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Feeding Ecology of Wading Birds

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WADING birds — herons, storks, ibises, and spoonbills — have elicited an exhaustive and exhausting literature describing their foraging ecology and food habits. Although many of their interesting behaviors and habits are rediscovered by succeeding generations of field biologists, detailed ecological studies are few and dispersed over three decades and several continents. In the present paper, I attempt to summarize what is known about the feeding ecology of wading birds in the hope of providing a foundation for future work, to build some structure upon that foundation, to seek generalities, and to provide tentative explanations for some of the patterns found. I hope these explanations will be useful as hypotheses to be tested by artificial and natural experiments. The discussion centers around two major and intimately associated facets of feeding ecology — foraging behavior and food habits. Together they suggest the evolutionary pathways wading birds have followed and their role in natural ecosystems. The review ends by providing some directions for future research.

Foraging Behavior

Understanding the ecological aspects of foraging requires use of a standardized nomenclature and knowledge of the distribution of various behaviors among wading bird species. Size of bird, behavioral plasticity, evolutionary history, and learning all influence feeding behavior. The use of various mechanisms for catching prey depends in part on a species' morphological and physiological adaptations and on the availability of various types of prey. Spacing systems, ranging from wide dispersion to aggregation, correlate with the nature and defensibility of the food resources. Aggregative foraging leads to behavioral associations such as commensalism and prey robbing.

Nomenclature of Feeding Behavior

The foraging repertoire of wading birds can be conveniently divided into postures, which are general physical attitudes, and feeding behaviors consisting of postures and actions directed toward obtaining prey. Although the distinction between postures and behaviors is certainly not precise, it is useful to distinguish postures because they are used in various behavioral settings and so provide subcategories for behaviors. The use of a particular posture may be ecologically significant as it is often correlated with habitat or prey variables.

Although postures used while foraging often blend together, several that are used by wading birds are usefully distinctive. In crouched posture the bird stands with its body parallel to the ground or to its perch, often with legs bent and head pointed down or lower than about 30 degrees below the horizontal. In upright posture the bird stands straight with body angled away from the water. In erect posture the head and neck are elevated, usually around 90 degrees to the horizontal, with bill level or pointed upward.

Several neck postures also are quite recognizable in wading birds. In peering over, the bird turns its head so that the bill is pointing down. In head tilting, the bird turns its head and neck to one side. In head cocking, the bird turns only its head to one side. In facing down, the bird's head and bill are pointed downward and submerged in the water during feeding.

Distinguishing different behaviors provides a useful tool for heuristic and analytical purposes. It is, however, a rather simplistic exercise since no named behavior is precisely alike from one species to the next. Furthermore, using the same name for a similar-appearing activity in two species does not in itself imply homology. The occurrence of similar behaviors in diverse groups may be the result of analogous solutions to pervasive ecological problems. Behaviors are nearly infinitely divisible. It may be useful for some purposes to distinguish, for example, various types of foot stirring or various types of bill probing. For other analyses, only broad categorization may be necessary. Nevertheless, since comparability between studies is important, a standardized nomenclature should be used when possible.

Thirty-eight feeding behaviors are presently distinguished in wading birds, some of which have been defined previously (Meyerriecks 1962; Kushlan 1976*a*, in press *a*). These are:

Standing — stands in one place

Bill vibrating — rapidly opens and closes bill in water

Baiting — places material that attracts prey in water

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Standing flycatching — while standing catches prey that is airborne

Gleaning — catches prey located on an object (e.g., an emergent plant) above water

Flipping — turns over objects (e.g., rocks, shells, dung) to feed underneath

Head swaying — moves head from side to side out of water, in either slow or rapid sweeps

Neck swaying — moves neck and sometimes body from side to side out of water

Head swinging — moves bill from side to side in water

Forward ploughing — walks with bill under water and projecting forward

Bill dragging — drags bill through water at side of the body

Probing — quickly and repeatedly moves bill tip into and out of water or substrate

Groping — places and holds open bill in water

Pecking — picks up item from substrate

Table 1. Occurrence of feeding behaviors among representative species of herons.

	Great Blue Heron	Black-headed Heron	Goliath Heron	Purple Heron	Great Egret	Reddish Egret	Black Heron	Louisiana Heron	Cattle Egret	Little Blue Heron	Snowy Egret	Eastern Reef Heron	Paddybird	Green Heron	Agami Heron	Yellow-crowned Night Heron	Black-crowned Night Heron	Boat-billed Heron	Bare-throated Tiger Heron	Least Bittern	American Bittern
Standing	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Bill vibrating					X				X		X						X				
Baiting														X							
Standing flycatching	X								X					X			X				
Gleaning					X				X												
Head swaying					X				X	X	X			X		X					
Neck swaying		X			X				X					X		X		X		X	X
Head swinging					X																
Probing	X								X												
Pecking	X				X			X	X		X					X					
Walking slowly	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X
Walking quickly						X		X	X	X	X										
Running	X				X	X	X	X	X	X	X										X
Hopping	X				X	X		X	X	X	X	X									
Leapfrog feeding					X			X	X	X	X										
Wing flicking	X				X	X		X		X	X									X	
Openwing feeding						X		X		X	X										
Underwing feeding						X		X			X										
Double-wing feeding						X															
Canopy feeding							X														
Foot stirring					X	X	X	X			X	X		X							
Foot raking						X		X		X	X			X							
Foot probing											X										
Foot paddling											X										
Hovering	X			X	X	X		X		X	X						X				
Hovering stirring						X		X			X										
Dipping					X			X		X	X	X									
Foot dragging								X		X	X										
Aerial flycatching									X												
Plunging	X				X												X				
Diving														X							
Feetfirst diving	X									X							X				
Jumping	X												X	X							
Swimming feeding	X		X		X			X						X			X				

Walking slowly — walks at slow speed
Walking quickly — walks at relatively fast speed
Running — moves quickly
Hopping — flies short distance and alights
Leapfrog feeding — flies from back of feeding flock to front
Wing flicking — quickly partially extends and retracts wings
Openwing feeding — completely extends and retracts one wing
Underwing feeding — puts head under extended wing for strike
Double-wing feeding — brings wings forward and holds them over head
Canopy feeding — bring wings forward and downward above head to form a closed canopy
Foot stirring — vibrates foot or leg
Foot raking — rakes substrate with foot
Foot probing — probes with foot
Foot paddling — moves feet up and down
Hovering — hovers over water or ground, picking up prey
Hovering stirring — hovers while patting, raking, or stirring with feet
Dipping — while flying puts head down and catches prey

Table 2. Occurrence of feeding behaviors among representative species of storks and relatives.

	Wood Stork	African Open-billed Stork	Abdim's Stork	White Stork	Black-necked Stork	Jabiru	Marabou	Shoebill	Hammerkop
Standing	X	X	X	X	X	X	X	X	X
Standing flycatching				X			X		
Gleaning									X
Head swinging	X								
Probing		X	X	X		X	X		X
Groping	X	X		X	X	X	X		
Walking slowly	X	X	X	X	X	X	X	X	X
Walking quickly				X					X
Running				X	X	X	X		X
Pecking							X		
Wing flicking	X								X
Openwing feeding	X							X	
Foot stirring	X								X
Hovering									X

Foot dragging — while flying drags toes or feet through water
Aerial flycatching — while flying catches airborne prey
Plunging — dives headfirst from air
Diving — dives headfirst from perch
Feetfirst diving — alights on water feetfirst
Jumping — jumps from perch feetfirst
Swimming feeding — swims or floats on surface of water

Uses of Feeding Behaviors

The uses of feeding behaviors by 37 herons, storks, and ibises are shown in Tables 1, 2, and 3. References are in Appendix 1. Species were selected to represent the major lines of wading bird adaptation with emphasis on those for which information is available.

Standing is a virtually universal foraging behavior among wading birds. In birds that feed nonvisually, standing involves some type of active foraging in place and includes such behaviors as probing or groping. All herons stand and wait for prey to approach. This behavior is used in the water, on a perch, on land, or on floating plants with any of the basic postures. Positions used are variable. In small herons, such as the Green Heron (*Butorides striatus*), standing may even involve hanging onto its perch by its feet with its head down. Standing in erect posture is often used when a bird is feeding in aggregations where agonistic encounters are common. Upright posture is an advertis-

Table 3. Occurrence of feeding behaviors among representative species of ibises.

	White Ibis	Glossy Ibis	Bald Ibis	Hadada	Sacred Ibis	African Spoonbill	Roseate Spoonbill
Standing	X	X	X	X	X	X	X
Running						X	X
Gleaning							X
Flipping			X				
Head swinging	X	X			X	X	X
Forward ploughing						X	
Probing	X	X	X	X	X		
Groping	X	X					X
Hopping						X	X
Pecking	X	X		X		X	X

ing display as well as a way of viewing a relatively wide area for potential prey. Crouched posture is used from land, perches, or in the water. It restricts the field of vision but brings the head closer to the strike zone. A standing bird may sometimes glean insects off nearby plants. Standing flycatching usually involves insects, but larger prey such as birds may also be taken.

Walking slowly also is a behavior used by most species. It usually involves carefully looking for or stalking prey. Both upright and crouched postures are used. The speed of walking differs among species, and this behavior often merges imperceptibly with standing. Walking differs markedly in different species. Little Blue Herons (*Florida caerulea*), for example, often appear to crisscross the same area, whereas Snowy Egrets (*Egretta thula*) appear to continuously move away from previous locations.

Movements and postures of the head and neck are often important components of standing or walking feeding (Meyerriecks 1962, Krebs and Partridge 1973, Beasley 1975). Head tilting is used to overcome glare from the sun by shifting the glare away from the striking zone. Head cocking and peering over are used to locate prey by birds with monocular and binocular vision, respectively, and probably to reduce refraction distortion. Walking birds may use head bobbing, a sinuous forward and backward movement of the head and neck. Although not considered a feeding behavior, it probably functions in obtaining parallax while walking. Head and neck swaying are commonly used (Meyerriecks 1962, North 1963, Ali and Ripley 1968, Blaker 1969*a*, Carpenter 1971, Siegfried 1971*b*, Dinsmore 1973) and also permit birds to obtain better parallax. Although herons have good binocular vision, thus reducing the need for such behavior, head swaying may be used to provide a precise estimate of distance and location when only a single strike is probable, such as on particularly cyptic prey or those that can readily escape. Head swaying in Cattle Egrets (*Bubulcus ibis*) is associated with unsuccessful feeding attempts, suggesting that the potential prey sought are rather difficult to catch. The function of neck swaying is obscure, although in some species, such as bitterns, it may increase camouflage. It may also permit a quicker strike, by having muscles in movement when the strike begins.

Behaviors such as walking quickly, running, and hopping are often categorized as disturb-and-chase feeding (Meinertzhagen 1949; Meyerriecks 1960*a* and *b*, 1962; Kushlan 1976*b*). However, they may be primarily used to move quickly from one location to the next and to better spot and overtake moving prey, rather than to disturb quiescent prey. Running is often accompanied by wing actions for balance and quicker movement. The extent to which prey are actually disturbed by such movement is unclear. Prey may seldom be frightened into drastic avoidance or escape reaction. It is more likely that disturbance feeding usually causes only slight movement of prey, and thus moderate rather than drastic behaviors are more likely to function in disturbing susceptible prey.

Leapfrog feeding has been described in several species, often as an example of joint feeding and communal beating (Meyerriecks 1960*a* and *b*, 1962; Blaker 1969*a*; Siegfried 1971*b*; Wiese and Crawford 1974). It appears, rather, to be a form of hopping in which a bird moves to the head of an on-moving aggregation and in so doing moves to the better, forward position in the group. There are several lines of evidence to support this. When Abdim's Storks (*Ciconia abdimii*) congregate in an area, individuals increase their walking speed to stay ahead of others (Condy 1965). Cattle Egrets run and hop to keep ahead of a herd of moving cattle (Dawn 1959), and they use pure leapfrog feeding when following farm equipment in a cleared field. In this case one bird moves to the head of the aggregation nearest the new food source exposed by the plow. It lands, forages awhile, and then hops to the head again. In tall grass, where this behavior is most common, flying may be the only practical way to catch up with the moving aggregation. Restlessness and the molification achieved by flying up and seeing other birds nearby are not required to explain the behavior but may function secondarily. There is no evidence to suggest that leapfrog feeding functions in communal beating. Cattle Egrets, the primary perpetrators, in general are well dispersed when feeding and maintain fairly large feeding territories within the aggregation.

Wings are often used in foraging (Ayres 1878; Loveridge 1922; Rand 1936; Jackson 1938; Delacour 1946; Curry-Lindahl 1960; Meyerriecks 1960*a*, 1962; du Plessis 1963; Markus 1963; Kahl 1964). Wing flicking and openwing feeding may be used to disturb prey. Underwing, double-wing, and canopy feeding help increase visibility by reducing glare. The canopy position is often, although not always, assumed with back to the sun, thereby producing a shadow in front of the bird. Fish may be better seen at the edges of this umbra made by the wings. Whether fish are actually attracted to the shade deserves further study. Meyer-

riecks (1960*a*) has seen fish swim toward the shadow made by the wing of a Reddish Egret (*Dichromanassa rufescens*) while it was canopy feeding. Black Herons (*Melanophoyx ardesiaca*) foot stir within the shadow. I distinguish the double-wing feeding of the Reddish Egret from the canopy feeding of the Black Heron because of differences in execution.

Special use of feet in foraging also is common among wading birds (Baird et al. 1884; McIlhenny 1936; White 1947; Haverschmidt 1948; Rand 1956; Hobbs 1957; Meyerriecks, 1959, 1962, 1966, 1971; Markus 1963; Kahl 1964, 1972*a*; Blaker 1969*b*; Benson and Penny 1971; Recher and Recher 1972). Foot stirring, raking, probing, and paddling are variations that in part reflect species differences. That several foot-stirring species, such as the Snowy Egret, Little Egret (*Egretta garzetta*) and Wood Stork (*Mycteria americana*), have differently colored feet suggests that this may be a morphological correlate of foot stirring. It is probable that foot movement causes prey to move from hiding rather than attracting them. Bright-colored toes more likely would startle than lure prey, and foot stirring is used most often in mud, aquatic and terrestrial vegetation, or in murky water where fish are less visible and must be forced to reveal themselves.

Other forms of behavior do attract prey (Stone 1937, Drinkwater 1958, Lovell 1958, Meyerriecks 1960*a*, du Plessis 1963, Parks and Bressler 1963, Buckley and Buckley 1968, Blaker 1969*a*, Kushlan 1973*a*, Sisson 1974, Norris 1975). Baiting uses a lure, such as bread or a feather, to attract fish and includes placing bait in the water. Bill vibrating uses the rapid opening and closing of mandibles in the water to accomplish the same purpose.

Catching prey in the air occurs infrequently (Audubon 1840, Clark-Kennedy 1875, Warburton 1948, Lovell 1958, Valentine Jr. 1958, Kahl 1966*a*, Hedeen 1967, Griffiths and Griffiths 1969). Aerial flycatching and standing flycatching involve catching flying or otherwise airborne prey. Pursuits of flying insects may occur, and flying or standing herons can catch birds while in flight, or they may even wait patiently while fish ascending a waterfall jump into their mouths.

Feeding from the air takes advantage of particular circumstances of prey availability (Wetmore 1920; Brooks 1923; Grimes 1936; Sprunt Jr. 1936; Fargo 1937; Dickinson 1947; Valentine Jr. 1958; Meyerriecks 1959; Marshall 1961; ffrench 1965; Abdulali 1967; Waters 1967; Jenni 1969; Kushlan 1972, 1973*b*; Reese 1973; Mock 1974; Rodgers 1974, 1975; Gochfeld 1976). Such behaviors are used when less energetic behaviors fail or when prey particularly vulnerable to these feeding methods becomes available. Dipping and hovering often involve foraging for dead or dying prey. Foot dragging differs from other aerial behaviors, in which feet happen to touch the water, in that they are dragged for long distances, presumably to disturb prey that is then taken while the bird is in flight. Hovering stirring similarly disturbs prey. Herons also pick up fish that jump from the water because of below-surface disturbances. Efficient use of aerial feeding may in some instances require wind.

Wading birds, generally limited to the use of water shallower than their leg lengths, have developed several behaviors for deeper water (Pearson 1850, Brooks 1923, Bent 1926, Jensen 1930, Dickinson 1947, Hawbecker 1949, Boyle 1967, Hedeen 1967, Stacey and Gervis 1967, Kushlan 1973*b*, Mock 1974). Aerial feeding is often used over deep water. Diving, plunging, feetfirst diving, and jumping involve entering relatively deep water to catch prey. Swimming and floating have been noted in many wading birds (Townsend 1912, Weston Jr. 1913, Bent 1926, Donaldson 1926, Hoffman 1941, Dickinson 1947, White 1947, Greene 1960, Allsopp and Allsopp 1965, Hedeen 1967, McCulloch 1967, Stimpson 1968, Kushlan 1976*a*, Mock 1976) and may be used to feed in deep water.

Nonvisual foraging behaviors such as head swinging, probing, and groping are used extensively by several species (Baird et al. 1884; Allen 1942; Parsons 1947; Kahl 1964; Kahl and Peacock 1963; Poorter 1969; Siegfried 1971*b*; Mock 1975; Vestjens 1975; Kushlan, in press *a*, in prep.). Most storks and ibises have nonvisual components to their feeding repertoire, and many herons, particularly Cattle Egrets, sometimes probe and peck nonvisually. Such tactolocation, especially groping, is most effective when prey density is relatively high. The ability of most tactile-foraging species to use vision, also, enlarges their fundamental foraging niche (Kushlan and Kushlan 1975; Kahl 1966*a* and *b*; Kushlan, in press *a*). Nonetheless, even when experimentally presented with clear water and high prey density, Wood Storks and ibises generally resort to tactile foraging.

Prey Capture

Methods of prey capture differ among wading birds and to some extent among individuals. A bill snap is a

rapid bill closure in reflex to tactile stimulation by a prey item. In the Wood Stork the bill-snap reflex averages about 25 milliseconds (Kahl and Peacock 1963). Kahl and Peacock postulated that bill closure is a myotatic response to stretching the jaw musculature. I think it likely that the stimulus of most prey items would be too small to cause such jaw stretching and suggest rather that the bill-snap response is mediated by tactile receptors beneath the tomia.

A bill grab consists of grasping prey in a forceps fashion without a quick darting of the neck. This is used by both visual and nonvisual foragers and is typically used by visually foraging storks. Ibises, spoonbills, and herons use it when a prey item is dead or slow-moving.

A bill thrust is a downward or lateral strike involving fast, directed movement of head, neck, and body. It is the usual technique of herons. The Louisiana Heron (*Hydranassa tricolor*) often crouches and strikes nearly horizontally to the water, while Little Blue Herons and Great Egrets (*Casmerodius albus*) often strike deeply and nearly vertically. Strikes may be made with neck curled into an S-shape or nearly extended and only slightly curved. The head may be lowered or extended slowly toward a prey item, and then the thrust made with the neck near full extension. A bill thrust may be accompanied by a body lunge, during which parts of the body may submerge. This occurs at times with neck drawn back but more often when the neck is nearly fully stretched. Reddish Egrets and Reef (*Egretta sacra*), Green, and Louisiana Herons spring up and then lunge downward into the water. Most bill thrusts are diagonal and must compensate for refraction (Cassin 1846, Zimmer 1918).

There is extended discussion in the literature as to whether striking birds pierce or grasp their prey (Audubon 1840, Coues 1872, Michael 1934, Roberts 1936, Hunter 1937, George 1941, Meyerriecks 1960*a*, Pringle 1964, Hedeen 1967, Recher and Recher 1968, Willard 1976). The method of capture depends mostly on bill and prey morphology. A strike is usually made with the bill slightly open. Small and thin fish are usually grasped; wide or large prey may be stabbed, more often with one than with both mandibles. The bill thrust itself is not therefore an adaptation for impaling prey, because impaling occurs in a minority of thrusts. Thick-billed herons seldom spear fish; thin-billed birds often do.

All species have tactics for handling and subduing prey that cannot be immediately swallowed (Clark-Kennedy 1875, Gabrielson 1914, Bent 1926, Saunders 1926, Jensen 1930, Andrews 1948, Goodwin 1948, Witherby et al. 1952, Hobbs 1957, Valentine Jr. 1958, Meyerriecks 1960*a*, Pringle 1964, Cunningham 1965, Kahl 1966*b*, Recher and Recher 1968, Blaker 1969*a*, Carpenter 1971, Dennis 1971, Vestjens 1973, Snow 1975, Kushlan, in prep.).

Most prey items are mandibulated with bites or bill snaps. The prey may move up the bill during the process, be released, then recaught at the bill tip. Large, hard, or dangerous prey may be battered, rubbed, shaken, dropped, or stabbed, and may be picked apart and eaten in pieces. Often a prey item will be carried to an exposed place. The Australian White Ibis (*Threskiornis molucca*) holds mussels against a rock with its feet while stabbing them. (This is not a case of tool use as Vestjens [1973] implied.)

Size and type of prey determine handling time. Large prey takes more handling, and time increases exponentially with prey size (Kushlan, in prep.). Defenses of prey, such as spines, hardness, violent contortions, wriggling, wrapping, or inflation, increase handling time and the chance that the prey may escape. Large birds can deal with defensive structures better than small ones can (Fig. 1, data from Recher and Recher 1968). Wading birds usually swallow small prey immediately after capture by either flipping the bill upward and catching the item or by releasing the prey and moving the mouth forward to catch it. Ibises using the latter method can swallow

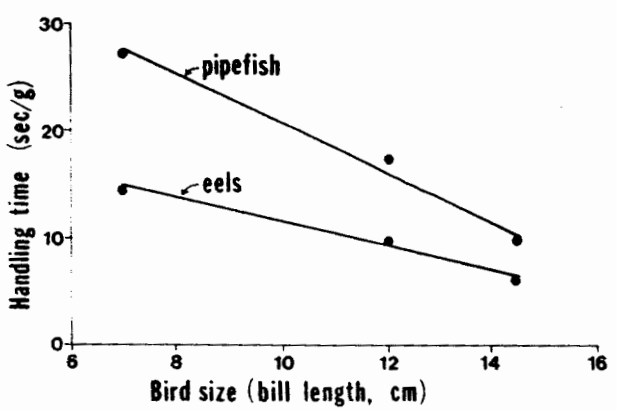

Figure 1. Relationship of handling time to size of bird. The size of heron is measured by bill length. Handling time for each prey type is expressed as seconds per gram of prey to eliminate the bias of different prey sizes being caught by different herons. Handling time therefore measures the difficulty of handling a type of prey rather than a size of prey.

prey nearly instantaneously without altering their head-down posture.

