidly moves feet up and down on the substrate to disturb prey.

AERIAL AND DEEP WATER FEEDING

In *hovering* (Meyerriecks 1960a: 89), a heron hovers over a single spot and reaches down with its bill to remove prey from the water. A variation of this behavior is *hovering stirring* (Meyerriecks 1959) in which a heron hovering above the surface of the water extends one foot and pats the surface of the water or stirs or rakes vegetation or floating debris. Strikes at prey are made from the hovering position. This behavior includes what Meyerriecks (1959) called hovering scraping.

In *dipping* (Dickinson 1947), a heron flying low above the water catches prey in the water while continuing in direct flight without hovering. A heron may also fly higher and descend to catch fish, fly a short distance, and dip again. Both hovering and dipping behaviors are also used to pick up other objects from the water, especially nesting material (e.g. Dickinson 1947, French 1965). A variation of dipping behavior is *foot dragging* (Kushlan 1972) in which a heron flying in direct flight near the surface of the water drags the toes or foot of one or both legs in the water. Strikes are made while the heron continues in forward flight. In *aerial flycatching*, a heron while in flight pursues and captures flying insects.

Hérons use several types of diving behavior. In *plunging* (Kushlan 1973b), a heron from forward flight or hovering position dives head first into the water to catch prey. After plunging the heron may either take flight immediately or float at the surface. In *diving* (Brooks 1923, Meyerriecks 1960a: 9), a heron perched on shore or on branches overhanging the water dives head first from its perch into the water. In *feet first diving*, a heron alights on the water feet first, usually from a hovering position, and usually stabs at prey immediately on landing.

A similar behavior called *jumping* occurs when a heron jumps from a perch feet first into the water.

In *swimming feeding* (Kushlan 1973b), a heron swimming at the surface of the water strikes at nearby prey. This is usually done after a feet first dive but may follow plunging, or a heron may wade into the water and begin swimming. Various herons have often been reported swimming without feeding. Herons swimming feeding may either swim for prolonged periods, or more commonly alight on the water and feed only for a matter of minutes before taking flight again.

OCCURENCE OF BEHAVIORS

The occurrences of various feeding behaviors of all species of North American herons are compared in Table 1. Primary sources of information are noted to aid future studies. No heron, according to current information, uses all 28 feeding behaviors listed in Table 1. Bitterns are generally the least versatile, followed by night-herons. The Black-crowned Night-Heron, however, does show a surprising number of specialized techniques such as bill vibrating, hovering, plunging, and swimming feeding. The report of bill vibrating in the Cattle Egret (Blaker 1969) is of some interest because of this species' terrestrial feeding habits.

The six species of typical day herons (Ardeini) have the greatest variety of feeding behaviors. The largest, the Great Blue, and the smallest, the Green Heron, have the fewest feeding behaviors attributed to them. Both rely primarily on stand or stalk techniques. Of the remaining typical herons, the Little Blue Heron and Great Egret are more circumscribed than the Snowy Egret, Louisiana Heron, and Reddish Egret, which are the most versatile and active of North American herons.

DISCUSSION

The pioneering studies of Huxley (1924), Verwey (1930), Lorenz (1938), and Noble et al. (1938) followed by the comprehensive comparative work of Meyerriecks (1960a) demonstrated that the Ardeidae are a suitable and rewarding group for behavioral study. Subsequent contributions by Meyerriecks (1962b) and others, including Weller (1961), Baerends and van der Cingel (1962), Hudson (1965), and Blaker (1969), have increased the ethological information available on this group. Such information may be a potentially useful tool in taxonomic, evolutionary, motivational, and, especially, ecological studies.