Wading birds may or may not pause after prey capture. Pause time is generally longer with larger prey. Swallowing in herons is often followed by head shaking and by dipping the bill in the water (Kalter 1932, Longley 1960, Meyerriecks 1960*a*, Carpenter 1971, Dennis 1971, Tomlinson 1974). The function of dipping undoubtedly is to ease food passage. Although bill dipping may not follow the capture of small prey, the behavioral sequence is so tightly bound that birds often dip following misses. Ibises and storks apparently do not bill dip after swallowing most prey but will take a drink after a large item by lowering their bills into the water. Herons use their long tongues (Gardner 1925) to wipe the edge of their bills after swallowing.

Correlates of Feeding Activity

There is a general correlation in wading birds between size and feeding activity (Meyerriecks 1960*a*, Kushlan 1976*a*). This is particularly apparent within a closely related group. Figure 2 shows the average activity value of the known feeding repertoire of various herons. Large and small species tend to be less active and use standing or walking behaviors. Medium-sized species tend to engage in many active behaviors. Larger herons are inactive because of the relatively large energy expenditure required to overcome their inertia. Small herons are inactive because their morphology inhibits wading to any great depth and therefore they feed by perching over the water or standing at the water's edge. The difference in activity between large and medium-sized herons is noted in several aspects of their biology, including breeding activity, and their tendency to be provoked to flight.

Given a repertoire of potential behaviors, a bird chooses one to fit its current circumstance. It might be expected that a bird would choose a behavior that provided the greatest net energy return. It may only be necessary, however, that the bird's net energy return be positive. The bird is more likely to choose a behavior based on its success rate or on the time between successes than on net energy return. Similarly, among various species it is expected that the species that is more successful at using a behavior will use it more often than a species that has less success with the same behavior (Fig. 3, data from Meyerriecks 1959). Thus, the Snowy Egret stirs more often than does the Green Heron, probably because

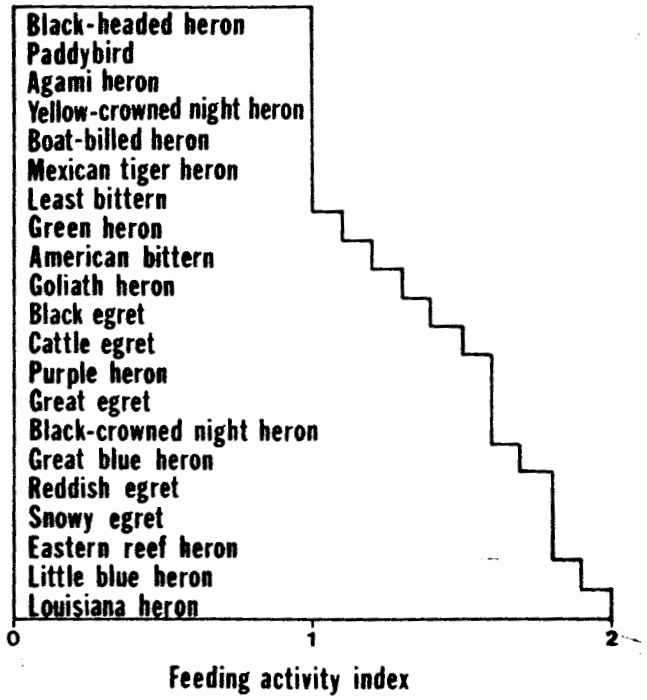

Figure 2. Feeding activity of herons. Feeding activity index measures the average activity value of a species' behavioral repertoire. The index was calculated by assigning activity values ranging from 0 (inactive) to 3 (very active) to each behavior in Table 1, summing the total for each species, and dividing by the total number of behaviors described for that species.

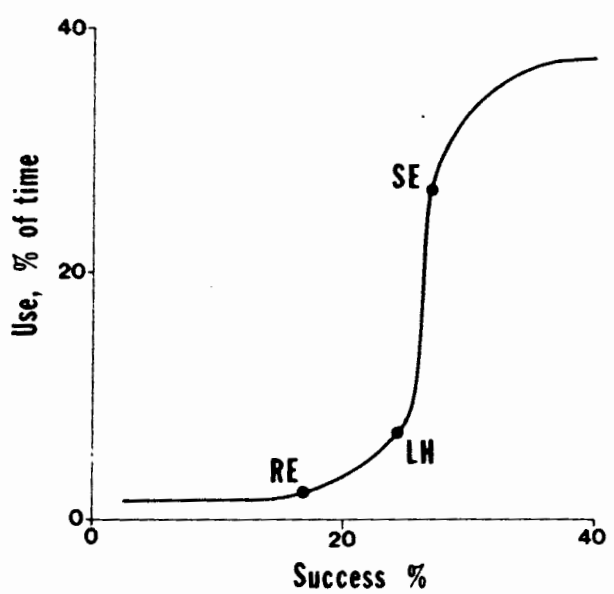

Figure 3. Relationship between frequency of use of foot stirring by three species of herons and their feeding success. (SE = Snowy Egret, LH = Louisiana heron, RE = Reddish Egret)

morphological and behavioral adaptations permit greater success with the behavior.

An individual may switch behaviors because of changes in the pattern of prey availability (Kushlan 1972, 1973*a*, 1976*c*; Mock 1974). The appearance of frogs, dying newts, or schooling fish in deep water may elicit aerial feeding. Nocturnal oxygen depletion can force fish toward the surface near dawn, and wading birds may best catch these fish by standing and waiting for them. As oxygen levels become less restrictive during the day, fish may become less available near the surface, and more active behaviors may be required of a foraging heron. Many such variations in prey availability may correlate with the selection of particular feeding behaviors.

Different habitats or structural niches may require different techniques. Active behaviors are ineffective in dense habitats. Thus, it is expected that individuals may vary their behavior from habitat to habitat, season to season, or even minute to minute. White Ibises (*Eudocimus albus*) alter their behavior when searching in different types of structural niches (Kushlan, in press *a*). Within several minutes a bird may make shallow multiple probes around the base of a plant, move to soft mud and probe deeply, and finally go into deep water and head swing.

Most foraging behaviors and postures also serve, to a greater or lesser extent, a display function by possessing a message content independent of the foraging function. In at least two cases an entire behavioral sequence has achieved display status of as yet unknown meaning (Cooper 1970, Kahl 1973). The flap-dash display of Saddle-billed (*Ephippiorhynchus senegalensis*) and Black-Necked (*E. asiaticus*) Storks mimics their active foraging behavior but terminates with ritualized rather than consumatory bill thrusts. The run, canopy/ run, canopy feeding sequence of the Black Heron is apparently used in communication, probably as an advertisement or territorial display. Agonistic behavior is temporally associated with feeding behavior. The erect foraging posture of Great Egrets and Great Blue Herons (*Ardea herodias*) is a low-intensity agonistic display used in response to disturbance or to a potential interindividual encounter, particularly prior to prey robbing (Hedeen 1967, Kushlan, in prep.). The upright foraging posture is also an alert and advertisement posture. Most foraging behaviors convey messages of alertness, nonalertness, and identification to other birds. The mere presence of a feeding individual signals foraging opportunity, the message being enhanced or degraded by co-occurring feeding behaviors and by the bird's apparent foraging success.

Evolution of Feeding Behaviors

The evolutionary links of many feeding behaviors are readily forged. Disturbance techniques that include foot and wing movement are probably derived from walking and balancing motions. The swimming ability of wading birds permits their developing deep-water feeding techniques. Prey attraction behaviors, such as bill vibrating and baiting, are probably derived from drinking and standing, respectively.

The similarity of behaviors in diverse wading bird groups poses difficulties in distinguishing behaviors that are convergent from those that represent primitive shared characteristics. The wide occurrence of some simple behaviors suggests they are primitively derived. An example is the spotty occurrence of wing flicking in some day herons, one bittern, one genus of storks, and the Hammerkop (*Scopus umbretta*).

The occurrence of bill vibrating in one night heron and one terrestrial and two aquatic egrets may be an example of convergence of feeding behaviors. Meyerriecks (1960*a*, 1962) concluded that wing flicking, openwing, underwing, double-wing, and canopy feeding represent an evolutionary sequence in the elaboration of increasingly complex behaviors. While a hierarchy of complexity undoubtedly exists within this sequence, it is possible that a common primitive behavior such as wing flicking was convergently elaborated upon by several species. In each species those behavioral and morphological adaptations coevolved that were suited for its particular foraging conditions. That each achieved somewhat similar results may be a testament to similarity of the original evolutionary fabric and common environmental pressures. The Black Heron has not yet been reported to use the simpler behaviors in the openwing sequence. It may have possessed and then lost them, or it may just use them infrequently because of its success in canopy feeding, or it may never have possessed them. Given alternative interpretations, it should not necessarily be considered that canopy feeding derives from simpler behaviors presently existing in other species.

Certain feeding patterns are apparent within ciconiiform groups. Wading bird taxa appear to specialize in one of two main foraging strategies, visual or tactile (Fig. 4). Secondary adaptive dichotomies also occur. Visual foraging predominates in the herons. *Ardea*, *Ardeola*, and *Tigrisoma* herons

primarily wait or search, while other groups are more active. Storks show a dichotomy between primarily visual foraging and primarily tactile foraging tribes. Ibises follow the tactile strategy and show two evolutionary trends, one adapted to probing and one to head swinging. The common ancestry of these evolutionary dichotomies is illustrated by the occasional use of probing by spoonbills and head swinging by ibises.

Learning

Juveniles must learn to feed effectively (Allen 1942, Palmer 1962, Recher and Recher 1969*a*, Milstein et al. 1970, Siegfried 1971*a*, Snow 1975, Kushlan, this paper). The usual feeding behaviors of a species are innate and are often practiced before fledging. Herons mock hunt at the nest; ibises probe the ground around the colony; spoonbills head swing in shallows adjacent to the colony site. Although it is apparent that juvenile wading birds are less proficient in foraging, data demonstrating this are limited. The best information is from Recher and Recher's (1969*a*) study on the Little Blue Heron. They found differences in success rate and net energy return in one area, although not in another area. However, in that plumage differences may alter foraging effectiveness

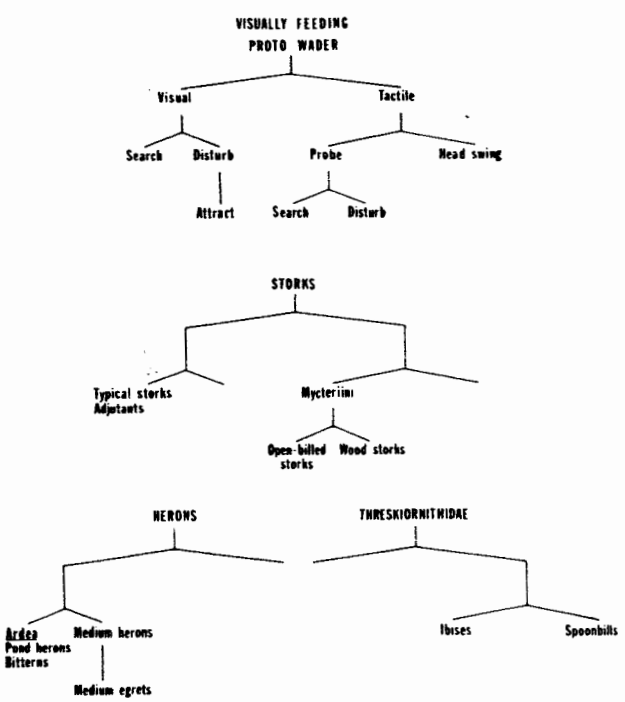

Figure 4. Elaboration of feeding strategies in the three groups of wading birds.

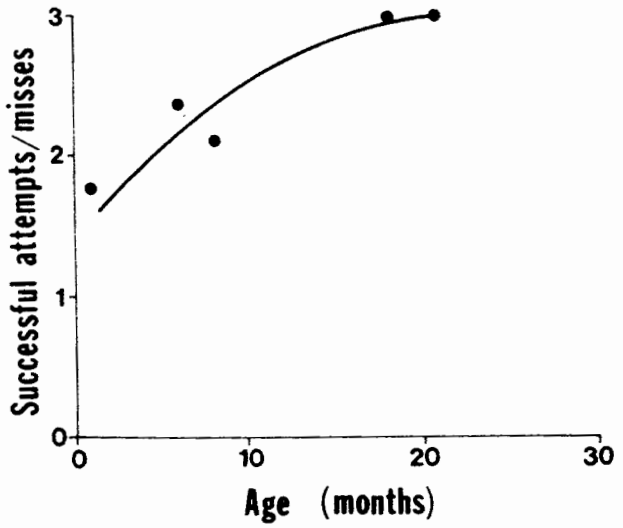

Figure 5. Foraging success of Little Blue Herons in relation to age of bird. Plumage color and geographic location differ among data sets.

irrespective of intrinsic differences in ability, this species may be a poor model for studying juvenile learning. Future studies should obtain information in which the variables of location and plumage color are eliminated. I suggest that such studies would show that juveniles increase their foraging efficiency with time, as is suggested in Figure 5 (data from Recher and Recher, 1969*b*).

Adults also probably learn foraging techniques and learn when to use them (Longley 1960; Marshall 1961; Recher and Recher 1968; Meyerriecks 1971; Siegfried 1971*a*; Kushlan 1973*a*, 1976*c*). Trial-and-error learning of prey handling, and learning about novel foraging opportunities, appear widespread. Locating new foraging locations or discovering potentially dangerous habitats also are often learned by trial and error. Social observational learning may be locally important in eliciting use of certain feeding behaviors, especially infrequently used ones such as bill vibrating or diving. The sporadic report of some behaviors in various wading bird species may result from interspecific observational learning. Habituation to disturbances and other environmental situations occurs commonly.

Foraging Schedule

Time-budget studies of wading bird foraging are needed to understand the uses of various behaviors. Most wading birds typically forage most actively near dawn and dusk and rest in midday, but other factors

may determine the feeding schedule. Tide is important in many coastal locations (Peacock Jr. 1850, Verwey 1930, Allen 1942, Recher and Recher 1972, Krebs 1974, Snow 1975). Most coastal wading birds roost during high tides and forage during falling and low tide. During nesting or other periods of high energy demand, more time is needed for foraging, and so birds will often forage at high tides or fly long distances into nontidal habitats where food is probably less available than at low-tide sites.

Species differences in timing of feeding can be seen in the feeding schedule of their nestlings (Kahl 1966*b*, Whitelaw 1968, Milstein et al. 1970, Kushlan, in press *b*). White Ibises generally have peaks of nestling feeding at 0900 and 2100 hours corresponding to early-morning and late-day adult foraging, whereas Marabou Storks (*Leptoptilos crumeniferus*) have a single peak between 1300 and 1400, because adults depend on thermals for transportation and return to the colony from midmorning to midafternoon (Fig. 6, data from Kushlan in press *b* and Kahl 1966*a*). In the White Ibis, the feeding activity pattern of nestlings in-

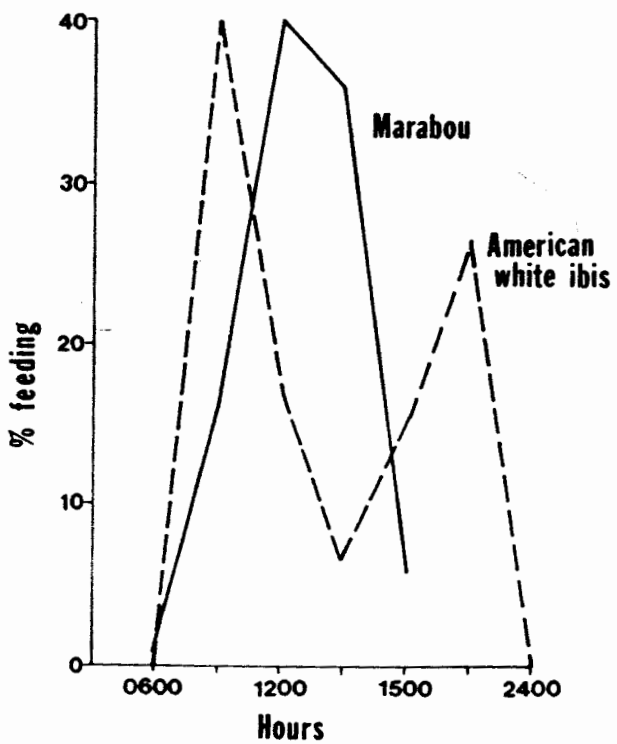

Figure 6. Feeding activity of nestling wading birds. Activity measured by the percentage of the total number of daily feedings provided within three-hour blocks.

nately corresponds to the feeding cycle shown in Figure 6.

Night foraging is widespread among wading birds, and some species specialize in this strategy (Waterton 1835; Baird et al. 1884; Hudson 1920; Dawson 1923; Saunders 1926; Jackson 1938; Witherby et al. 1952; Taylor 1957; Curry-Lindahl 1960; Mackworth-Praed and Grant 1962; Kahl and Peacock 1963; Kahl 1964, 1965; Markus 1963; Milstein et al. 1970; Mukherjee 1971; Krebs 1974; Mock 1975). Tactile foragers such as Wood Storks sometimes feed at night, but ibises apparently seldom do. It is possible that the nocturnal night herons, Boat-billed Heron (*Cochlearius cochlearius*), and Shoebill (*Balaeniceps rex*) will be shown to sometimes feed tactilely. Although night herons typically forage at dusk, some, especially Yellow-crowned Night Herons (*Nyctanassa violacea*), often forage during the day, particularly where their foraging schedule is determined by tides. Black-crowned Night Herons (*Nycticorax nycticorax*) also feed diurnally during periods of high energy demand or high food availability. *Ardea* herons — particularly the Great Blue, Gray (*A. cinerea*), Cocoi (*A. cocoi*), and Purple (*A. purpurea*) — the Striated Heron (*Butorides striatus*), pond herons, and (*Ixobrychus*) bitterns feed at dusk and at night. Although foraging efficiency is undoubtedly reduced at night in diurnal herons, the food obtained then may be an important component of the energy budget, particularly during nesting.

Morphological Adaptations for Feeding

Structure

Structural adaptations of wading birds have been studied often (Baird et al. 1884; Shufeldt 1889; Mitchell 1913; Gardner 1925; Witherby et al. 1952; Hofer 1954; Adams 1955; Bock 1956, 1960; Verheyen 1959; Hartman 1961; Huxley 1962; Parks 1962; Humphrey and Parkes 1963; Král 1965; Wetmore 1965; Kokshaysky 1966*a*; Lange and Staaland 1966; Dubale and Mansuri 1969; Vanden Berge 1970; Payne and Risley 1976).

Of all the structural adaptations for feeding, the bills of wading birds may be the most obvious (Fig. 7). Thick heron bills are probably an adaptation for prey handling, while thin bills are adapted for securing fast-moving prey. The elongated bills of Agami (*Agamia agami*) and Louisiana Herons increase the effectiveness of their darting stroke. Bills that are long and thin are generally adapted for catching fast-moving prey,

while bills that are large and thick permit taking large prey of several types. Long bills do not necessarily correlate with a bird striking deeply, as has been suggested. Louisiana Herons, long-billed birds, most often strike horizontally. On the other hand, the relatively short, thick, slightly down-curved bill of the Little Blue Heron is often used for deep striking. Small bills are associated with terrestrial habits in both herons and ibises. In ibises, probing requires a deeply down-curved bill; head swinging requires a bill with large surface area. Storks show much the same range of bill shapes as do herons and ibises together. Tactile foraging is associated with a heavy ibislike bill in the Wood Storks. The specialized gaping bill of the Open-billed Stork (*Anastomus lamelligerus*) is used for handling and extracting mollusks, probably by providing opposing bill tips that effect a forceps-type action on hard, slippery shells. The bill of the Shoebill is convergent with the Boat-billed Heron's in gross shape. These bills may function in nighttime foraging on relatively slow-moving prey and also very likely to provide structural strength for handling large prey. The typical storks have heronlike bills which are used for grabbing and bill snapping more than for striking and are therefore relatively thicker and larger.

The head and neck are similarly adapted for feeding. The eye position of herons and ibises permits binocular focus beneath or at the tip of the bill. The eyes of night herons, the Boat-billed Heron, and Shoebill are enlarged for night foraging, and night herons have tapeta. Night herons have short, stout neck vertebrae which may assist their lunging strikes. Day herons are adapted for using the darting stroke by prolongation of the sixth cervical vertebra and shortening of the seventh vertebra, which forms a lever system.

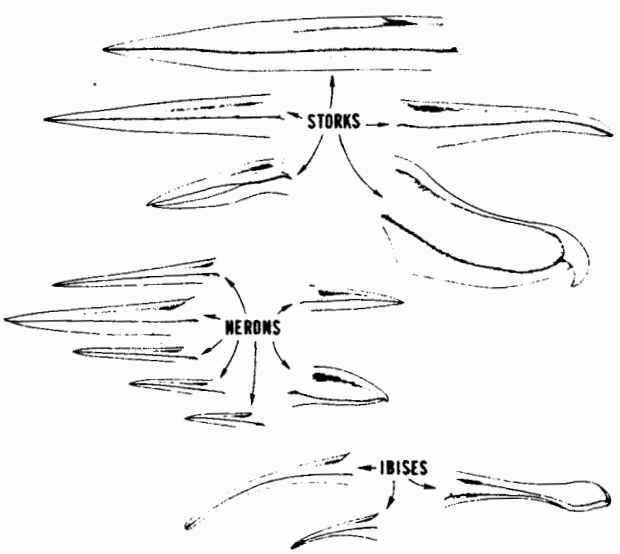

Figure 7. Adaptive radiation of bill morphology in wading birds. Clockwise from top: Storks — Black-necked Stork, Wood Stork, Shoebill, Open-billed Stork, White Stork. Herons — Black-crowned Night Heron, Boat-billed Heron, Cattle Egret, Little Blue Heron, Louisiana Heron, Great Blue Heron, Agami Heron. Ibis — Roseate Spoonbill, Green Ibis, White Ibis. (Drawing to ½ scale)

The trunk of bitterns is relatively compressed for movement through dense vegetation. Morphological differences between Reddish Egrets and Louisiana Herons may be correlated with feeding behavior. Muscular adaptations for soaring flight occur in storks and are correlated with differing foraging behaviors of Little Blue Herons and Snowy Egrets. The legs of *Ardeola* herons are relatively short and associated with shoreline crouching. The feet of the Reddish Egret are relatively small, probably as an adaptation for its active feeding behavior. The Purple Heron and Shoebill have long toes that permit standing on vegetation. Green Herons and bitterns have relatively short outer toes, which may be adaptations for holding onto and climbing on vegetation. Bitterns, pond herons, and the Purple Heron have long, slightly curved claws, which lend support while the birds move through grass.

Sexual dimorphism in body structure, particularly in body size and trophic appendages, is potentially an adaptation for use of different food resources (Selander 1966, 1972). Sexual dimorphism in body structure of wading birds has been little appreciated (Clancey 1968; Kahl 1972*a*, *b*, and *c*; Browder 1973*a*; Kushlan, in press *c*). Males of most spoonbills, ibises, and storks are pronouncedly larger than females in overall size and bill length. Males of some herons, particularly Cattle Egrets, average larger statistically, but unlike the above groups, the dimorphism is not apparent in the field. The bills of male and female White Ibises have a character ratio above that of many sympatric congeneric species pairs showing character displacement (Schoener 1965, 1970). This means that selection for character divergence has resulted in differences of a magnitude similar to that occurring in competing species, suggesting the possibility that males and females partition available resources. Yet I found no significant differences in feeding behavior or food taken between the two sexes of White Ibis. As in all such competition studies, negative results are never conclusive because the search for divergence can con-

tinue ad infinitum. Sexual dimorphism is functional in nest-site defense and pair formation and that, rather than ecological considerations, may be the principal factor in its evolution in some wading birds.

Plumage color

The plumage color of wading birds has been a subject of considerable discussion, often as it relates to feeding ecology. Much of the discussion has concerned color polymorphism and age-dependent plumage phases (Palmer 1909; Mayr and Amadon 1941; Mayr 1945, 1956; Carpenter 1948; Koenig 1952; Amadon 1953; Huxley 1955; Meyerriecks 1957; Milon 1959; Berlioz 1961; Palmer 1962; Fabian and Sterbetz 1966; Recher and Recher 1969*a* and *b*, 1972, in prep.; Benson and Penny 1971; Murton 1971*a*; Recher 1972*a*; Holyoak 1973; Voisin and Voisin 1975; Bolen and Cottam 1975). Plumage polymorphism is prevalent in herons, including the Gray Heron, Great Blue Heron, Reddish Egret, Western Reef Heron (*Egretta gularis*), Eastern Reef Heron, the Least Bittern (*Ixobrychus exilis*), and the Mangrove Bittern (*I. flavicolis*). Whether there is a distinct Dimorphic Egret (*Egretta dimorpha*) and whether the Little Egret is polymorphic are disputed. For this account, I consider the Little Egret to be dimorphic. The Little Blue Heron, White Ibis, and Scarlet Ibis (*Eudocimus ruber*) have juvenal color phases. Pond herons have breeding phases. Some species such as the Roseate Spoonbill (*Ajaia ajaja*), while not having a distinct juvenal plumage phase, assume adult plumage color gradually. Biochemical changes associated with carotenoid metabolism (Fox 1962, Fox and Hopkins 1966) may occur with age in such species. Other reported color forms, such as in the Crested Ibis (*Nipponia nippon*), result from cosmetic coloration (Uchida 1970), and some age-dependent plumages, such as in the Cattle Egret, may be adventitial.

Obvious cryptic coloration, usually considered to be an antipredator adaptation (Cott 1940, Robinson 1969, Hamilton 1973), occurs in many wading bird species (Hudson 1920, Stone 1937, Witherby et al. 1952, Palmer 1962). Although the cryptic plumage of some small species, such as bitterns and pond herons, may serve an antipredator function, it also complements their slow behavior or standing foraging behavior. Since adult wading birds of most species are seldom subject to predatory attack, crypsis in wading birds probably functions primarily to reduce conspicuousness to prey and competitors rather than to predators. Many species have stripes ventrally that camouflage the bird from its prey. Birds of dense vegetation, such as *Botaurus* bitterns and tiger herons, have striped plumage, which probably decreases their conspicuousness to other birds and thereby permits solitary foraging. Generally, I suggest that much of the plumage color of wading birds functions either to reduce or to increase conspicuousness and is an adaptation for foraging.

Explanations put forth to account for plumage color in wading birds often advocate morphological, physiological, and protective functions or nonfunctional linkages to characteristics such as disease resistance (Cott 1947, Fabian and Sterbetz 1966, Recher and Recher 1969*a*, Recher 1972*a*, Hamilton 1973). I discount structural strength associated with melanistic feathers as functional in total plumage coloration in wading birds. I also discount a role for the physiological advantages of dark plumage. Caloric gain from heat absorbed by dark plumage is probably an insignificant factor in maintaining body temperature of large birds that seldom endure significant environmental heat loss. Protective coloration is unimportant in the large species of wading birds because as adults they are relatively immune from predation. Although polymorphism in small species such as the bitterns may correspond to substrate, as noted before their foraging requires inconspicuous coloration and probably is the dominant factor over predation avoidance. This is illustrated by the Lava Heron (*Butorides striatus sundevalli*) (Snow 1975), in which the predator-free dark morph is cryptically colored to match its foraging habitat on lava shores. The possibility that plumage coloration is nonfunctionally linked to other characteristics also is discounted as being unlikely.

While the functional significance of plumage color in wading birds is by no means clearly known, it is useful to make some testable suggestions. There appears to be a general dichotomy among wading birds between dark and light plumage, with plumage color polymorphism and age-dependent coloration being subsets of this wider phenomenon. I suggest that the primary factors in the development and persistence of plumage color are conspicuousness to prey and conspicuousness to other birds, and that secondary factors include alleviating the potential excess heat load on dark-plumaged birds foraging in highly insolated environments (Palmer 1909; Pirenne and Crombie 1944; Craik 1944; Armstrong 1946, 1970; Murton 1971*a*; Cowan 1972; Holyoak 1973; Kushlan, in prep.). I propose then the following hypotheses:

(*1*) Diurnal birds with light dorsal plumage are more conspicuous from above than those with dark dorsal plumage.

(*2*) Diurnal birds with light ventral plumage are less conspicuous from below than those with dark ventral plumage.

(*3*) Nocturnal, crepuscular, or shadow-feeding birds with dark ventral plumage are less conspicuous from below than birds with white ventral plumage.

(*4*) Diurnal birds with dark dorsal plumage have a higher heat load than birds with white dorsal plumage.

Some evidence supports these hypotheses:

(*1*) Birds that have light dorsal plumage are more conspicuous to human eyes. This is apparent without formal test to workers on the ground or in airplanes.

(*2*) Craik (1944) and Cowan (1972) demonstrated that birds with light or partially light ventral plumage show less contrast from below than birds with dark ventral plumage. Birds with less contrast should be less conspicuous. The role of a light ventral surface in aquatic systems is further demonstrated by the analogous countershading of pelagic fishes.

(*3*) Dark plumage would be less conspicuous in shadow or when light is poor. When there is no light, plumage color should make little difference. But some light is often present, even for nocturnal feeders, and dark plumage may therefore be less conspicuous.

(*4*) Differential absorption of radiant energy by dark plumage is well documented (Heppner 1970, Lustick et al. 1970, Lustick 1971). Under conditions of high temperature and insolation, heat absorption probably can produce hyperthermia if behavioral and physiological relief mechanisms are inoperable. An example is the rapid death of the dark hatchlings of the White Ibis when exposed to intense sunlight prior to the time they develop the ability to thermoregulate or to move away from areas of thermal stress. Since adult wading birds have a number of adaptations to reduce heat load, especially through heat exchange across unfeathered body areas (Kahl 1963*a*, Hafez 1964, Steen and Steen 1965), heat loading may be readily compensated for in all but the most intensely insolated environments. But the cost of such compensation may become relatively high.

As corollaries to the first three hypotheses above, it can be further suggested: (*1*) Diurnal birds that have light dorsal plumage would better attract other birds to a feeding location than birds that have dark dorsal plumage. (*2*) Diurnal birds that have light ventral plumage would frighten prey less than birds that have dark ventral plumage. (*3*) Nocturnal or shade-feeding birds that have dark ventral plumage would frighten prey less than birds that have light ventral plumage. Each of these corollaries is testable. (*1*) I (Kushlan, in prep.) conducted an experiment that showed that more wading birds were attracted to feeding locations by white models than by dark models. (*2*) D. W. Mock (pers. comm.) found more fish more times near a light wading bird model than near a dark model. (*3*) There has been no test of the third corollary.

Thus, adaptive pressures associated with plumage color may include conspicuousness and heat loading. Their effect depends on habitat and on foraging behavior. Selective pressure for ventral lightness would be strongest in active birds that may have a difficult time approaching prey. It should also be strong for birds foraging in open, bright habitats with high solar reflectance. If such pressures acted independently, several predictions about plumage color would be possible: (*1*) Birds that are nocturnal, crepuscular, or feed in the shade or by creating shade should have dark ventral plumage. (*2*) Diurnal birds that feed gregariously should have light dorsal plumage or otherwise be obviously colored, whereas solitary birds should have dark dorsal plumage. (I postpone to a later section the question of why it might be advantageous for a bird to be gregarious.) (*3*) Diurnal birds that feed by moving actively should have light ventral plumage to permit them to approach prey closer before attempting capture. (*4*) Diurnal birds that feed in very clear, open aquatic habitats with light substrate in which a bird may be maximally visible to prey should have light ventral plumage. (*5*) Birds that feed in very dense cover should have cryptically colored ventral plumage. (*6*) Birds in areas of intense insolation, primarily in the tropics, should tend to have white plumage to reduce heat load.

These predictions are based on independently operating selective pressures. But the many pressures affecting plumage color occur simultaneously, conflictingly or synergistically, and plumage color results from the concurrent resolution of all critical selective pressures. A first attempt at determining these factors is shown in Figure 8. By categorizing a species as to its feeding ecology, we can predict its plumage color and then see how well the actual color fits the predictions. Species are categorized as nocturnal or diurnal; gregarious or solitary; active or passive in foraging; inhabiting open, sunny, clear, bright habitat, intermediate habitat, or dense cover; and inhabiting highly insolated tropical habitats or other habitats. I have made difficult decisions such as general gregariousness or

feeding activity based on the overall tendency of the species throughout its range. There are uncritical steps for birds that are inactive foragers and birds from habitats other than very dense or highly isolated ones.

Table 4 shows the results of testing the procedures shown in Figure 8 on the species that were used for previous analyses (Tables 1, 2, 3). Overall, the agreement of predictions to the actual plumage color is surprisingly good, with 27 of 31 species having plumage colors properly predicted. Entirely white species such as Cattle Egrets, White Ibises, Wood Storks, and spoonbills are accurately predicted as are bicolored birds such as Louisiana Herons and Black-necked Storks. The dorsal plumage of nonactive, nongregarious feeders is predicted, but their ventral plumage varies, reflecting a gradient of selection pressures. The system does not explain gregarious dark species such as the Glossy (*Plegadis falcinellus*) and Bald (*Geronticus calvus*) Ibises. The bitterns and tiger herons have become entirely cryptic rather than having cryptic ventral plumage and dark dorsal plumage. Total cryptic plumage indicates a highly dispersed solitariness. The white breeding plumage of the Paddybird (*Ardeola grayii*) is not predicted, and it is possible that conspicuousness may be important to these birds while nesting. The colors of adult Little Blue Herons and White Ibises are accurately predicted, but the colors of their juveniles are not. Perhaps the gregariousness of the young differs from that of the adults — that is, juvenile White Ibises may be less gregarious and juvenile Little Blue Herons may be more gregarious than the adults.

Although this exercise is not meant to provide final answers as much as to provide an illustrative tool and to clarify questions to be asked, it does emphasize the importance of considering the compromise of selective pressures rather than a single factor in analyzing plumage color. Table 4 suggests also that polymorphic species may be responding to the simultaneous pressures for different plumage colors. In the various species, the pressure for dark dorsal plumage, to decrease the time spent in defending a feeding territory, is opposed by pressure for light dorsal plumage, to reduce heat load. Pressures for light plumage in open habitats may be opposed by pressures for darker plumage in other habitats.

Since polymorphism exists because of a selective balance between the morphs, explanations for its existence should be sought in the nature of the balance. Differing conditions whether disjunct or along a gradient should be reflected by different proportions of

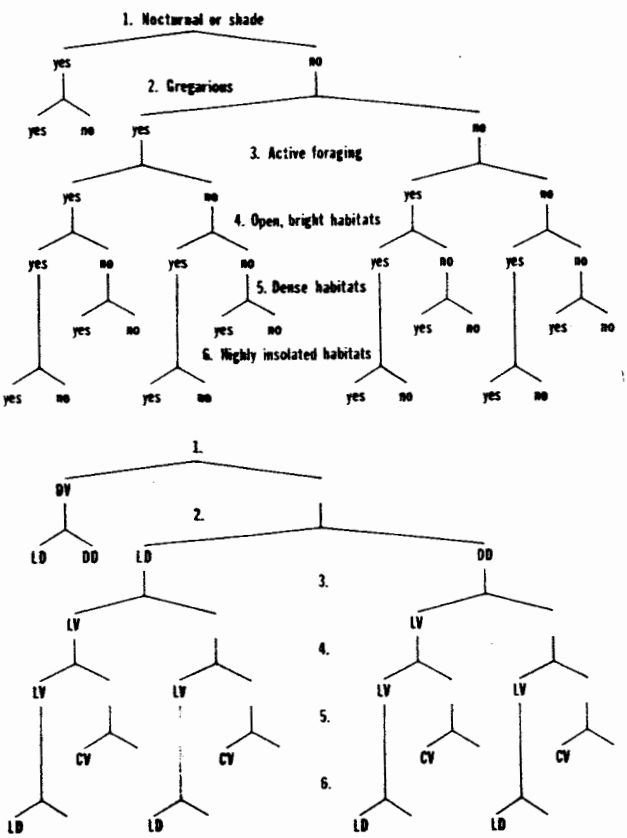

Figure 8. Evolutionary-decision tree for predicting the plumage color of a bird based on its feeding behavior and habitat use. Criteria are explained in text. (LD = light dorsa, DD = dark dorsa, LV = light ventra, DV = dark ventra, CV = cryptic ventra)

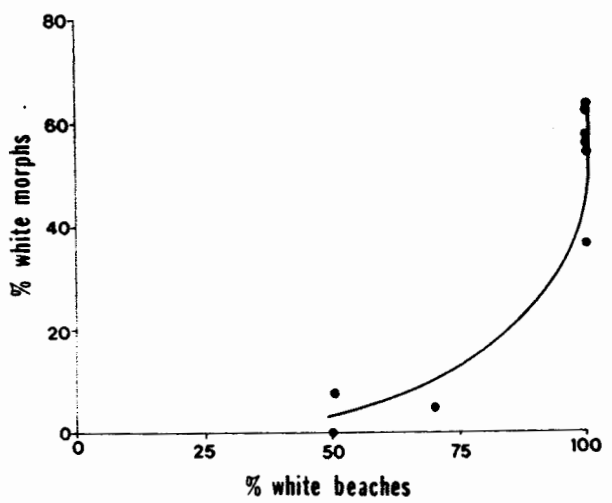

Figure 9. Clinal variation in morph ratios with environmental conditions. The percent white morphs of the Eastern Reef Heron correlate with the percent white beaches.

Table 4. Predicted and actual plumage color of the wading bird species in Tables 1, 2, and 3, based on Figure 10.

	Nocturnal or shade	Gregar-ious	Active foraging	Open bright habitat	Dense habitat	Highly insolated habitat	Predicted plumage dorsal	Predicted plumage ventral	Actual plumage dorsal	Actual plumage ventral
Great Blue Heron	N	N	N	N	N	N	D	—	D	C
Great White Heron	N	N	N	Y	N	Y	D+L	L	L	L
Black-headed Heron	N	N	N	N	N	N	D	—	D	C
Goliath Heron	N	N	N	N	N	N	D	—	D	C
Purple Heron	N	N	N	N	N	N	D	—	D	C
Great Egret	N	Y	N	N	N	N	L	—	L	L
Reddish Egret (dark)	N	N	Y	Y	N	Y	D+L	L	L	L
Reddish Egret (light)	N	N	Y	Y	N	Y	D+L	L	D	D
Black Heron	Y	N	Y	N	N	N	D	D	D	D
Louisiana Heron	N	N	Y	N	N	N	D	L	D	L
Cattle Egret	N	Y	Y	N	N	N	L	L	L	L
Little Blue Heron (adult)	N	N	N	N	N	N	D	—	D	D
Little Blue Heron (juv.)	N	N?	N	N	N	N	D	—	L	L
Snowy Egret	N	Y	Y	N	N	N	L	L	L	L
Eastern Reef Heron (dark)	N	N	N	Y	N	Y	D+L	L	D	D
Eastern Reef Heron (light)	N	N	N	Y	N	Y	D+L	L	L	L
Paddybird (breeding)	N	N?	N	N	Y	N	D	C	L	L
Paddybird (winter)	N	N	N	N	Y	N	D	C	D	C
Green Heron	N	N	N	N	Y	N	D	C	D	C
Agami Heron	N	N	N	N	Y	N	D	C	D	C
Yellow-crowned Night Heron	Y	N	N	N	N	N	D	D	D	D
Black-crowned Night Heron	Y	N	N?	N	N	N	D	D	D	L
Boat-billed Heron	Y	N	N	N	N	N	D	D	D	D(L)
Tiger Heron	N	N	N	N	Y	N	D	C	C	C
Least Bittern	N	N	N	N	Y	N	D	C	D	C
American Bittern	N	N	N	N	Y	N	D	C	C	C
Wood Stork	N	Y	Y	N	N	N	L	L	L	L
African Open-billed Stork	N	N	N	N	N	N	D	—	D	D
White Stork	N	Y	Y	N	N	N	L	L	L	L
Abdim's Stork	N	Y?	Y	N	N	N	L	L	D	L
Black-necked Stork	N	N	Y?	N	N	N	D	L	D	L
Jabiru	N	Y	N?	N	N	N	L	—	L	L
Marabou	N	N	Y	N	N	N	D	L	D	L
Shoebill	Y	N	N	N	N	N	D	D	D	D
Hammerkop	N	N	Y	N	N	N	D	L	D	D
White Ibis (adult)	N	Y	Y	N	N	N	L	L	L	L
White Ibis (juv.)	N	Y?	Y	N	N	N	L	L	D	L
Glossy Ibis	N	Y	Y	N	N	N	L	L	D	D
Bald Ibis	N	Y?	Y	N	N	N	L	L	D	D
Hadada	N	N	Y	N	N	N	D	L	D	L
Sacred Ibis	N	Y	Y	N	N	N	L	L	L	L
African Spoonbill	N	Y	Y	N	N	N	L	L	L	L
Roseate Spoonbill	N	Y	Y	N	N	N	L	L	L	L

N = no
Y = yes
D = dark
C = cryptic
L = light

morphs in various populations. Important selective pressures that vary along gradients include heron population levels (large to small), insolation (temperate to tropical), clear, bright habitats (temperate to tropical, dark to light substrate, and murky to clear water). Heron populations should vary similarly (dark to light), compromising any opposing trends. Studying ratio clines of morphs may result in identification of the significant operating pressures. I have suggested some in the exercise conducted above, but more undoubtedly exist. A ratio cline in the Reef Heron (Fig. 9, data from Holyoak 1973) corresponds to a gradient between high-reflecting white beaches and darker beaches. According to Figure 8, this would affect the

relative pressures for light ventral plumage. In light habitats, the pressures for being inconspicuous to prey may be relatively greater than the pressures to avoid excessive defense of a feeding territory. In dark habitats, pressures for being inconspicuous to prey are relaxed, and the relative value of being inconspicuous to other birds searching for a feeding area increases. A proportional difference also exists between the morphs of the Reddish Egrets of Florida and the Bahamas, and between inland Great Blue Herons and marine Great White Herons (*Ardea herodias occidentalis*) in Florida.

Resolution of the environmental pressures producing dimorphic plumage color should be sought on a populational rather than on an individual level. To discern differences on the individual level, all costs and benefits associated with the different plumage types must be considered, including heat loading and the energy used and gained in foraging. Over a short period one need not expect individual morphs to exhibit differences in feeding efficiency because individuals of either morph remaining in an area can obtain sufficient energy there. Although one could expect long-term depression of reproductive output of the atypical morph, this may not be obvious on the short term since morphs that persist in the habitat do so because in any place some percentage of the population composed of the atypical morph should be adequately adapted for persistence. The reason is that limiting factors on the atypical morph include long-term reproductive success, particularly in times of stress, rate of immigration from adjacent populations, degree of competition (territorial exclusion) by individuals of the more abundant morph, amplitude of environmental fluctuations that change the relative adaptive value of each of the morphs, and the frequency of disruptions that provide short-term advantage to the otherwise suboptimal morph. Thus, it is not surprising that studies have found no differences in foraging behavior and efficiency between morphs. Because they are members of the same species and often, to a greater or lesser extent, members of the same interbreeding population, individuals of a species should feed generally in the same way, in the same places, on the same prey. Questions of polymorphism will be resolved by studies of long-term reproductive output that span episodes of rigorous times and by examining statistical distributional differences.

Spacing

Territorial spacing systems are important factors in the ecology of many species of birds (Howard 1920, Nice 1941, Conder 1949, Lack 1968, Crook 1965, Brown 1969). Herons may defend relatively large feeding territories, but they also may feed in dense aggregations. Understanding the apparent variety of heron territoriality requires analyses of the various ecological circumstances involved.