Behavior is playing an increasingly important role in current thought regarding the taxonomy and evolution of herons. Curry-Lindahl (1971) for example has recently proposed a taxonomic revision based on etho-

TABLE 1
COMPARATIVE BEHAVIOR CHART: COMPARISON OF THE FEEDING BEHAVIOR OF TWELVE SPECIES OF NORTH AMERICAN HERONS

Behavior	Least Bittern		Yellow-crowned Night-Heron		Cattle Egret		Green Heron		Little Blue Heron		Louisiana Heron		Reddish Egret		Snowy Egret		Great Egret		Great Blue Heron		
	1 ¹	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	
Stand and wait																					
Bill vibrating																					
Baiting																					
Standing flycatching																					
Gleaning																					
Walk slowly																					
Walk quickly																					
Running																					
Hopping																					
Leapfrog feeding																					
Wing flicking																					
Openwing feeding																					
Underwing feeding																					
Canopy feeding																					
Foot stirring																					
Foot raking																					
Foot probing																					
Foot paddling																					
Hovering																					
Hovering stirring																					
Dipping																					
Foot dragging																					
Aerial flycatching																					
Plunging																					
Diving																					
Feet first diving																					
Jumping																					
Swimming feeding																					

¹ Key: 1, commonly reported behaviors; 2, Kushlan (1973a) and references therein; 3, Lovell (1958); 4, Valentine (1958); 5, Warburton (1948); 6, Audubon (1840); 7, Kushlan (MS); 8, Jenni (1969); 9, Meyerricks (1960a) and references therein; 10, Meyerricks (1960b); 11, Wise and Crawford (1974); 12, Meyerricks (1962a); 13, Meyerricks (1960a: 151, only in comparative behavior chart); 14, Holt (1961); 15, Meyerricks (1959) and references therein; 16, Meyerricks (1966); 17, Meyerricks (1971); 18, Rodgers (1974); 19, Grimes (1936); 20, Kushlan (1972); 21, Dickinson (1947) and references therein; 22, Fargo (1937); Kushlan (1972); 23, Meyerricks (1962b, 1971); 24, Kushlan (1973b) and references therein; 25, diving was recorded for Great Egret and Great Blue Heron by Meyerricks (1960a: 151); this is interpreted to be plunging; 26, Mock (1974); 27, Bent (1926); Hedeen (1967); 28, Hawbecker (1949).

logical and ecological characters, although he did not detail the data on which he founded his revision. Such systems, which depart from current North American usage (A.O.U. 1957, 1973) and from morphologically based revisions (e.g. Verheyen 1959), are important steps toward a revision of heron systematics and demonstrate the potential importance of behavior, especially agonistic and sexual behavior, in this group. Although feeding behavior will probably not be so amenable to taxonomic interpretation, at least one taxonomic question, the conspecificity of *Egretta thula* and *Egretta garzetta*, revolves in part around their feeding behavior (Voous 1960 and Murton 1972 vs. Curry-Lindahl 1971).

Learning in herons, especially the role of interspecific and intraspecific learning of feeding behavior, is a field in which study has scarcely begun. Both Meyerriecks (1971) and I (Kushlan 1973a) briefly noted possible examples of such learning. Studies of this aspect of heron behavior are essential to a clear understanding of the significance of the occurrence of various feeding behaviors noted in Table 1.

Feeding behavior can contribute importantly to the understanding of heron ecology. Studies such as Jenni (1969), Recher and Recher (1969, 1972), Siegfried (1971), Murton (1972), and Kushlan (1972, 1976) provide a beginning. The role of habitat in determining heron feeding behavior is an often overlooked variable in such studies. For example, my observations suggest that variation in availability of prey may in some instances determine feeding behavior (Kushlan 1972). In that differences in type and density of prey, predator density, water depth, plant cover, and other parameters of the feeding site differ from one location to the next, feeding efficiency and behavior may be expected to vary also. Such variables must be considered in the ecological analysis of heron feeding behavior. Future studies of both the ethological and ecological aspects of heron feeding behavior require standardized terminology, clear understanding of the descriptive aspects of each behavior, and knowledge of the occurrence of various behaviors in different species. It is hoped that the present paper will provide a common background for such future studies.

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SUMMARY

North American herons use at least 28 different feeding behaviors, each of which is briefly described in this paper. The occurrence of various

behaviors in 12 species of North American herons is documented in a comparative behavior chart that shows that bitterns and night-herons are the least versatile species whereas the medium sized day herons are the most versatile and most active species. No species is known to use all 28 feeding behaviors. Heron feeding behavior is an especially useful tool in ecological studies.

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