Territorial foraging

Several types of territories are held by wading birds (Lorenz 1938, Noble et al. 1938, Meyerriecks 1962, Hedeen 1967, Recher and Recher 1972, Snow 1975, Woolfenden et al. 1976). The Lava Heron defends a feeding territory which may include its nest site. The Eastern Reef Heron defends a feeding territory apart from its nest site. Some individuals may establish feeding territories seasonally; other individuals may defend a feeding area throughout the entire year. All wading birds defend the individual distance around them, which may enlarge or contract according to conditions. It is minimally the length of the head and neck. Feeding territories, such as those of Great Blue Herons around lakes, may be defended throughout the day, whereas territories in coastal areas may be defended only when tide is suitable for foraging. Individual birds may defend a feeding territory but may also forage periodically in an undefended area. More than a single bird may defend a single territory, but with Reef Herons, defense of co-owned territories is accomplished by a single bird at a time rather than cooperatively. Boundaries between territories may be sharply or weakly defined, and feeding territories are not absolutely inviolate. A particular nonterritorial bird may more or less permanently insinuate itself within a territory, whereas feeding by other individuals may be permitted for only very short periods of time. In other cases territorial birds may divide available high-quality habitat among themselves, while nonterritorial birds may be relegated to lower-quality habitat.

Intraspecifically, immature birds are often at a social disadvantage in feeding disputes and are dominated by adults. I have observed this in Little Blue Herons, White Ibises, Glossy Ibises, Wood Storks, and Snowy Egrets. Little Blue Herons are particularly prone to indulge in cross-generation antagonism. Such adult dominance may cause habitat differences between young and adults. In a natural experiment where dispersal of subdominant birds was impossible, younger birds were dominated by older birds at feeding sites and so suffered greater mortality (Woolfenden et al. 1976).

Wading birds also defend feeding areas interspecifically. Interspecific defense involves all sizes of birds, not just similarly sized birds that might be potential competitors; the smaller species in such conflicts seldom win. In more than 2,500 one-minute observations of feeding wading birds, the winners were without exception larger or the same size as the losers (Fig. 10, data this paper). Wading birds therefore divide their feeding habitat territorially with dominance by size of bird. Smaller species may be permitted within feeding territories that are large but will generally be displaced when entering the territory core area near larger birds.

The expression of territorial behavior in wading birds is plastic, and one species may exhibit the entire range of feeding sociality. In some areas a Great Blue Heron may be overdispersed throughout its habitat. In other areas it may establish large feeding territories or may forage aggregatively with other birds at localized food patches. In such cases the size of its defended area shrinks to the species' characteristic individual distance. The size of wading bird territory can be thought of as compressible with its realized size varying under different conditions. Territory size may be expressed areally or linearly (such as along a riverbank).

The realized size of the territory of a single individual may be related to the area's defensibility, which can be measured by the time between aggressive encounters. A highly defensible area is one in which the time between defenses is relatively long. Costs of defense are lower when encounters occur less frequently. Such costs must be offset by the gain derived from the resources being defended. The costs of particular defenses are not equivalent; some defenses may consist only of a forward threat whereas others may require active pursuit. Since the measure of defensibility in terms of minutes between encounters is not weighted by the cost of defense, it is a somewhat simplified, but useful, approximation.

Figure 11 proposes a hypothetical model of the relationship between the size of wading bird territory and its defensibility. Asymptotic limits are set by individual distance and by the limits of practical defense, beyond which nondefensive avoidance spacing occurs. As defensibility increases, so does territory size. At a given initial territory size, high numbers of encounters will cause a shrinking of size to the point where the number of encounters is balanced by foraging return. The mechanism of operation can be visualized by birds holding initial territories of the sizes indicated by point *a* and point *b*. A bird holding a territory at point *a* experiences a frequency of encounters too great to be offset by the return it obtains and will decrease its territory size to the curve. A bird holding a territory at point *b* will have relatively few encounters and can expand its territory size to the curve.

Factors that influence the defensibility of an area are critical to the establishment of territory. The most important consideration may be the degree of dispersion of the resource, which may be clumped, highly dispersed, or in any intermediate condition. Territory

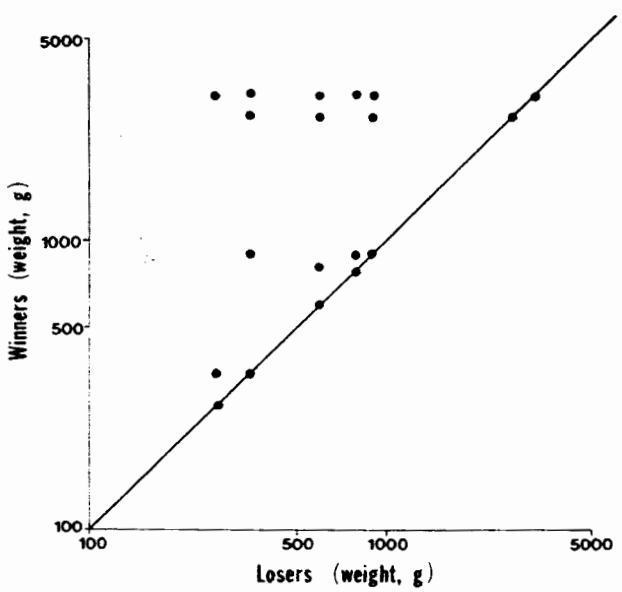

Figure 10. Relationship of size of bird to its winning territorial encounters in southern Florida. Incidents of winning and loosing are plotted by body size of participants.

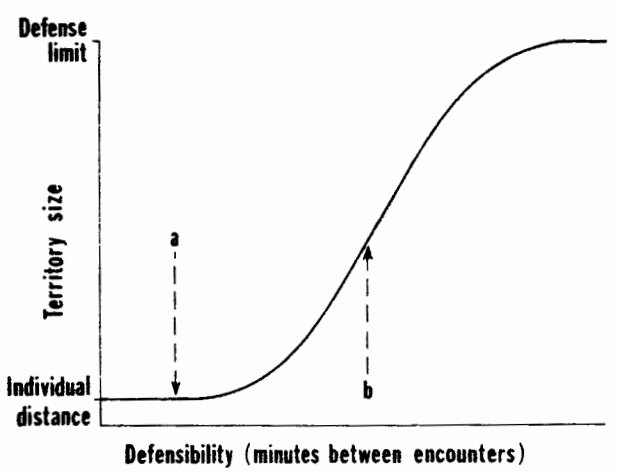

Figure 11. The role of defensibility in change in territory size. Birds at points a and b will change territory size to that represented by the curve.

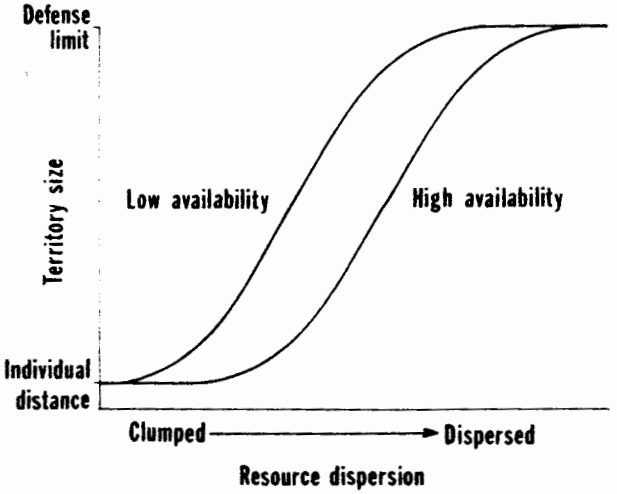

Figure 12. Proposed relationship of territory size to resource dispersion.

size is small when resources are highly clumped but large when they are dispersed (Fig. 12). For a given prey dispersion, prey availability may be high or low, depending on abundance. High prey availability may be correlated with a smaller territory size than is low availability. Both clumping and high availability increase the frequency of defense of the area, and territory size shrinks because the extra return from a larger territory is not compensated for by costs of defense. Conditions become particularly critical when availability is low and food is clumped. Then territory size is relatively large and must be defended despite its low yield. Under such conditions the excessive cost of defense would cause movement in search of a more economical foraging location. When dispersal is impossible, benefits accrue to the few dominant birds able to defend the food source from others; the others must then forage in even poorer habitats.

Additional factors influence territory defensibility when comparisons are made between habitats, geographic areas, or seasons. Defensibility also varies with the size of the competing predator population and habitat availability. The greater the population competing for resources in an area and the smaller the available high-quality habitat, the more encounters occur and the less defensible a given-sized territory becomes. Availability of resources, shown in Figure 12, varies between locations and times. Thus, the higher densities of suitable prey or the greater abundance of vulnerable prey (such as dying fish), the less defensible the resource. All these factors can cause the size of a territory to shift.

These hypotheses require that a bird balance the costs of defending territory against the energy gained as a result of its exclusive feeding rights. Although many factors influencing either costs or gain determine territory size, a bird need only monitor intake versus defense costs and adjust its defensive posture accordingly. When food is dispersed, defense of a large territory is required. When it is not, perhaps only avoiding interference within its individual distance is practical. It is possible, as noted in the case of clumped food of low abundance in a competitor-rich habitat, that the required territorial defense does not allow sufficient energy gain. In such cases, shifts in feeding area occur, or foraging occurs that is sub-energetically sufficient.

Aggregated foraging

Aggregated foraging and flock feeding are widespread among birds (Rand 1954, Moynihan 1962, Morse 1970, Murton 1971*b*, Krebs 1973, Krebs et al. 1972, Hamilton 1971, Pulliam 1973, Ward and Zahavi 1973). There is little evidence that wading birds form associations based upon individual recognition, consistent interindividual contact, or other social interactions that characterize flocking species. When a small number of a gregarious species occupy an area, consistently use the same roosting and feeding grounds, and move together over periods of days, they may develop dominance hierarchies, such as typically occur in captive wading birds. In most other circumstances, wading birds feed in aggregations formed through local enhancement. Aggregations form when feeding territory is reduced because of low defensibility of the resource, which at the extreme may be correlated with clumped prey dispersion, high availability, and large numbers of searching wading birds. Thus, food although not highly defensible is highly available, and it is advantageous for a bird to be attracted to an aggregation, provided its behavior and morphology permit effective foraging under such conditions. Birds that forage daily in aggregations would decrease search time between food patches, increase likelihood of foraging in beneficial locations, decrease risk of obtaining no food, and increase energy consumption. The last may be the most critical factor because the stability and persistence of an aggregation depend on energy gain per bird, measured in terms of either net energy gain per time or the time between prey items (Krebs 1974; Kushlan, in prep.). Aggregations form when feeding birds achieve a sufficient net energy gain or frequency of capture for them to remain in a place and thereby attract other birds.

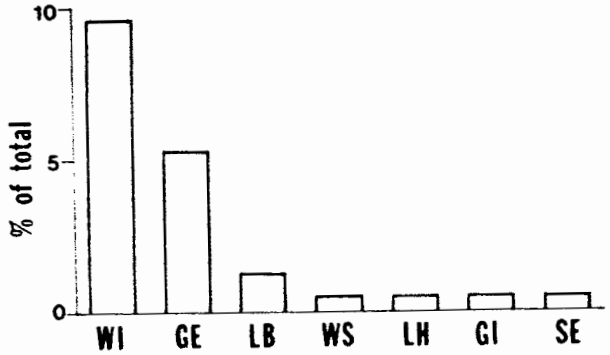

Figure 13. Frequency of occurrence of seven types of single-species aggregations in southern Florida. Data expressed as the percentage of 209 observed mixed- and single-species aggregations that were comprised solely of one of the seven species.

Some wading birds form single-species aggregations. In such species-rich regions as southern Florida, single-species aggregations constitute only a small proportion of the total aggregations (Fig. 13, data this paper, n = 209 flocks). Although it might be expected that species that form single-species aggregations might also form the core of mixed-species aggregations, this is not necessarily so because the tendency for a species to participate in a mixed aggregation is a function of its foraging behavior, habitat selection, and competitive interactions, which may differ between single- and mixed-species aggregations. Dark plumage inhibits some species from initiating mixed-species aggregations. The single-species aggregations of some birds, such as Little Blue Herons and Louisiana Herons, are rather dispersed, and these herons generally assume peripheral positions in mixed aggregations. In southern Florida the numbers of these herons using a feeding site decreased as the total size and diversity of the aggregation increased (Kushlan 1976*c*). Some species are at a social disadvantage because their active feeding methods cause encroachment on an area defended by larger birds. Species that use methodical searching behavior are at a disadvantage in disturbed conditions such as those within aggregations. Thus, species that form the core of mixed aggregations feed either by standing or by slow nonvisual feeding. Other species are forced by territorial constraints or by lowered foraging efficiency to feed at the periphery of or away from the aggregation.

Composition of aggregations differs geographically (Fig. 14, New Jersey data from Willard 1975, flock n = 196; Everglades data, this paper, flock n = 209). Some of the differences are accounted for by relative abundances of different species in each area.

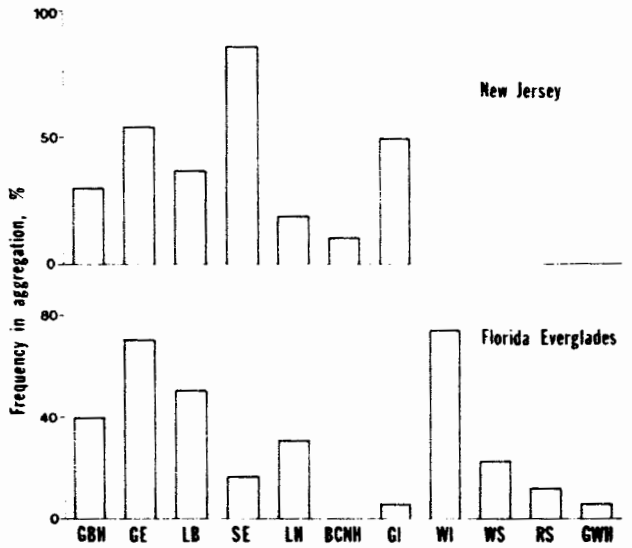

Figure 14. Frequency of occurrence of various species in mixed- and single-species aggregations in New Jersey coastal marshes and the Florida Everglades.

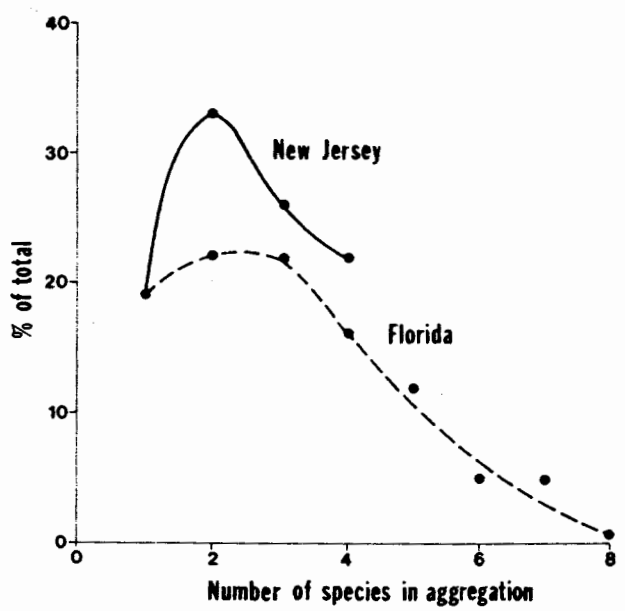

Figure 15. The richness of aggregations in temperate (New Jersey) and subtropical (Florida) areas.

For example, Black-crowned Night Herons and Glossy Ibises make up a larger proportion of the total number of birds in temperate areas where additional species occur. Because of this, the number of species in an aggregation depends in part on the number of species in the pool of regional species (Fig. 15). Both maximum and mean species richness of aggregations increase along a temperate-to-tropical gradient.

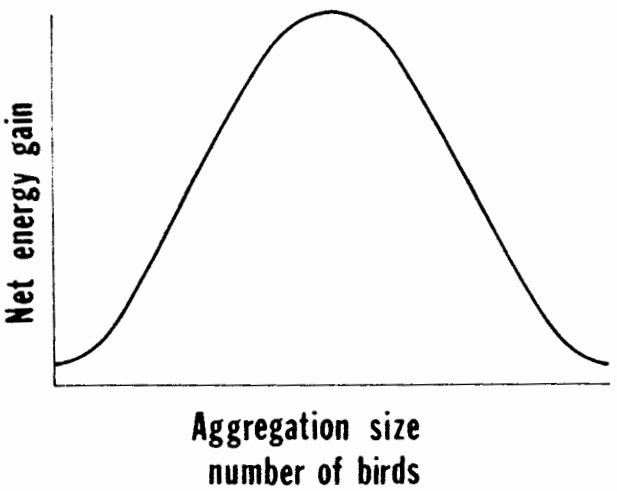

Figure 16. Proposed relationship between aggregation size (number of birds per area) and energy gain.

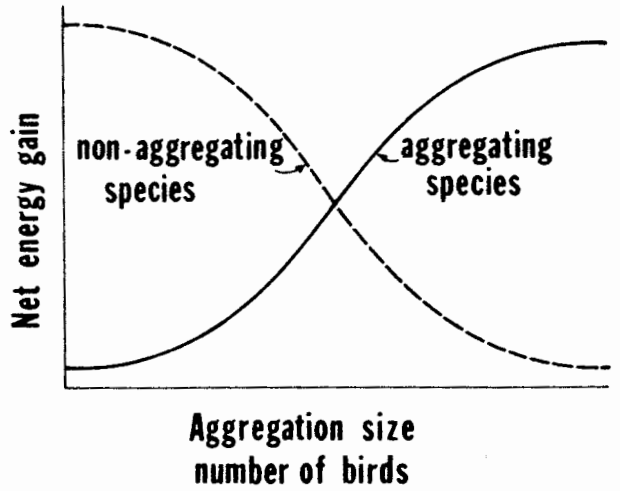

Figure 17. Proposed relationship between aggregation size and energy gain for species with different feeding behaviors.

While it is obviously advantageous for a bird to join an aggregation, it is unclear why a bird feeding at a good location should attract other birds to its feeding site, irrespective of the quantity, dispersion, or ephemeral nature of the food supply there. I suggest that net energy gain may be in part a function of aggregation size (Fig. 16), with energy gain first increasing and then decreasing as aggregation size increases. Species should differ in their maximal effective aggregation size, and since there are both generally aggregating and generally nonaggregating species, the curve should shift along the x axis for different species. For two extreme examples, a peripherally aggregating species (e.g., Louisiana Heron) would exhibit greatest gain at low aggregation size, whereas an aggregating species (e.g., Great Egret) might achieve higher gain with increasing predator density up to some maximum (Fig. 17). The right half of the curve would not be realized in an aggregating species because interference associated with increased predator density will cause birds to move to another feeding site. Although data with which to test this hypothesis are limited, Krebs (1974) measured the relationship between gross food intake and aggregation size for Great Blue Herons. In this case gross food intake was proportional to net energy gain, since foraging behavior, and therefore energy use, of aggregating and nonaggregating birds was the same. Krebs' mean data points (although not the regression model he chose) well describe the curve proposed for an aggregating species (Fig. 17).

Demonstrating the relationship between aggregation size and energy intake (Fig. 16) is confounded by other variables. Because aggregations form where prey is abundant, increased energy gain could be only a function of higher availability. Furthermore, aggregation size itself may increase with increased prey availability. I suggest, however, that at a given prey density, aggregative feeding alters the functional relationship between prey and predator, so aggregating individuals of some species obtain more net energy than nonaggregating individuals (Fig. 18). Aggregating may increase effectiveness of foraging in several ways: by increasing the rate of successful stabs, by increasing the number of stabs with no change in success, or by decreasing energy expenditure per gross energy intake. All may be correlated with increased vulnerability of prey to the birds of an aggregation. In support of this hypothesis, it is known that Little Blue Herons foraging with White Ibises obtain more energy than those feeding without ibises in the same habitat and with the same prey availability (Kushlan, in prep.). Krebs' data (1974) provided a direct test of the model (Fig. 18). He determined the relationship between energy gain and prey abundance of individually feeding birds and compared it to that of aggregating birds. Of seven aggregation samples, three fell below the curve for individual birds, and four above it. Krebs concluded that aggregating does not make prey more available. By vote of four to three, one might suggest an opposite trend. Neither conclusion is justified by this scant data base, but further testing would be relatively straightforward.

If nature works as above, it would be advantageous

for some species of wading birds to feed in aggregations because net yield is greater. For birds feeding in such associations it may also be advantageous to attract other birds to a site because it may increase their net energy yield. Thus, birds that feed in aggregations should be conspicuous. Species associated only peripherally with aggregations may "parasitize" the group to locate food patches. These birds are inconspicuous because their foraging methods result in a decreased yield with aggregation size, and so they feed near but not in the aggregation. The alternative hypothesis is that birds exhibit mutual altruism in locating food sources. The former hypothesis is appealing on two counts — it doesn't require altruism among nonrelated birds, and it is testable.

Coloniality

Because coloniality is analyzed elsewhere in this volume (Krebs 1977), I will only emphasize that coloniality and communal roosting are often correlated with patchy food distribution (Crook 1965, Lack 1968). It has been proposed that communal roosting and colonial nesting permit local enhancement (Siegfried 1971*c*, Ward and Zahavi 1973, Krebs 1974, Kushlan, in prep.). The opposing argument is that communality functions in predator avoidance because of site safety (Gadgil 1972). Lack (1968) suggested that colonial nesting cannot be an adaptation to food availability because various species in mixed colonies use different resources. However, several species, each presumably using available resources somewhat differently, feed in aggregations and so can use each other for social food finding (Kushlan, in prep.). Lack (1968) suggested also that solitary-feeding species nesting in colonies cannot benefit from social food finding. On the other hand, the dispersal of feeding wading birds depends on many factors, and even such predominantly solitary species as the Great Blue Heron often feed in aggregations. To understand the colonial tendencies of such species, it is necessary to account for their dispersion throughout the range of conditions encountered.

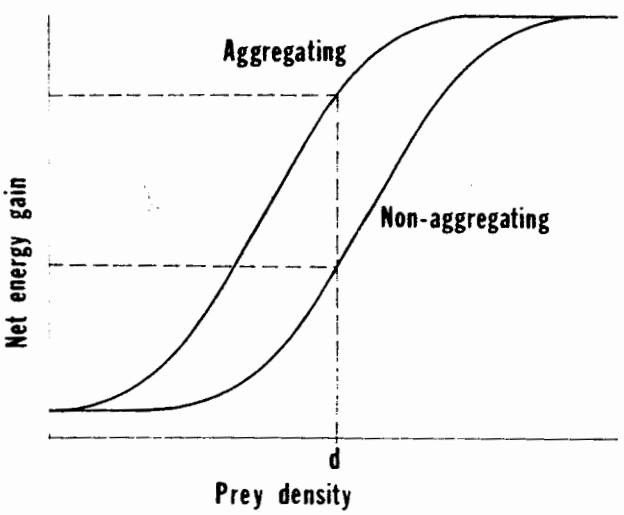

Figure 18. Proposed functional relationship between energy gain of an individual foraging at a particular prey density in an aggregation and not in an aggregation.

Foraging Sociality

Feeding in aggregations increases chances for the development of more cooperative forms of feeding behavior. Many potentially commensal associations have been reported (Fig. 19; Aquatic: Christman 1957, Pitman 1962, Parks and Bressler 1963, Reynolds 1965*a*, Emlen and Ambrose 1970, Kahl 1971*a*, Leck 1971, Mueller et al. 1972, Fraser 1974, Courser and

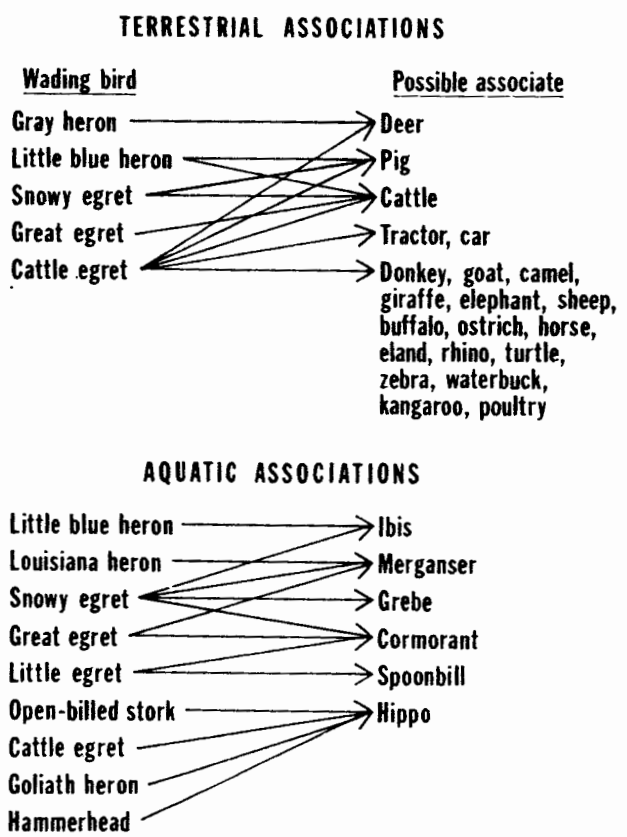

Figure 19. Potentially commensal associations of wading birds.

Dinsmore 1975, Kushlan, in prep.; Terrestrial: Howell 1932, Rand 1936, Bannerman 1953, Haverschmidt 1953, Rice 1954, Caldwell 1956, Valentine Jr. 1958, Denham 1959, Owre 1959, Curry-Lindahl 1960, Austin 1962, Pitman 1962, Skead 1963, Reynolds 1965*a*, Wetmore 1965, Skead 1966, Michael 1967, Blaker 1969*a*, 1971, Benson and Penny 1971, Browder 1973*b*, Dinsmore 1973). Nevertheless, the commensal nature of these associations has been proved only in the case of the Little Blue Heron–White Ibis association and the Cattle Egret–cattle association.

The intensity of commensal relationships in wading birds varies from casual to highly dependent, but in no cases is it obligatory. If aggregation feeding increases net return for some species, as I have proposed above, it may be considered a moderately discriminating form of commensal behavior. The next stage of complexity is a deliberate attempt to use another animal in a more or less casual manner. This is illustrated by the Little Blue Heron. The final step is a heavy dependence on, and additional interactions with, the associate. This is illustrated by the Cattle Egret. The Little Blue Heron–White Ibis association is generally short-lived. The heron often follows the ibis for a short time before moving away to something or someplace it noted while it was near the ibis. Herons near White Ibises caught more prey with no greater energy expenditure than herons in the same habitat feeding apart from ibises (Kushlan, in prep.). Cattle Egrets attending cattle catch more or larger prey with less energy expenditure than Cattle Egrets not attending cattle in the same habitat (North 1945; Sprunt Jr. 1954; Skead 1956, 1966; Gross 1964; Heatwole 1965; Blaker 1969*a*, 1971; Siegfried 1971*b*; Browder 1973*a*; Dinsmore 1973; Grubb 1976). Egrets following farm machinery also obtain more prey than do nonattending birds, but with greater energy expenditure. The Cattle Egret–cattle association dominates the species' feeding ecology in that more than 90 percent of the egrets in an area may be associated with another animal. The association includes additional interspecific interactions such as provoking resting cattle to move, cleaning, riding, and feeding from cattle, and communicating with them by warning flights (Rice 1954, Dawn 1959, Skead 1963, Skead 1966, Snoddy 1969).

The success of commensal feeding depends on habitat conditions and may be more useful when prey abundance is low (Valentine Jr. 1958, Blaker 1969*a*, Siegfried 1971*b*). Additionally, habitat and behavioral variables make various associated animals differentially valuable (Fig. 20 — data from Blaker 1969*a*). The territorial behavior common to all feeding associations carries over to commensal feeding (Grubb 1976; Kushlan, in prep.). Wading birds may defend the area around an associate and thereby increase foraging effectiveness.

Wading birds serve as "beaters" in commensal associations (Parks and Bressler 1963; Meyerriecks and Nellis 1967; Leck 1971; Kushlan, in prep.). White Ibises serve Little Blue Herons and Snowy Egrets. Great Egrets and Snowy Egrets may increase prey for kingfishers and grebes, although this has not been proven quantitatively. Neither has the proposed symbiosis of grebes and Snowy Egrets. The possibility that Cattle Egrets reduce populations of the invertebrate competitors of cows might merit investigation. The extent to which Cattle Egrets clean or warn cattle would render this at least partially a symbiotic association.

The success rate of feeding does not necessarily increase because of commensal feeding (Siegfried 1971*b*; Kushlan, in prep.). Only Dinsmore's (1973) study of Cattle Egrets has shown an increase in success rate. It has been argued that commensal animals serve as beaters, making prey easier to catch (Rand 1954, Meyerriecks 1960*b*, Heatwole 1965), but this is not necessarily so. Commensals may make prey more vulnerable by exposing them or by inducing them to move slightly, but ultimately the success of an individual strike depends on the prey species and nature of the habitat. Increased prey capture associated with commensal feeding results primarily from the exposure of more prey, which increases the strike or feeding rate rather than the success rate.

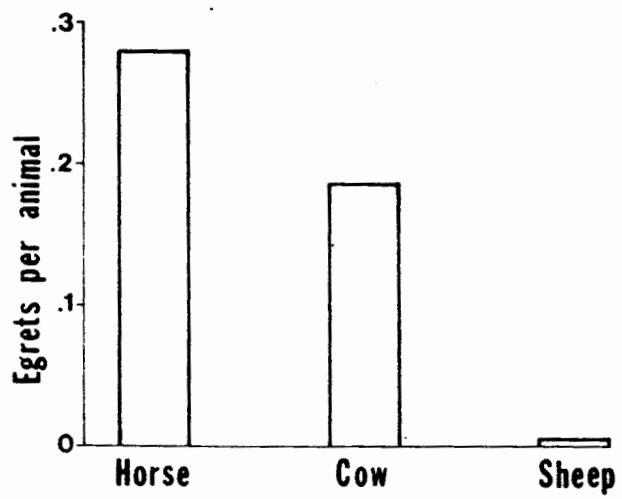

Figure 20. Relative use of several commensals by Cattle Egrets.

Prey Robbing

Aggregated foraging provides the opportunity for development of negative associations such as prey robbing. Robbing is widespread among birds (Sprunt Jr. 1941, Meinertzhagen 1949, Hatch 1970, Grant 1971, Hopkins and Wiley 1972, Andersson 1976, Payne and Howe 1976, Stenzel et al. 1976). Despite the potential for its widespread development, prey robbing has seldom been reported in wading birds (Audubon 1840; Sprunt Jr. 1941; Belknap 1957; Kahl 1966*a* and *b*; Temple 1969; Benson and Penny 1971; Recher and Recher 1972; Kushlan, in prep., this paper). Grackles rob Glossy Ibises, White-faced Ibises (*Plegadis chihi*), and White Ibises of crayfish. Turkey Vultures (*Cathartes aura*) rob nestling Great Blue Herons by forcing them to regurgitate. Great Blue Herons pursue Osprey (*Pandion haliaetus*) for fish. The Gray Heron robs Little Egrets. The Eastern Reef Heron robs Noddy (*Anous stolidus*) and Crested (*Sterna bergii*) Terns. Marabous depend on stealing carrion torn from carcasses by other scavengers.

In the Everglades, robbing is a commonly employed feeding tactic of wading birds (Kushlan, in prep.). In an aggregation of seven species of wading birds, each species robbed other birds, with robbing consuming up to 10 percent of a bird's feeding time. The tendency to rob depends on size, with larger birds having a high probability of success but also a large energy expenditure, and small birds lacking potential victims. As a result, medium-sized birds are often the predominant robbing birds in the Everglades aggregations. Principal victims of robbing are birds that have prey requiring a long handling time, especially large prey or those with special defenses. Robbing can limit the sizes of prey taken by victim species in aggregations and provides a mechanism of resource division through interference competition. Prey robbing in many cases is characterized by high energy costs and a low success rate (Dunn 1973; Kushlan, in prep.). In the Great Egret, it was less energetically beneficial than foraging alone, but it is nonetheless widespread and an important part of the feeding ecology of a number of species of wading birds.

Food Ecology

Despite their mutual importance, the effect of prey availability on feeding behavior and the role of behavior in prey selection have been little studied (Kokshaysky 1966*b*; Kushlan 1972, 1973*b*, 1976*a*). A wading bird can select the most appropriate foraging behaviors for its needs, and the choice of a successful foraging behavior should reinforce repeated use. It is of considerable interest to determine the causes of behavioral changes and prey shifts. I have shown that active, flying foraging is used when other behaviors become less productive. On a more precise scale, however, the effects of slight behavioral changes on prey selection are nearly unknown. In fact, when the study of potentially competing species resolves to foraging variables, it is often assumed, without critical examination, that prey differs. Since foraging behavior must determine to a large extent what prey is captured, the question is to what extent it does so. The answer must lie in study of the prey available and taken.

Food Consumption

Somewhere, sometime, individual wading birds have probably eaten just about any item that they could swallow. Items such as beads, paper, or butcher knives may be of little more than novelty interest. Of more concern is delimiting prey that make up the bulk of the energy consumed by a bird. Although the critical questions involve the relationship of food taken to availability, insight may be gained from the many studies that have been conducted on food habits. In Tables 5, 6, and 7, I summarize the food habits of species I have previously selected, with the addition of the Gray Heron because its food is so well documented. References for these summaries are listed in Appendix 2. Of interest is the wide variety of prey taken by the various species, even by such specialists as Wood Storks. The limited known prey of other apparent specialists such as Agami Herons may indicate lack of data. By far, aquatic prey, especially insects, crustaceans, fish, and amphibians, dominate the array of food taken by wading birds.

Adult wading birds deliver the same size and composition of prey to nestlings that they themselves consume (Owen 1955; Siegfried 1971*a*, 1972; Kushlan and Kushlan 1975; Ogden et al. 1976). Kahl (1964) stated that the size of food eaten by Wood Stork nestlings generally increases with size of young, but this was not confirmed by actual food collections (Ogden et al., in press). Rather than selecting small prey, adult wading birds often deliver well-digested food to young nestlings. As nestlings grow, they receive food that may be digested less or not at all. When an item is too large to be consumed by the nestlings, the adults usually reswallow it, but most nestlings can handle adult-sized food early in life.

Table 5. Foods consumed by selected species of herons.

	Great Blue Heron	Gray Heron	Black-headed Heron	Goliath Heron	Purple Heron	Great Egret	Reddish Egret	Black Heron	Louisiana Heron	Cattle Egret	Little Blue Heron	Snowy Egret	Eastern Reef Heron	Paddybird	Green Heron	Agami Heron	Yellow-crowned Night Heron	Black-crowned Night Heron	Boat-billed Heron	Bare-throated Tiger Heron	Least Bittern	American Bittern
Leeches									X						X		X	X			X	
Earthworms		X								X		X		X	X			X				
Aquatic insects	X	X	X		X	X			X	X	X	X		X	X		X	X	X		X	X
Land insects	X	X	X		X	X	X		X	X	X	X		X	X			X	X		X	X
Crabs	X		X			X					X	X		X	X		X	X	X			X
Prawns, crayfish	X					X			X		X	X	X		X		X	X	X		X	X
Other or unidentified crustacea					X		X				X	X	X	X				X	X			
Ticks										X												
Spiders					X				X	X	X				X							X
Other arthropods										X												
Snails	X				X				X	X		X			X		X				X	
Mussels																		X				
Other or unidentified mollusks										X			X					X			X	X
Freshwater fish	X	X	X	X	X	X		X	X	X	X	X		X	X	X	X	X	X	X	X	X
Marine fish	X	X			X	X	X		X		X	X	X	X	X		X	X	X			
Frogs, toads	X	X	X	X	X	X	X		X	X	X	X		X	X		X	X			X	X
Tadpoles, newts	X						X		X	X	X				X		X	X			X	X
Snakes, lizards	X	X	X		X	X			X	X	X	X		X	X		X	X			X	X
Turtles											X						X					
Crocodilians	X																					
Rodents	X	X	X		X	X				X					X		X	X	X		X	X
Other mammals	X	X	X		X	X															X	X
Birds	X	X	X		X	X				X							X	X				X
Eggs																		X				
Carrion	X		X															X				

Nestlings may have requirements that determine what types of prey are acceptable (Kahl 1964, 1966*b*, 1971*b*). Certain fish that contain high levels of thiaminase cannot constitute a large part of a growing bird's diet. Marabous require whole vertebrate prey early in nesting for bone development, and adults will shift feeding sites to supply it. Nestling Open-billed Storks show an innate preference for snails and may reject other food.

Juvenile wading birds regurgitate food when disturbed, and adults cast pellets of undigested material (J. G. 1834; Gross 1923; Hibbert-Ware 1940; Kirkpatrick 1940; Haverschmidt 1949; Lowe 1954; Owen 1955; Siegfried 1966; Skead 1966; Jenni 1969; Milstein et al. 1970; Kushlan and Kushlan 1975; Ogden et al., in press). Although adults' pellets containing such material as fur, bones, feathers, and chitinous exoskeletons have in the past been used in food analysis, due caution must be exercised because the digestion of wading birds is rapid and selective. Fish and frogs may be digested within six hours (Vinokurov 1960). Adults as well as nestlings of some species will regurgitate unpelleted food. I suggest such regurgitation is primarily an antipredator device used to lure predators away from nestlings. In support of this, it has been observed that Turkey Vultures, which may kill wading bird chicks, have learned to collect and to consume regurgitations instead (Temple 1969).

Food Requirements

Wading birds are relatively large animals requiring a considerable quantity of food to maintain a positive energy balance and to reproduce successfully. Wide-

Table 6. Foods consumed by selected species of storks.

	Wood Stork	African Open-billed Stork	Abdim's Stork	White Stork	Black-necked Stork	Jabiru	Marabou	Shoebill	Hammerkop
Earthworms		X							
Aquatic insects	X	X		X		X			X
Land insects	X		X	X			X		X
Crabs	X	X	X	X					
Prawns, crayfish	X								X
Other arthropods			X						
Snails	X	X				X			
Mussels		X							
Other or unidentified mollusks				X				X	
Freshwater fish	X	X		X	X	X	X	X	X
Marine fish	X								
Frogs, toads	X	X		X		X	X	X	X
Tadpoles, newts	X			X			X		X
Snakes, lizards	X			X		X		X	
Turtles	X							X	
Crocodilians	X						X	X	
Rodents	X			X			X		
Other mammals	X			X					
Birds				X			X		
Eggs							X		
Carrion							X	X	

Table 7. Food consumed by selected species of ibises.

	White Ibis	Glossy Ibis	Bald Ibis	Hadada	Sacred Ibis	African Spoonbill	Roseate Spoonbill
Leeches	X	X					
Earthworms	X	X		X	X		
Aquatic insects	X	X		X	X	X	X
Land insects	X	X	X	X	X		X
Crabs	X	X					
Prawns, crayfish	X	X		X		X	X
Other or unidentified crustacea				X	X		X
Spiders	X			X	X		
Other arthropods				X	X		
Snails	X			X	X		X
Mussels	X						
Freshwater fish	X				X	X	X
Marine fish	X						X
Frogs, toads	X	X			X		
Tadpoles, newts	X	X			X		
Snakes, lizards	X	X		X			
Eggs					X		
Carrion					X		

spread adaptations — such as social food finding; soaring flight to feeding grounds; asynchronous hatching; differential feeding of larger siblings; intersibling aggression; food competition, fighting, pecking, and cannibalism among nestlings; differential sibling survival; and nestling abandonment when food resources fail — demonstrate the importance and potential difficulty wading birds have in meeting their food requirements (Verwey 1930, Strijbos 1935, Moseley 1936, Owen 1960, Kahl 1964, Bauer and Glutz von Blotzheim 1966, Král and Figala 1966, Vespremeanu 1968, Dusi and Dusi 1970, Milstein et al. 1970, Kushlan 1977). Low food intake is particularly critical for fish-eating birds because of their load of symbiotic gastric nematodes, which attack the host when food consumption is reduced.

Nestlings suffer greatest mortality in their first two weeks. At this time, growth is rapid, the relative size difference between siblings is great, and parents forage one at a time while the other remains to guard the nest. Food shortages can impair weight gain, although probably not organ maturity. Growth-rate conpensation can occur if food delivery increases after growth is slowed. Reduction of feeding and abandonment of large chicks to increasing hunger may lead to fledging. Mortality is also high in the first months after independence (Lack 1949; Hickey 1952; Meanley 1955; Owen 1959, 1960; Dusi 1963; Kahl 1963*b*; Ryder 1967; Ricklefs 1969; Siegfried 1970; Wolford and Boag 1971*a*; Henny 1972).

The food requirements of wading birds depend on both environmental and physiological factors, the most important of the latter being metabolic rate. Although this paper does not review wading bird energetics, it must be emphasized that understanding energetics is indispensable in determining food use. Metabolic rates are simple allometric functions of body weight (Calder 1974). Higher-order metabolic parameters, including existence metabolism and daily energy expenditure, also appear to be allometric functions (King 1974), although better resolution of these relationships for large birds such as ciconiiforms is necessary.

The daily food requirements of birds depend on time budget, activity level, assimilation efficiency, and energy content of food. None of these variables is well known in wading birds. Within an ecologically similar

group of birds such as ciconiiforms that are either related or closely convergent, it is possible that differences in assimilation efficiency, food value, and time budget are small enough not to significantly affect the food requirements of various species. Data on daily food requirements of wading birds are few and are arrived at in different ways (Table 8, data on Wood Stork from Kahl 1964; Marabou, Kahl 1966*b*; Cattle Egret, Siegfried 1969, 1971*b*, Shanholtzer 1972; Snowy Egret, Shanholtzer 1972; Striated Heron, White-backed Heron (*Nycticorax leuconotus*), and Goliath Heron (*Ardea goliath*), Junior 1972; White Ibis, Kushlan 1977). Despite the disparity of the data, they demonstrate a relationship between bird size and daily food consumption (Fig. 21, data from Table 8, regression model: $\log y = .966 \log x - .640$, where x is weight in grams). The points lie remarkably close to the regression line. The usefulness of this approach in determining the food requirements of wading bird communities may merit further consideration.

The food required by larger birds therefore increases with body weight. Similarly, the total amount of food required for growth and maintenance of nestlings increases with the size of the bird because maintenance costs increase with larger biomass and a longer nestling period. Of ecological importance is the daily food delivery required of adults. Some data are summarized in Table 9 (Kahl 1962, 1966*a*; Siegfried 1972; Kushlan 1977). Although studies are few, the results suggest that the total daily food requirements of nestlings decrease with increasing species size even though the total nesting requirements increase.

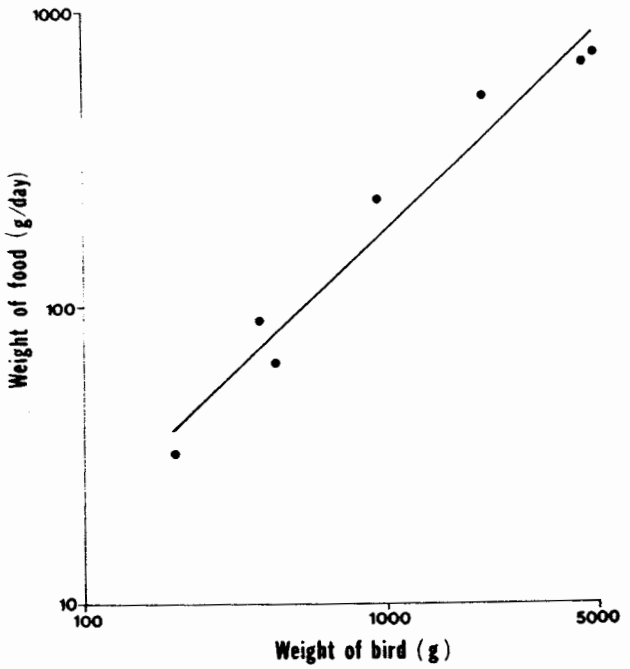

Figure 21. Relationship of daily food requirements of wading bird to size of bird.

Table 8. Daily food requirements of various wading birds.

	Daily energy requirement (kcal/d)	Daily food requirement (g/d)	Calculation
White Ibis	206	203	DER = DEE/(assimilation efficiency of .80) DFR = DER/1.01 kcal/g (Kushlan 1977)
Wood Stork	570	520	DER = DEE/(assimilation efficiency of .79) DFR = DER/1.1 kcal/g (Kahl 1964)
Cattle Egret	187	90	DFR for grasshoppers (Siegfried 1971)
Marabou	900	720	DER = DEE/(assimilation efficiency of .80) DFR = DER/1.1 kcal/g (Kahl 1966)
Striated Heron		32	DFR = .16(W) (Junior 1972)
White-backed Heron		65	DFR = .15(W) (Junior 1972)
Goliath Heron		700	DFR = .155(W) (Junior 1972)

DER = daily energy requirement
DEE = daily energy expenditure
DFR = daily food requirement
W = weight of bird

Feeding Risks

Feeding is not necessarily a safe way to spend a day (Langdale 1897, Cottam 1938, Trautman 1940, Hull 1944, Ryder 1950, Greene 1959, Benson and Penny

Table 9. Energy requirements for some nestling wading birds.

Species	Total energy kcal	Period measured	Kcal/day	
Wood Stork	16500	120d	137.5	Kahl 1962, 1964
White Ibis	8620	40d	215.5	Kushlan 1977
Cattle Egret	6453	21d	307.3	Siegfried 1972, calculated (1676 gm insects) (5.5 kcal/g)

1971). Herons have been choked by frogs and have had large fish lodged permanently between their bills. Least Bitterns have been consumed by snapping turtles, and Little Egrets "curiously" chased by sharks. Meyerriecks (1971) noted a Snowy Egret hitting its head on mangrove roots during a strike and then moving back to open water. A Great Egret reported by Weigel (1962) impaled its head on a mangrove stick. Great Blue Herons may get into spectacular trouble. Audubon (1840) related how one impaled a large fish which then dragged the heron underwater for several yards. Pringle (1964) told of a heron striking between its legs, loosing balance, and floating downstream on its back. Even such inoffensive animals as clams may securely trap an unwary bird's foot (Semple 1937). Thus, there are unobvious considerations in a wading bird's choice of behavior, food, or foraging location.

Use of Habitat

Wading birds include species of both wide and restricted habitat preferences. Whereas the White Ibis, for example, is generalized in its habitat (Kushlan and Kushlan 1975), bitterns are often restricted to a single habitat — dense emergent vegetation (Trautman 1940, Weller 1961). Although one might expect the requirements of wading birds to be met by their use of aquatic habitats, the birds are not always that obliging. Terrestrial habitats are important to many aquatic species (Hudson 1920; McIlhenny 1936; Davis 1941; Van Rossem 1943; Vincent and Symons 1948; Van Someren 1956; Dawn 1959; Curry-Lindahl 1960; Carrick 1962; Slud 1964; Wetmore 1965; Kahl 1966*a* and *b*, 1971*b*; Benson and Penny 1971; Kushlan and Kushlan 1975; Kushlan, in press *a*). Species such as the Bald Ibis nest in semiarid regions and feed in dry habitats, and the Black-headed Heron (*Ardea melanocephala*) characteristically feeds in dry habitats. The most terrestrial heron, the Cattle Egret, may be more of a marsh bird than commonly appreciated. It often forages along pond margins and in both freshwater and salt marshes, and in Africa it requires access to such habitats for nesting (Valentine Jr. 1958, Post 1970, Siegfried 1971*b*). Shifts between terrestrial and aquatic habitats are correlated with the relative availability of prey and the ability of birds to use it (Grater 1938, Valentine Jr. 1958, Carrick 1959).

Another pattern of habitat use is the specialization of some wading bird species for marine or freshwater sites (Scott and Sharpe 1912, Bent 1926, McIlhenny 1936, Sprunt Jr. 1937, Allen 1942, Palmer 1962, Recher and Recher 1969*a*, Murton 1972, Robertson Jr. and Kushlan 1974). Some species, such as Reef Herons and Reddish Egrets, may have behavioral or morphological adaptations for foraging in marine habitats. Most apparently marine species occur in freshwater habitats to a greater or lesser extent and forage successfully there.

Habitats possess particular characteristics to which birds respond either innately or through learning (Lack 1933, 1940; Miller 1942; Klopfer 1963; Welch 1963; Hilden 1965), but little is known about the mechanics of habitat selection of wading birds. Cattle Egrets respond innately to dry land (Lowe-McConnell 1967), whereas White Ibises apparently undergo habitat learning, as evidenced by the atypical habitats used by fledglings. Certain characteristics enhance the usefulness of habitats to particular species. Cattle farming with resultant improved pasturage is one such factor (Rice 1954, Carr 1965, Blaker 1971). In North America, species such as the Snowy Egret have altered their pattern of habitat selection because of the introduction of improved short-grass pasturage and intensive cattle farming. This same habitat enhancement has proved the requisite for establishment and spread of Cattle Egrets in the western hemisphere. Fires increase habitat use by upland birds, such as Marabou, Maguari (*Ciconia maguari*), and Woolly-necked (*Ciconia episcopus*) Storks, Cattle Egrets, and Sacred Ibis (*Threskiornis aethiopicus*) (Kahl 1966*a*, 1972*c*; Chapin 1932; Priest 1933; Van Someren 1956; Cypert 1961; Kushlan, this paper). Marsh fires open dense stands of vegetation and increase available nutrients, a fact which is reflected in food availability.

The population levels of wading birds depend on the existence and preservation of feeding habitat (Allen 1937, Skead 1952, Weller et al. 1958, Lebret 1964, Siegfried 1965, Craufurd 1966, Vespremeanu 1968, Robertson Jr. and Kushlan 1974, Weller and Fredrickson 1974). Along the Atlantic Coast of North America, for example, the amount of coastal wetlands correlates with the numbers of coastally nesting wading birds (Fig. 22, data from Custer and Osborn, in press).

Prey Availability

Seasonality of prey

Prey abundance varies seasonally, and in temperate areas winter–summer seasonality is quite critical. Many temperate wading bird species typically migrate

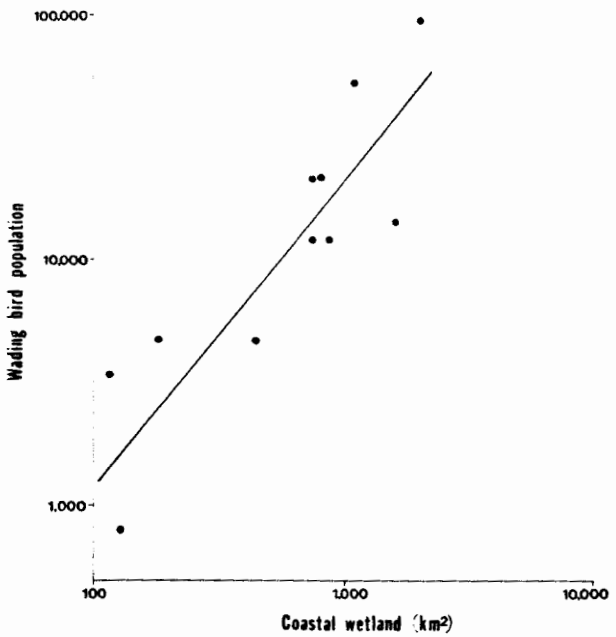

Figure 22. Relationship of habitat availability to the number of nesting wading birds. The populations of nesting wading birds in states along the Atlantic Coast of North America are plotted against the area of coastal wetlands. States with less than 100 km² of coastal wetland habitat are not graphed.

to tropical or subtropical areas during winter and return to more temperate areas to nest (Cooke 1913; Lowery Jr. 1946; Larrison 1947; Coffey Jr. 1948; Haverschmidt 1949; Siebenaler 1954; Meanley 1955; Rydzewski 1956; McClure 1957, 1958, 1974; Stevenson 1957; Simmons 1959; Curry-Lindahl 1960; Meyerriecks 1960*a*; Owen 1960; Mackworth-Praed and Grant 1962; Palmer 1962; Sapetin 1962; Witherby et al. 1952; Slud 1964; Dusi and Dusi 1967; Ryder 1967; Smith 1970; Milstein et al. 1970; Kahl 1971*b*, 1972*b*; Henny 1972; Browder 1973*a*). In such areas nesting occurs almost exclusively in spring and summer, cold weather being limiting. The dispersal of many herons and other wading bird species at the conclusion or failure of nesting is generally radiative, although one component may dominate because of topographic features (Lonnberg 1938; Coffey Jr. 1943; Rydzewski 1956; Carrick 1962; Palmer 1962; Dusi and Dusi 1967; Siegfried 1970; Medway and Lim 1970; Henny 1972; Hopkins 1972; Byrd, this volume; Ryder, this volume). Birds nesting in tropical continental areas may tend to disperse in late summer toward temperate marshes where food may be maximally abundant. The influx of temperate migrant birds into the tropics increases the impact on the wading birds in those areas and renders the pattern of food availability critical to the survival of birds nesting over a much larger area. For example, the marshes of southern Florida support birds from much of eastern North America (Robertson Jr. and Kushlan 1974). Winter food availability may limit population levels of nonmigrating temperate species (Lack 1951, 1953, 1966). The expanding Cattle Egret population in the United States is apparently not yet limited by winter food availability, but adverse weather conditions impact population levels, probably through changes in food availability (Bock and Lepthien 1976).

For most species of wading birds, the critical seasonality is that of the wet–dry cycle (Carrick 1962; North 1963; Ruwet 1963, 1964; Kahl 1964, 1966*b*, 1971*b*; Carroll 1967; Lowe-McConnell 1967; Klug and Boswell 1970; Siegfried 1971*b*, 1972; Vernon 1971; Urban 1974; Ogden et al., in press; Kushlan, in prep.). Depending on the habitat, wet or dry season correlates with the greatest availability of prey, and many wading birds nest during these times. In most tropical areas, prey is more abundant and available during the rains. Depending on the area, either the big rains or the little rains are the primary nesting period. In subtropical marshes, the drying season is the time of maximum availability. The critical role of the hydrologic cycle in prey availability is such that heavy rains may cause abandonment of colonies of dry-season nesting birds, and drought can do the same for wet-season nesting birds (Mountfort and Ferguson-Lees 1961, Dusi and Dusi 1968, Kushlan et al. 1975). Similarly, proper hydrologic conditions irrespective of time of year can often cause some species to initiate nesting (Ruwet 1964, Kushlan 1976*c*).

The proximate factor initiating nesting in tropical wet–dry areas is not definitely known (Keast and Marshall 1954; Kahl 1964; Ruwet 1964; Kushlan 1976*c*, this paper). In the subtropics, photoperiod apparently has some effect, because captive White Ibises become sexually active during their usual spring nesting season. However, ibises also nest at other times of year when water conditions become suitable. Thus, food availability may be the overriding proximate factor in eliciting nesting, although the nature of prey availability differs somewhat in different wading bird species. In Africa, two storks may nest at the same site but, because they respond to different patterns of prey availability, nest on different cycles.

Nesting sites are situated at or near available foraging habitat. Solitary species may use the same or immediately adjacent habitat for foraging and nesting

(Gabrielson 1914, Saunders 1926, Weller 1961, Kushlan 1973*c*). Except for fledglings, colonial species generally do not feed at nesting sites because food there is quickly depleted. Adaptations for low-energy long-distance flight, particularly soaring, extend the permissible distance from colonies to feeding sites (Campbell 1892; Witherby et al. 1952; Forster 1955; Rand 1956; Palmer 1962; Cone Jr. 1962; Kahl 1964, 1966*a*, 1972*a*, *b*, and *c*, 1973; Ogden et al., in press).

The decline, movement, or disappearance of birds from particular colony sites is correlated with habitat change (Nicholson 1929; Moseley 1936; Ryves 1948; Valverde 1958; Carrick 1962; Noskiewicz 1964; Hopson 1966; Skead 1966; Kerns and Howe 1967; Ryder 1967; ffrench and Haverschmidt 1970; Milstein and Jaka 1970; Milstein et al. 1970; Grant 1971; Waterman et al. 1971; Kushlan 1976*b*; Custer and Osborn, in press). Colonies may be relocated because of disturbance or site alteration, including that caused by nutrient accumulation and other impacts on the birds themselves, but in most such cases the colony relocates in the same area and birds use the same foraging habitat as before (Kerns and Howe 1967; Weseloh and Brown 1971; Wiese, this volume; Kushlan, in prep.).

Species differ in their propensity to change colony sites. Some, such as Wood Storks, return to former colony sites each year. Degradation of nesting habitat, reflected by site changes, occurs only slowly, with a complete colony movement happening over a period of years. At the opposite extreme, in climates where habitat conditions vary from year to year, some species wander widely prior to breeding, which results in the establishment of colony sites near currently available foraging habitat (Carrick 1962, Kushlan 1976*b*). Nevertheless, tradition plays a role in most species, regardless of their tendencies. Many birds will return to the previous year's site and begin nesting activity. If conditions are suitable, they may remain; if not, they may move to another area. When exceptionally good habitat conditions at a site are followed by average but suitable conditions the following year, birds may return to nest. In this way nesting may recur in an area after the original conditions no longer exist.

Regional movements undertaken by many wading birds are also made in response to seasonal changes in prey availability (Chapin 1932; Curry-Lindahl 1960; Carrick 1962; Craufurd 1966; Dowsett 1969; Britton 1970; Urban 1974; Kushlan 1976*a*, in prep; Ogden et al., in press). Population levels in an area being used by birds undertaking regional movement depend on the available feeding habitat (Fig. 23, data from Craufurd 1966). Responses of wading birds to drought and high water illustrate the importance of feeding conditions in marsh habitats (Trautman 1940; Cypert 1958; Kahl 1964; Robertson Jr. and Kushlan 1974; Kushlan 1976*b*, in prep.). Great Egrets decrease in numbers in marshes during droughts and move to permanent bodies of water such as lakes. In southern Florida, both drought and high water inhibit habitat use and cause movement to other habitats. Water-level fluctuations, however, are necessary to make many habitats available (Weller and Spatcher 1965; Weller 1967; Kushlan et al. 1975; Browder 1976; Kushlan 1976*b*, in press *a*).

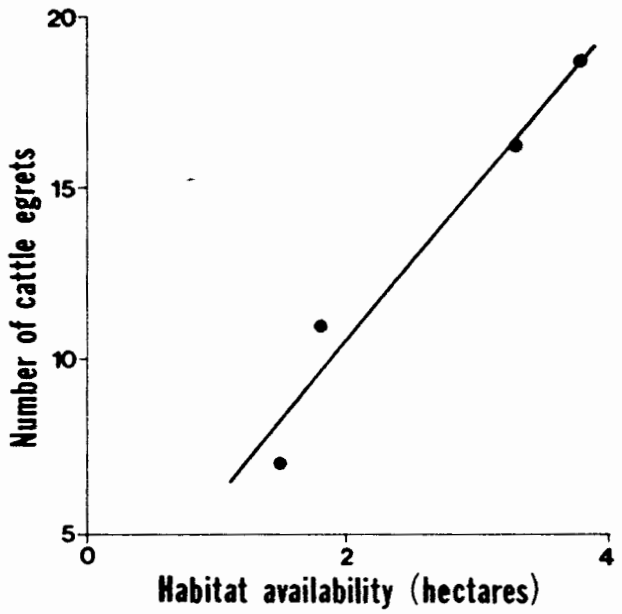

Figure 23. Relationship of habitat availability to the number of Cattle Egrets in a region. The habitat is garden plots in an area used by Cattle Egrets during the African dry season.

Prey dispersion

The degree of dispersion of food resources determines the tactics of predation. As discussed before, relatively unconcentrated prey often results in overdispersion of feeding birds or in territorial feeding (Recher 1972*b*, Recher and Recher 1972, Snow 1975, Siegfried 1975). Lava Herons fishing along rocky shores and Eastern Reef Herons fishing over reef crests defend relatively uniform habitats in which patchiness of food distribution is small enough to per-

mit defense. Changes in bird dispersion within a habitat are associated with changes in prey distribution (Kushlan 1973*c*, 1976*c*). In the southern Florida wet season, Great Egrets and Great Blue Herons are well dispersed through the Everglades; during the Everglades dry season, however, they feed aggregatively. Bitterns, normally solitary, may nest in densities approaching coloniality when food is patchily concentrated.

Although highly concentrated food resources may provide a superabundant food supply in that more prey occur than can be quickly consumed, at least at the beginning of exploitation, in most cases the superabundance is of short duration in a single location because birds soon reduce the concentration. A succession of such patches, however, may produce a continued availability of locally superabundant food through most of a season. Finding and using new patches of food may be accomplished by intraregional movement. Thus, when seasonal conditions produce a succession of suitable foraging areas, wading birds move from one patch of abundant food to another (Kushlan 1976*b* and *c*).

The environmental determinants of food dispersion are complex but critical to understanding the feeding ecology of wading birds. Detailed studies are few (Owen 1957, Kahl 1964, Vespremeanu 1967, Kushlan et al. 1975, Browder 1976, Kushlan 1976*c*, Ogden et al. 1976). The relationship of food dispersion to nesting success in the Wood Stork is an example of the complexity involved. The tactile-feeding Wood Stork forages at patches of relatively concentrated prey which develop because seasonal drying forces aquatic animals from shallow marshes into deeper pools and ponds. Storks follow a predictable pattern of regional movement. Use of an area corresponds to the time when it dries and becomes available for foraging. Time of nesting is predicated on food availability. In the Big Cypress Swamp, nesting begins when the swamp's surface water reaches a certain level. In the broad marshes of the Everglades, time of nesting is correlated with the rate at which the marshes dry (Fig. 24 — data from Kushlan et al. 1975). If water levels rise, storks disperse from their normal feeding pattern. Water-level rises greater than or equal to 3 cm in the first two months of nesting cause desertion of colonies. Thus, environmental conditions affecting prey availability determine the pattern of feeding dispersion and success of nesting, but the nature of the conditions differs in the two adjacent wetland systems of southern Florida. In the Big Cypress Swamp, fish concentrate in many small localized depressions where storks can feed only when water depth becomes shallow enough for foraging. In the Everglades, fish are concentrated in broad, gently sloping marshes and pools along an edge of drying habitat caused by progressively falling water levels. This provides a continual supply of available food along the topographic gradient as water levels fall. Rising water refloods the higher marshes, allowing remnant fish to disperse. The rate at which fish become available depends on the rate of water-level recession. A slow rate will mean slow concentration. Thus, the rate of change in the Everglades determines food availability and nesting success.

Prey Selection

Prey selectivity is the consumption of a prey item in relatively greater proportions than it occurs in the environment (Ivlev 1961). It is the "preference" of a predator for a certain prey. A convenient index of selectivity is $S = (C_i - A_i)/(C_i + A_i)$, where S is selectivity, C_i is the proportion of the diet composed of consumed prey type i, and A is the proportion of prey type i available in the environment. This index

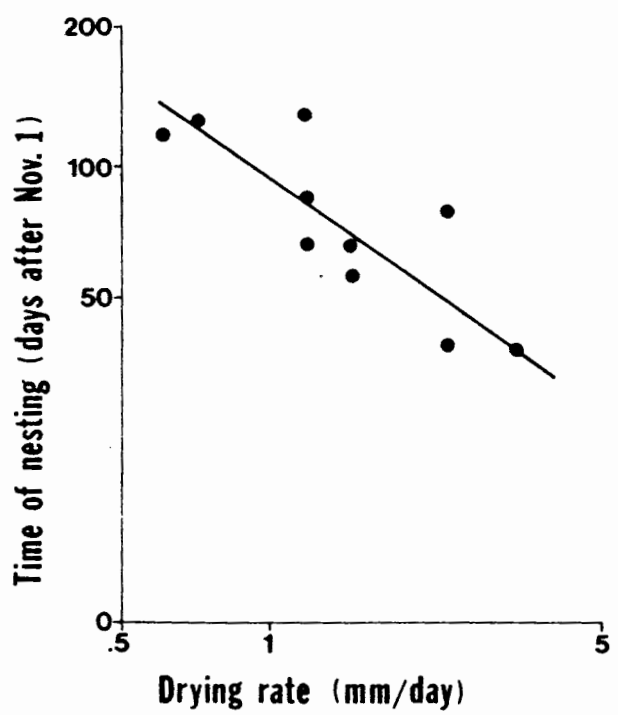

Figure 24. Relationship of timing of Wood Stork nesting in southern Everglades to hydrologic conditions.

ranges from near +1 when a prey type is consumed proportionally well above its relative availability, to near −1 when a prey type is consumed proportionally well below its relative availability. Thus, prey items are positively or negatively selected. Index values near 0 indicate selection of a prey item in direct proportion to its relative abundance. C and A may be expressed in terms of numbers, biomass, or energy content. Wading birds apparently exhibit food "preferences" to a greater or lesser degree (Baynard 1913; Carrick 1959; Siegfried 1971*a*, 1975; Kushlan and Kushlan 1975; Recher, in prep.). Apparent preferences often noted among wading birds mean that certain prey appear in the diet more often than might be expected and that they are selectively consumed. It seldom means that the total diet is restricted to a few kinds of prey.

Individuals also show food preferences (Owen 1955, Carrick 1959, Milstein et al. 1970, Siegfried 1971*a*, Browder 1973*b*). Data collected from individual birds foraging in the same general area or nesting at the same location have shown marked differences in food taken. Some differences result from selective use of habitat, but differences in both type and proportions of prey vary in individual birds collected while feeding in the same aggregation.

Feeding location is an important factor influencing the type and size of food taken, both within and between species. Differences in the proportions of prey taken in several habitats reflect variance in density, size, or vulnerability of a prey species in each habitat. A prey type may occur at identical densities in two habitats but may be less visible in one habitat, and therefore less vulnerable, and hence will make up a smaller proportion of the diet there. Density is usually considered a critical factor in prey capture (Owen 1955; Kahl 1964; Ogden et al. 1976, in press; Kushlan, in prep.). Changes in the proportions of particular fish species in the Gray Heron's diet corresponded to their increased abundance in the feeding habitat. Wood Storks depend on concentrated prey and choose feeding habitats containing high prey densities. However, of their 11 most important prey species, only one was taken near the proportion it occurred in the habitat. The other ten were either relatively overrepresented (selected) or underrepresented (negatively selected) in the diet. Thus, high densities alone do not increase selectivity.

The functional relationship between prey density and capture also differed in the various prey of the White Ibis (Kushlan, in prep.). There is a typical sigmoid-type correlation with water beetles, but density makes no difference for crayfish since they are selectively consumed by ibises at all densities, and fish do not become important in the diet until their densities are extremely high. Switching can occur when a less susceptible prey occurs at high density and selection of the more susceptible prey drops. This may often result from a swamping effect of the dense prey rather than from a deliberate change on the bird's part if its foraging tactics do not change. Thus, there are several patterns relating selection to increasing prey density (Fig. 25). The selectivity of a prey species may increase, decrease, or be unchanged by fluctuations in density.

Increasing prey size should affect susceptibility to capture (Owen 1955; Ogden et al. 1976; Kushlan, in prep.). A greater total range of prey sizes and a greater mean and median size of prey should be taken by larger birds. The lower limit may be set either by ineffectiveness of a bird in catching relatively small prey or by the bird's choice not to strike at small prey. This could be functional if strikes at a small fish decrease the probability of subsequently catching larger fish. The upper limits of prey size may be set by capture ability or handling time. White Ibises feeding in aggregations often release large prey, apparently because long handling time increases the probability of loosing the item to robbing species. The entrance of a species into the Gray Heron's diet corresponds with

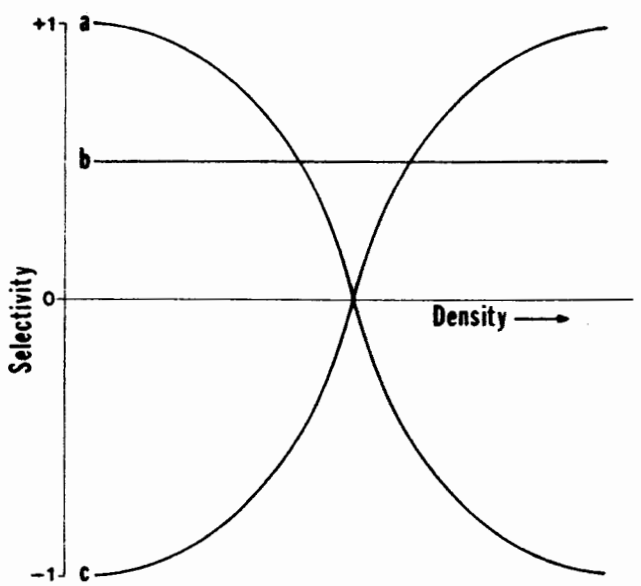

Figure 25. Relationship of density of certain prey to selectivity of wading birds. a — birds select some prey only at lower densities. b — birds show consistent selection of some prey regardless of density. c — birds select some prey at higher densities.

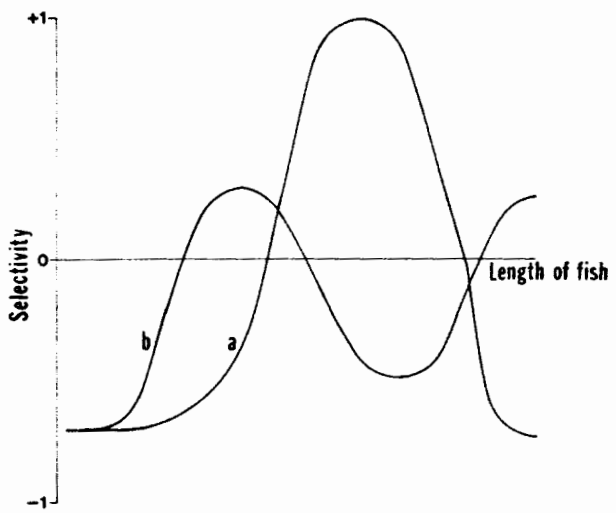

Figure 26. Two patterns of the relationship of length of fish to prey selectivity.

growth to a susceptible size. The Wood Stork shows selectivity for larger fish and consistently takes relatively large prey. The critical size for positive selection varies for different species of Wood Stork prey. Figure 26 shows two size selectivity patterns. The usual pattern is shown by curve *a*. Curve *b* reflects changes in selectivity caused by behavioral changes in the prey. Selectivity increases with increasing size of the prey until growing to a size when schooling behavior decreases selectivity. Further growth of the prey may again increase selectivity.

It appears therefore that characteristics of the prey species are important factors in predator selectivity. In the examples cited above, such characteristics can alter the role of other factors. Prey behavior, size, density, and similar factors influence catchability, handling time, and escape probability. Cattle Egrets, for example, specialize on grasshoppers and other prey that are cryptic, often ground dwelling, and respond to a predator by remaining stationary or taking short, rather than long, escape flights (Browder 1973*b*). Such effects are apart from any possible energy differences among prey. In the White Ibis, energy content of prey plays little or no role in prey selection (Kushlan, in prep.).

It is the interaction of predator and prey characteristics that determine whether a prey type is taken. Initially, tactics of predation involve choice of habitat having an adequate density of suitable prey. Secondarily, predators select prey they are capable of catching. Visual predators such as herons can weigh cost and benefits of attempting to capture an item before striking. A nonvisual predator can make no a priori balancing of costs and benefits and should attempt to capture any prey encountered, although a balancing of costs of additional handling may occur afterward. A bird that expends energy in searching must decrease search time by habitat selection and by behavioral modifications such as observational or trial-and-error learning.

In terms of prey selection, birds that mostly search for prey should be generalists, while birds that actively pursue prey and those that wait for prey to approach them should have more restricted diets. The nonvisual predator, being a searcher, should have a generalized diet, but its foraging behavior is such that it will invariably be somewhat specialized on prey it can most easily catch. This is supported by the documented diets of Wood Storks and White Ibises in southern Florida (Ogden et al. 1976; Kushlan, in prep.). The difference between searchers and pursuers is supported by data on Little Blue Herons and Snowy Egrets in north Florida (Jenni 1969). Little Blue Herons, searchers, consumed 36 prey types, and the four most important items made up 59 percent of the diet. Snowy Egrets, pursuers, consumed 29 prey types, and the four most important items made up 73 percent of the diet. Thus, searchers were more generalized than pursuers. In this same study the Louisiana Heron fed primarily by standing. It consumed 26 prey types, and the top four most important prey made up 81 percent of the diet. This standing species therefore had a fairly restricted diet. Thus, the predictions are generally upheld by these few data.

Impact on Prey

The impact of wading birds on their prey has concerned many a game warden and modern hatchery guard (Hickling 1961, Nikolski 1963, Vinokurov 1965, Mills 1967). Wading bird predation on fish artificially concentrated in shallow hatching pools can be severe, but information on the role of predation in natural environments is slim. Carrick (1962) found that locusts were eaten by ibises at all densities but that the ibises had no impact on the locusts' population dynamics because of the availability of more highly preferred prey. Predation on fish populations in a pond reduced their numbers by 77 percent without loss of species richness (Kushlan 1976*c*). When predation does not occur, oxygen can be reduced to the extent that fish kills take place, which can eliminate 99

percent of a population and extirpate most species of fish.

Sympatric Foraging

The ways in which animals partition available resources have aroused considerable interest, particularly in efforts aimed at demonstrating the competitive exclusion principle or at determining the limiting similarity of coexistence (Cole 1960; Hardin 1960; MacArthur and Levins 1967; Miller 1967; Lack 1971; May and MacArthur 1972; Cody 1974; Pianka 1974, 1975). Several studies of species pairs or species groups of wading birds have uncovered differences sufficient to elicit judgment that the species did not sufficiently overlap in resource use to be competitive (Carrick 1962; Meyerriecks 1962; Jenni 1969; Kahl 1972*a*; Willard 1975; Kushlan 1976*c*; Custer and Osborn, this volume).

The rough cut of resource partitioning within a wading bird community is straightforward, as demonstrated by the diverse wading bird community in southern Florida (Fig. 27). On a regional basis, 16 species appear to be ecologically isolated by a number of mechanisms, including habitat use, time of activity, feeding behavior, and size of each species. This leads to the conclusion that they share the resource base noncompetitively or that different species do indeed differ. The result, while sufficient to demonstrate mechanisms of regional persistence, is unsatisfactory for detailed consideration. Most of the primarily inland birds feed in marine habitats and also nest there. Aquatic herons and ibises sometimes feed terrestrially. Many species feed together in aggrega-

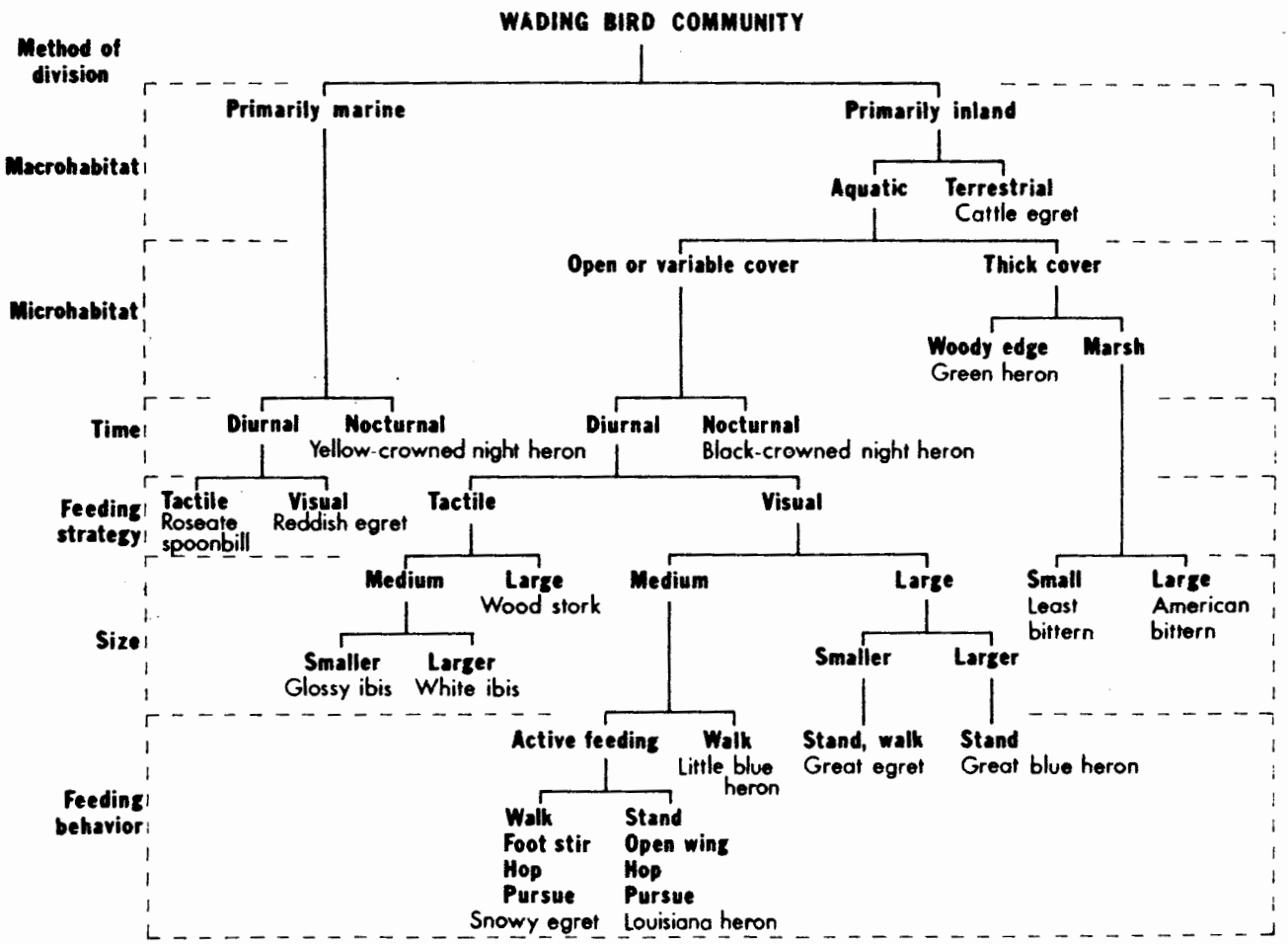

Figure 27. Methods of resource partitioning in the southern Florida wading bird community.

tions. Night herons are not entirely nocturnal, and day herons are not entirely diurnal.

Of more interest is exploring the partitioning mechanisms and relations among similar birds feeding in similar habitats or feeding together in aggregations. Several studies of wading birds have touched upon some of these considerations and have generally shown that congeneric wading birds differ by their size, behavior, feeding sites, or food (Carrick 1959; Meyerriecks 1962; Jenni 1969; Kahl 1972*a*; Recher and Recher 1972, in prep.; Recher 1972*a*; Kushlan 1973*b*, 1976*c*; Willard 1975; Custer and Osborn, this volume). Several species of the *Ardea-Egretta* complex often feed together. In Florida habitats, these species appear to differ by a combination of feeding behaviors and habitat choice, but some data may also be interpreted to suggest marked similarity in the diets of several smaller species, particularly Louisiana Herons and Snowy Egrets. Although data from temperate marshes are somewhat contradictory, they too suggest that diet similarities exist among the smaller egrets. Each of these studies found some aspect of feeding ecology that could separate the species, and usually it was feeding behavior. However, considering behavior to be the critical resolving factor glosses over striking similarities in diet that are sometimes found in two or more of the medium-sized herons, similarities that have not yet been adequately explained.

With some wading birds overlapping in diet, studies of how the diet is obtained become important. Several characteristics of wading bird foraging bear noting. There is no reason to expect that a species in a guild of similar species is less effective a hunter than any of the others. Each species should be equally good in supplying its own energy needs. Each species is adapted to its environment and adequately meets its energy demands in most circumstances, probably without excess effort and without compressing its time-budget allotments to other activities. We can expect that within a species energy gain will be similar over a wide range of habitats, decreasing only in those that are exceptionally poor and therefore presumably little used. We can also expect energy gain per time to be similar for similarly sized birds but to vary directly with size of bird. This is supported by data (Recher, in prep.) that show similar weight of prey taken per minute by each of the species in habitats as diverse as Florida and New Jersey.

Maximization of net energy intake need not necessarily occur at any given time (Kushlan, in prep.). Under rigorous conditions of low food availability or high energy demands, strict optimization may be expected. When conditions are not rigorous, however, a bird may need to obtain only an adequate energy balance, and this can often be achieved by less than maximal foraging return.

Intense resource-based competition also need not occur at any given time. To meet its energy demands, a bird selects a feeding location and a behavior to match prey and habitat. Because species differ in their ability to use a behavior effectively, each species may choose a different set of behaviors under identical conditions. Similarly, individuals in populations probably choose behaviors based upon individual abilities. On the other hand, two species may change and even switch habitat and behavior use between two different areas. Feeding behaviors are probably selected based on energy return, which is determined in part by the number and types of other birds present. As the defensibility of a resource decreases, more contact is made between birds, and the range of behavioral options decreases. Therefore, combinations of behavior and habitat are chosen that reduce time lost to aggression relative to energy gained. Within an area, resource-based competition may seldom occur because of the many possible ways of partitioning the resources, and, under conditions of nonrigorous foraging, noncompetitive prey overlaps may develop.

Functional Relationships

Community Structure

The diversity of wading bird communities generally increases from the temperate zone to the tropics, reflecting a higher diversity of habitats and prey. Increased habitat diversity in the tropics may have led to the evolution of such specialized herons as those that feed on open tropical shores and reef crests. It is not certain whether productivity available to wading birds increases in the tropics; to the contrary, Recher and Recher (1972) found that increased productivity does not occur on reefs where overall habitat productivity is high but is only marginally available to wading birds. It is possible that the available productivity of habitats in the tropics at any given time may not be very different from similar types of habitats in temperate areas in the summer. Therefore, it may be the addition of habitat types and trophic compartments in the prey community that brings about an increase in the diversity of the tropical wading bird community.

Ecosystem Function

The role of wading birds in the functioning of ecological systems is little understood. It is probable that populations of such large and locally numerous predators may play an important role in some ecosystems. Their total impact may be surmised from their food requirements. Seven nesting wading bird species in southern Florida require about 170 tons of food per day (population from Kushlan and White, 1977; daily food requirement from Fig. 2). This intake may either have significant impact on prey or, alternatively, may only be utilizing surplus prey. The magnitude of the food intake suggests the former. Under some conditions in southern Florida this predation is required to provide population reduction necessary for survival of prey populations through a dry season (Kushlan 1976*a*). It is not expected, however, that wading birds would be a critical component of all habitats in which they occur. Coral reefs, for example, may be little affected by the foraging of the Eastern Reef Heron, although its impact on particular prey species might be important.

The role of wading birds affects a system not only through biomass reduction but through control of the pathways of energy flow. Figure 28, using the energy language of Odum (1972), shows the functional role of wading birds in one such system — a pond in a seasonally fluctuating marsh (based on data in Kushlan 1974, 1976*c*). Water overflows the edge of the pond for most of the year, but water levels fall in the dry season. As water depth in the pond and surround-

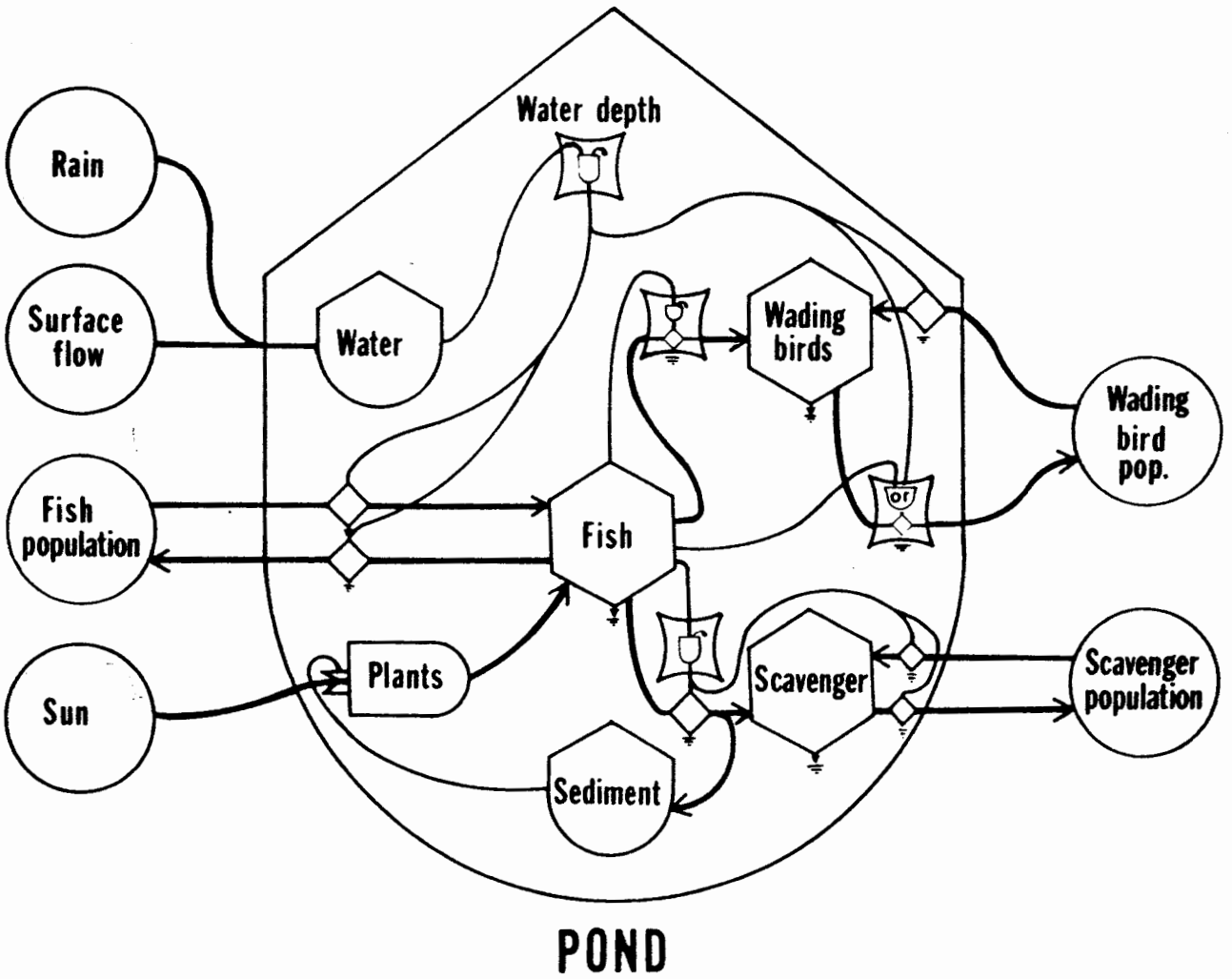

Figure 28. Model of the role of wading bird predation in controlling the pathways of energy flow in a pond ecosystem (see text for details).

ing marsh decreases, fish migrate into the pond and there density increases. Lowered water depths attract wading birds from the mobile regional population. Length of their stay at the pond depends on catch rate, which is in part determined by fish density. More birds remain as fish density increases. In the model, wading bird biomass increases through immigration, and fish biomass decreases through predation. The aggregation remains until prey density falls below the threshold of effective foraging or until water depth increases to a point where wading is impractical. At such time wading bird biomass in the pond decreases from emigration. If wading birds do not feed in the pond during the dry season while fish density increases, a critical threshold density occurs in which oxygen depletion causes a fish kill. As a result, biomass flows to scavenger populations and into the sediment. The fish kill ceases when fish density reaches a point where oxygen levels can support the remaining fish population.

Predation by wading birds is one of the forces determining the functional characteristics of this system by exerting control over pathways of energy flow. The tactical aspects of predation, such as the relationship between prey availability and prey consumption and between defensibility and territory size, function in determining the nature of the fish to wading bird energy flow. Similar relationships should exist in other feeding habitats that taken together determine the regional pattern of habitat use, prey consumption, and the ways wading birds meet daily and seasonal food requirements. It is reasonable to expect analogous relationships in systems elsewhere and to expect to discover that the role of wading bird feeding may be significant in many aquatic systems throughout the world.

Directions for Future Research

The extensive literature on feeding ecology of wading birds, summarized in this paper, provides a broad foundation for future study. Certain directions deserve emphasis.

Habitat

The relationship of the type, extent, and quality of habitat to wading bird population status deserves extensive study. Such data become particularly important in land-use planning and wild-area management. Planning and management decisions are necessary to provide for the conservation of adequate habitat for wading birds. The limits of habitat use must also be determined. The quality of habitat may fluctuate with little effect on the viability of a dependent wading bird population, but once critical thresholds are exceeded, the usefulness of the habitat decreases despite an unaltered outward appearance. Wintering habitat is crucial to the survival of many temperate populations. Similarly, many areas may be used for only a short period during the year by species making regional movements, but such areas are important in preserving regional populations. The primary function of habitat is to provide nesting sites and food, and these become critical aspects of wading bird ecology to be investigated.

Foraging Behavior

The relationships of feeding behavior to habitat use and prey consumption are important areas of study. Understanding the plasticity both of individuals and of species in altering behavior to meet energy requirements and environmental opportunities can illuminate many aspects of feeding ecology. Comparative studies of the relationship between morphology and feeding behavior may suggest limits on the choice of behaviors that can be made by various species. Basic observational study of who uses what, how, remains important since the behavior of many species is little known. Determining how feeding success relates to behavior, age of bird, habitat choice, food type, and prey availability may best be achieved by experimental studies. The dark-light plumage dichotomy and the functional significance of plumage polymorphism deserve continued thought. It is important to consider the total array of selection pressures operating in determining plumage color rather than to attribute color to the effect of a single factor. Proposals are made in this paper to bring this way of thinking into focus. Evidence of the function of polymorphism should be sought by study of clinal or discontinuous changes in selective pressure rather than by single-site studies of individual birds. The role of spacing in behavior, food use, and population regulation should prove to be critical, as is the role of interaction among aggregated birds. Most critical questions are susceptible to both observational and experimental study.

Food

Determining the food requirements of wading birds over their range of sizes may be important to understanding their total ecological impact and the role of

prey availability. Although studies of food habits remain useful, more critical questions involve the way wading birds select items from the range of potential prey available and the role of such factors as prey density, species type, and prey size in determining selectivity. Environmental conditions determine which prey are available to be selected. Similar birds taking similar prey in similar habitats provide test cases for determining the role and mechanism of possible resource division.

Functional Relationships

The structure of wading bird communities relative to patterns of prey availability may provide insight into components of faunal diversity. The role that wading birds play in their ecosystem has been little studied. Wading birds may control the composition of prey communities and have an impact through biomass reduction. More subtle but important relationships include those influencing the control of energy flow within their ecosystem.

Most wading bird studies have been primarily descriptive, and such information is exceptionally important and useful. Nevertheless, questions are often more decisively answered by testing hypotheses through critical natural or artificial experiments. Some hypotheses to be tested have been suggested in this paper. They are intended less as explanations than to point the direction toward suitable questions that, when answered, may advance our understanding of wading bird feeding ecology.

Acknowledgments

I thank T. W. Custer, J. C. Ogden, D. W. Mock, S. Bass, and J. Browder for discussing aspects of this paper. I especially thank M. S. Kushlan and J. Aresty for their able assistance in putting the paper together. M. S. Kushlan drew the figures. My research has been supported by the Maytag Chair of Ornithology at the University of Miami, the U.S. National Park Service, and the interest of my colleagues and co-workers, especially M. S. Kushlan, O. T. Owre, J. C. Ogden, and W. B. Robertson Jr.

Summary

This paper attempts to summarize what is presently known about the feeding ecology of wading birds and attempts to provide some generalizations, testable hypotheses, and direction for future work.

Thirty-eight feeding behaviors, three body postures, and four head and neck postures are described, and their characteristics and occurrence in the various species discussed. Methods of prey handling and prey capture differ among wading birds and between prey types. There is a general correlation between size of bird and its feeding activity. A bird may select a behavior from its repertoire on the basis of its relative success. Some species are more successful than others at using particular behaviors. Feeding behaviors and postures contain a message content. The evolutionary basis of some behaviors is fairly clear. There is a strong possibility, however, that because of the similarity of the original evolutionary fabric and common environmental pressures affecting different species, feeding behaviors have converged. Visual and tactile foraging constitute two major foraging strategies. Learning is important to both juveniles and adults. Night foraging occurs in most groups. Structural modifications for feeding include divergence and convergence of bill types. It is proposed that light-dark plumage dichotomy and polymorphism are associated primarily with conspicuousness of the bird to its prey or to other birds and are secondarily associated with heat loading. Several pressures may act together or in opposition to determine plumage color. Polymorphic species may be compromising opposing selective pressures. Study of plumage polymorphism should center on the environmental correlates of statistical differences in distribution of the morphs.

Territorial spacing occurs in all wading birds. Feeding territory expands or contracts depending on its defensibility, which is affected by resource dispersion, prey availability, the number of possible competitors, and habitat availability. Aggregative feeding is widespread, and the diversity of aggregations increases toward the tropics. Depending on their behavior, some species characteristically aggregate, while others either do not aggregate or forage only peripherally to aggregations. Since aggregations form at food concentrations, it is advantageous for a bird to join such an aggregation if its foraging behavior permits. It is proposed that aggregating species benefit from attracting additional birds to a site by an increase in their own foraging effectiveness. Commensalism and prey robbing are phenomena commonly associated with aggregative feeding.

The food taken by wading birds is variable, but some specialization is evident in most species. The food of nestlings apparently does not differ from that of adults. The daily food requirements of wading birds

increase with size as does total food required for nesting. Time budgets, seasonality, and prey dispersion affect prey intake. Wading birds selectively consume prey from the array of potential prey. Both species and individuals demonstrate such preferences. Feeding location, prey density, prey size, and prey behavior affect selectivity, which is ultimately determined by the interaction of characteristics of both prey and predator. Among wading birds, searchers should be generalists while pursuers and standing-feeding species should be more specialized. Sympatric species can be shown to be ecologically separated on a regional scale, but there are critical unanswered questions involving the ecological relationships among similar species within a guild feeding in similar habitats. Such questions may be resolved by studying the relationship of specific foraging behaviors to the capture of specific prey types. Wading birds may choose behaviors and habitats that permit adequate energy intake, have similar energy intake in various habitats, and maximize energy intake only during certain periods.

The habitat requirements of wading birds are very broad in many cases but restricted in others. Habitat availability correlates with population abundance. Winter or other seasonal use of habitat may be critical for maintaining population levels. Habitat enhancements, such as fire, flood, or tide, affect food availability. Nesting sites are located near or in available foraging habitat.

The structure of wading bird communities changes from temperate to tropical areas. The increased diversity in the tropics probably corresponds to increases in habitat types and in trophic compartments of the prey community. The role of wading birds in their ecosystems includes that associated with the reduction of standing crops of prey populations and control of the pathways of energy flow within the system.

Directions for future research in habitat use, feeding behavior, food relationships, and ecosystem function were noted.

Questions

MICHAEL ERWIN: I was interested in the plumage color-feeding strategy correlations you suggested. Might the exceptions to the rule be more plastic in their feeding behavior? In other words, the end result of plumage color might be a selective trade-off or compromise with selective pressures often being antagonistic.

JAMES A. KUSHLAN: We should not expect birds to respond to only a single selective pressure. A number of pressures will be operating synergistically or antagonistically, and these may vary in different geographical and ecological situations. Plumage polymorphism may be one such compromise; some single-plumage systems may also be compromises. One of the primary values of considering the models I've proposed is that those species that refuse to conform become the most intriguing because they indicate where information is lacking or where we have failed to recognize additional selective pressures. The hypotheses that I have presented are attempts to generate new perspectives and new questions rather than provide pat explanations, which tend to stifle further thought.

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Appendix 1

References for Feeding Behaviors of Selected Species

Great Blue Heron. — Audubon 1840; Taverner 1922; Dawson 1923; Pearson 1923; Bent 1926; Michael 1934; Roberts 1936; Dickinson 1947; Meyerriecks 1957, 1960*a*, 1962; Greene 1960; Hutt 1960; Palmer 1962; Pringle 1964; Hedeen 1967; Dennis 1971; Krebs and Partridge 1973; Krebs 1974; Kushlan 1976*a*.

Black-headed Heron. — Chapin 1932, Jackson 1938, Curry-Lindahl 1960, Mackworth-Praed and Grant 1962, North 1963, Taylor 1972.

Goliath Heron. — Chapin 1932, Jackson 1938, Winterbottom 1957.

Purple Heron. — Rand 1936, Witherby et al. 1952, Winterbottom 1957, Mackworth-Praed and Grant 1962, Tomlinson 1974.

Great Egret. — Michael 1934; Davis 1941; Clarke 1955; Oliver 1955; Caldwell 1956; Meyerriecks 1960*a*, 1962, 1971; Rodgers 1974; Wiese and Crawford 1974; Willard 1975; Kushlan 1976*a*.

Reddish Egret. — Baird et al. 1884; Allen 1954–1955; Meyerriecks 1959, 1960*a*, 1962; Kushlan 1976*a*.

Black Heron. — Ayres 1878; Loveridge 1922; Rand 1936; Jackson 1938; Delacour 1946; Winterbottom 1957; Curry-Lindahl 1960; Meyerriecks 1960*a*, 1962; Broekhuysen and Broekhuysen 1961; Farkas 1962; Milstein and Hunter 1974; Irwin 1975.

Louisiana Heron. — Michael 1934; McIlhenny 1936; Meyerriecks 1959, 1960*a*, 1962, 1971; Jenni 1969; Kushlan 1972, 1976*a*.

Cattle Egret. — Valentine Jr. 1958, Meyerriecks 1960*b*, Heatwole 1965, Blaker 1969*a*, Jenni 1969, Siegfried 1971*b*, Browder 1973*b*, Dinsmore 1973, Grubb 1976, Kushlan 1976*a*, Schupp 1976.

Little Blue Heron. — Dickinson 1947; Meyerriecks 1960*a*, 1962, 1971; Jenni 1969; Mock 1974; Kushlan 1976*b*.

Snowy Egret. — Audubon 1840; Baird et al. 1884; Bent 1926; Forbush 1929; Walsh 1929; Bond 1934; Michael 1934, 1936; Grimes 1936; McIlhenny 1936; Sprunt Jr. 1936; Fargo 1937; Hickey 1937; Dickinson 1947; Haverschmidt 1948; Diedrich 1949; Rand 1956; Meyerriecks 1959, 1960*a*, 1962, 1966, 1971; Buckley and Buckley 1968; Helbig 1968; Jenni 1969; Emlen and Ambrose 1970; Kushlan 1972, 1973*a*, 1976*a*; Rodgers 1974; Wiese and Crawford 1974; Willard 1975.

Eastern Reef Heron. — Oliver 1955; Recher and Recher 1969*b*, 1972; Recher 1972*b*.

Paddybird. — Smythies 1953, Lamba 1963, Ali and Ripley 1968.

Green Heron. — Barker 1901; Brooks 1923; Kalter 1932; Warburton 1948; Hawbecker 1949; Lovell 1958; Meyerriecks 1960*a*, 1962, 1966, 1971; Hoyt 1961; Norris 1975; Kushlan 1976*a*.

Agami Heron. — Slud 1964, Wetmore 1965, Karr 1971.

Yellow-crowned Night Heron. — Audubon 1840, Maynard 1896, Bent 1926, Wetmore 1965.

Black-crowned Night Heron. — Audubon 1840, Wetmore 1920, Gross 1923, Bent 1926, Stone 1937, Peters and Burleigh 1951, Drinkwater 1958, Meyerriecks 1960*a*, Voisin 1970, McAllister and Maxwell 1971, Kushlan 1973*b*.

Boat-billed Heron. — Wetmore 1965, Carpenter 1971, Dickerman and Juarez 1971, Mock 1975, 1976.

Bare-throated Tiger Heron (*Tigrisoma mexicana*). — Dickey and van Rossem 1938, Slud 1964, Wetmore 1965.

Least Bittern. — Baird et al. 1884, Gabrielson 1914, Bent 1926, Saunders 1926, Eastwood 1932, Sutton 1936, Simpson 1939, Weller 1961.

American Bittern (*Botaurus lentiginosus*). — Baird et al. 1884, Abbott 1907, Gabrielson 1914, Bent 1926, Saunders 1926.

Wood Stork. — Audubon 1840; Bent 1926; Dixon 1930; Rand 1956; Rechnitzer 1956; Kahl and Peacock 1963; Kahl 1964; Wetmore 1965; Ogden et al., in press.

African Open-billed Stork. — Jackson 1938; Huxley 1960; Root 1963; Mackie Niven and Mackie Niven 1966; Kahl 1971*a*, 1972*d*.

White Stork (*Ciconia ciconia*). — Beetham 1910, Jackson 1938, Haverschmidt 1949, Witherby et al. 1952, Löhrl 1957, Kahl 1972*b*.

Abdim's Stork. — Kahl 1972*b*, *a*.

Black-necked Stork. — Ali and Ripley 1968; Kahl 1973; Kushlan, this paper.

Jabiru (*Jabiru mycteria*). — Bent 1926, Naumburg 1930, Slud 1964, Kahl 1973.

Marabou. — Pitman 1957; Mackworth-Praed and Grant 1962; Kahl 1966*a*, *b*.

Shoebill. — Jackson 1938, Mackworth-Praed and Grant 1962, Kahl 1965, Gilliard 1967.

Hammerkop. — Cowles 1930, Jackson 1938, Stowell 1954, Mackworth-Praed and Grant 1962, Kahl 1967, Siegfried 1975.

White Ibis. — Baird et al. 1884, Bent 1926, Dawn 1959, Slud 1964, Kushlan, in press *a*.

Glossy Ibis. — Sprunt Jr. 1941; Buckalew 1949; Witherby et al. 1952; Sanson et al. 1954; Dilly 1955; Dawn 1959; Mackworth-Praed and Grant 1962; Slud 1964; Bauer and Glutz von Blotzheim 1966; Kushlan, this paper.

Bald Ibis. — Elliot 1877, Vincent and Symons 1948, Cooper and Edwards 1969.

Hadada (*Hagedashia hagedash*). — Skead 1951, Ossowski 1952, Van Someren 1956, Raseroka 1975.

Sacred Ibis. — Rand 1956, Van Someren 1956, Taylor 1957, Ruwet 1963, Benson and Penny 1971.

African Spoonbill (*Platalea alba*). — Chapin 1932, Taylor 1957, Curry-Lindahl 1960.

Roseate Spoonbill. — Allen 1942, Dilley 1955, Slud 1964.

Appendix 2

References for Food Habits of Selected Species.

Great Blue Heron. — Audubon 1840; Bain 1885; Knight 1908; Howell 1911, 1932; Wetmore 1920; Bent 1926; Forbush 1929; Jensen 1930; Moseley 1936; Grater 1938, 1939; Cottam and Knappen 1939; Cottam and Williams 1939; Cushing 1939; Vestal 1939; Kirkpatrick 1940; Trautman 1940; Packard 1943; Cottam and Uhler 1945; Sutton 1946; Allen 1950; Ryder 1950; Peters and Burleigh 1951; Peterson 1953; Giles and Marshall 1954; Sprunt Jr. 1954; Palmer 1962; Robertson Jr. 1962; McAllister and Maxwell 1971; Olson and Johnson 1971.

Gray Heron. — Rowley 1869; Collinge 1924–1927; Bent 1926; Brown 1927, 1928, 1930; Moltoni 1936, 1948; Rand 1936; Hibbert-Ware 1940; Vasvari 1948; Witherby et al. 1952; Lowe 1954, 1966; Owen 1955, 1957, 1960; Palmer 1962; Skokova 1963; Jones 1966; Dement'ev and Gladkov 1968.

Black-headed Heron. — Chapin 1932, Pitman 1942, North 1963, Winterbottom 1957.

Goliath Heron. — Chapin 1932, Winterbottom 1957.

Purple Heron. — Chapin 1932, Winterbottom 1957.

Purple Heron. — Chapin 1932, Rand 1936, Moltoni 1936, Witherby et al. 1952, Dement'ev and Gladkov 1968, Tomlinson 1975.

Great Egret. — Baynard 1912, Wetmore 1916, Bent 1926, Howell 1932, Rand 1936, Sprunt Jr. 1939, Trautman 1940, Peters and Burleigh 1951, Witherby et al. 1952, Hunsaker 1959, Palmer 1962, Genelly 1964, Houck 1967, Dement'ev and Gladkov 1968, Reed 1971.

Reddish Egret. — Cahn 1923, Sprunt Jr. 1954, Palmer 1962.

Black Heron. — Rand 1936, Delacour 1946.

Louisiana Heron. — Audubon 1840, Baynard 1912, Wetmore 1916, Bent 1926, Howell 1932, Sprunt Jr. 1954, Palmer 1962, Jenni 1969, Recher and Recher 1972.

Cattle Egret. — Kirkpatrick 1925; Ticehurst 1931; Chapin 1932, 1956; Bates 1933, 1937; Priest 1933; Golding 1934; Rand 1936; Kadry 1942; North 1945; Beven 1946; Cockburn 1946; Holman 1946; Guichard 1947; Van Someren 1947; Vincent 1947; Witherby et al. 1952; Sprunt Jr. 1954; Middlemiss 1955; Seaman 1955; Ikeda 1956; Skead 1956; Haverschmidt 1957; Winterbottom 1957; Valentine Jr. 1958; Valverde 1958; Palmer 1962; Duxbury 1963; Skead 1963; Cunningham 1965; Reynolds 1965*b*; Siegfried 1966, 1971*a*; Martin et al. 1967; Ali and Ripley 1968; Burns and Chapin 1969;

Jenni 1969, 1973; Snoddy 1969; Hopkins Jr. 1970; Mukherjee 1971; Shanholtzer 1972; Browder 1973*b*; Dinsmore 1973; Fogarty and Hetrick 1973; Van Ee 1973.

Little Blue Heron. — Audubon 1840; Howell 1911, 1924; Baynard 1912; Wetmore 1916; Hallinan 1924; McIlhenny 1936; Trautman 1940; Van Tyne 1950; Peters and Burleigh 1951; Meanley 1955; Palmer 1962; Jenni 1969; Hopkins Jr. 1970; Recher and Recher 1972; Owre 1975.

Snowy Egret. — Audubon 1840, Lantz 1907, Baynard 1912, Wetmore 1916, Howell 1932, Michael 1936, Trautman 1940, Knowlton and Harmston 1943, Peters and Burleigh 1951, Sprunt Jr. 1954, Palmer 1962.

Eastern Reef Heron. — Oliver 1955, Recher and Recher 1972.

Paddybird. — Ali and Ripley 1968.

Green Heron. — Baird et al. 1884, Bowdish 1902, Baynard 1912, Bent 1926, Howell 1932, Kalter 1932, Cottam and Uhler 1945, Grant 1945, Hawbecker 1949, Peters and Burleigh 1951, Sprunt Jr. 1954, Palmer 1962, Wauer 1969.

Yellow-crowned Night Heron. — Audubon 1840; Maynard 1896; Anthony 1898; Bowdish 1902; Wayne 1906, 1910; Wetmore 1920; Hallinan 1924; Bent 1926; Howell 1932; Cottam and Uhler 1945; Price 1946; Kenyon 1947; Peters and Burleigh 1951; Palmer 1962; Parmer 1968.

Black-crowned Night Heron. — Vennor 1865, Baynard 1912, Wetmore 1920, Gross 1923, Bent 1926, Allen 1937, Allen and Mangels 1940, Trautman 1940, Marshall 1942, Witherby et al. 1952, Giles and Marshall 1954, Winterbottom 1957, Valverde 1958, Palmer 1962, Skokova 1963, Beckett 1964, Kale II 1965, Teal 1965, Hoogerwerf 1966, Nickell 1966, Wolford 1966, Stronach 1968, Collins 1970, Voisin 1970, Woods 1970, Wolford and Boag 1971*b*, Hunter and Morris 1976.

Boat-billed Heron. — Hallinan 1924, Van Tyne and Berger 1959, Haverschmidt 1969, Dickerman and Juarez 1971, Mock 1975.

Least Bittern. — Audubon 1840, Lantz 1907, Gabrielson 1914, Wetmore 1916, Dawson 1923, Howell 1932, Roberts 1936, Oberholser 1938, Simpson 1939, Carpenter 1948, Nero 1950, Peters and Burleigh 1951, Sprunt Jr. 1954, Weller 1961, Palmer 1962.

American Bittern. — Aughey 1878, Lantz 1907, Fisher 1909, Norton 1909, Gabrielson 1914, Soper 1923, Howell 1932, Trautman 1940, Ingram 1941, Cottam and Uhler 1945, Byers 1951, Peters and Burleigh 1951, Witherby et al. 1952, Sprunt Jr. 1954, Palmer 1962.

Wood Stork. — Daggett 1903, Lantz 1907, Wayne 1910, Wright and Harper 1913, Grinnell et al. 1918, Bryant 1919, Suthard 1926, Dixon 1930, Howell 1932, Abbott 1938, Tashian 1953, Palmer 1962, Kahl 1964, Ogden et al. 1976.

Open-billed Stork. — Chapin 1932, Rand 1936, Jackson 1938, Root 1963, Kahl 1971*a*.

White Stork. — Chapin 1932, Haverschmidt 1949, Witherby et al. 1952, Dement'ev and Gladkov 1968.

Abdim's Stork. — Chapin 1932.

Jabiru. — Pelzeln 1868–1871, Lloyd 1895, Chubb 1916, Kahl 1971*c*.

Black-necked Stork. — Jackson 1938, Ali and Ripley 1968, Kahl 1973.

Marabou. — Chapin 1932, Pitman 1957, Schneider 1952, Brown 1958, Dean 1964, Kahl 1966*a* and *b*.

Shoebill. — Chapin 1932, Van Tyne and Berger 1959, Kahl 1965, Gilliard 1967.

Hammerkop. — Cowles 1930, Chapin 1932, Rand 1936, Kahl 1967, Siegfried 1975.

White Ibis. — Audubon 1840; Wayne 1910, 1922; Baynard 1912, 1914; Pearson 1925; Allen 1955, 1963; Palmer 1962; Kale II 1965; Nesbitt et al. 1974; Kushlan and Kushlan 1975.

Glossy Ibis. — Baynard 1912, 1913; Witherby et al. 1952; Sprunt Jr. 1954, Belknap 1957; Palmer 1962; Skokova 1963; Stronach 1968, Mumford and Lehman 1969.

Bald Ibis. — Vincent and Symons 1948.

Hadada. — Chapin 1932, Skead 1951, Van Someren 1956, Basilio 1963, Raseroka 1975.

Sacred Ibis. — Nicoll 1906, Bolster 1931, Chapin 1932, Van Someren 1956, Stronach 1968, Urban 1974.

African Spoonbill. — Chapin 1932, Rand 1936, Friedmann and Loveridge 1937.

Roseate Spoonbill. — Audubon 1840, Hallinan 1924, Howell 1932, Cottam and Knappen 1939, Allen 1942, Palmer 1962.