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ANTIPREDATOR BEHAVIOR OF AMERICAN AVOCET AND BLACK-NECKED STILT CHICKS

By Tex A. Sordahl

American Avocet (*Recurvirostra americana*) and Black-necked Stilt (*Himantopus mexicanus*) chicks are precocial, leave the nest within 24 h after hatching, and are flightless for their first 4–5 weeks. During this period they occur in open environments, where they are exposed to a variety of predators. The most important antipredator strategy of young avocets and stilts is to seek cover and hide or simply crouch (posture described by Hamilton 1975:88) in the open when danger threatens, and then rely on the aggressive and/or diversionary behavior of their parents. Chicks and especially their parents are highly vigilant; this is probably essential, in view of the large number of potential chick predators and the inability of the parents to actually rout most of them (Sordahl 1981). Gibson (1971:452) noted that avocet chicks are very difficult to find when hiding, and that "hiding behavior lasted until at least the third week, after which they just ran." In this paper I examine the antipredator behavior of young recurvirostrids and show that it differs between avocets and stilts and varies with age and context in an apparently adaptive manner.

STUDY AREA AND METHODS

During the summers of 1977 and 1978, I studied avocets and stilts at 2 sites in northern Utah: the Barrens Company Hunting Club in Cache County and the Bear River Migratory Bird Refuge in Box Elder County. Both areas are managed by dredging, diking, and regulation of water flow. Their vegetation and topography are essentially identical. The general aspect of these marshes is one of broad ponds <1 m deep, usually bordered by dikes seldom >1 m high. Vehicles can be driven on the main dikes, which are paralleled by "borrow" channels that are often relatively deep. The big ponds lie on salt flats that are frequently exposed by fluctuating water levels. The flats become parched and cracked by June, water levels dropping as the season progresses.

Vegetation is absent in many places. *Salicornia* spp. are the only plants growing on most of the salt flats. The *Salicornia* may grow as a sparse cover of sprigs 5–10 cm high or as widely-spaced sturdy bushes of 20–40 cm height and 40–70 cm diameter. On some of the drier areas a few greasewood (*Sarcobatus vermiculatus*) shrubs occur. The dominant plant along channels and other relatively stable water boundaries is desert saltgrass (*Distichlis stricta*), which grows in dense mats and reaches 15–40 cm in height. In parts of the Bear River Refuge and at the edge of the Barrens, more typical "marsh" vegetation occurs—e.g., cattails (*Typha* spp.), rushes (*Scirpus* spp.), sedges (*Carex* spp.), and reeds (*Phragmites communis*). However, neither adult recurvirostrids nor their young regularly use such habitats.

I banded 172 young avocets and 120 young stilts. Of these, 49 avocets (33 nestlings, 16 older chicks) and 51 stilts (18 nestlings, 33 older chicks) were captured at the Barrens; captures were made opportunistically during daily field work and during 42 h of nightlighting on 17 nights. The remaining 123 avocet and 69 stilt chicks were captured at the Bear River Refuge. Weekly trips were made to the refuge once hatching had begun. I searched for chicks by driving the dikes in an automobile; an assistant watched the broods with binoculars or spotting scope while I approached them, then directed me to their hiding places with hand signals. A small boat was used to negotiate the deeper waterways.

Each chick received a U.S. Fish and Wildlife Service band (on the tibio-fibula), which quickly became dull-colored and difficult to see in the field. Since color bands might reduce the ability of chicks to hide from predators, only 2 avocet and 6 stilt chicks that were captured near fledging were color-banded. Eighteen avocet and 15 stilt chicks were recaptured prior to fledging.

I attempted to record the following data for each young bird captured: (1) species and estimated age; (2) time of capture; (3) what substrate it was captured on; (4) whether it tried to hide when approached or simply ran; (5) whether or not it called when captured. I measured the wing chord of each chick to the nearest millimeter with vernier calipers. Age estimates were based on personal experience and the knowledge that fledging normally occurs at ca. 28 days. Since I never misjudged the age of a recapture by >1 day (most recaptures had been banded originally during their hatching day and were therefore of known age), I believe the age estimates are accurate to ±2 days.

Whenever water of sufficient depth was located near a capture site, I tested the underwater swimming ability of chicks. Each bird was placed in the water and given a standard "scare treatment" that consisted of my wading after and reaching for it; it was then classified as either a diver or nondiver. Dive durations were timed to the nearest .1 sec with a stopwatch. I paced the distance between submergence and emergence points along the chicks' underwater paths, and converted the paces to meters (I had earlier calibrated myself for accuracy and consistency by pacing a football field while wearing hip boots; during 12 trials I paced the 100 yd in 123 to 125 paces, so 124 paces per 100 yd was used as a standard). Most chicks were given 3 diving trials, in rapid succession, and the best performance was used for calculations; distance and duration usually decreased on consecutive dives.

RESULTS AND DISCUSSION

Diurnal vs. nocturnal escape behavior.—The habitats where avocet and stilt chicks were captured in the daytime differed from those where they were captured at night (Fig. 1; although the data for both species yield highly significant χ^2 values, the statistical test for avocets may not be valid because of the low expected frequencies at night). During the day I usually caught chicks hiding in grass or, less commonly, crouching on

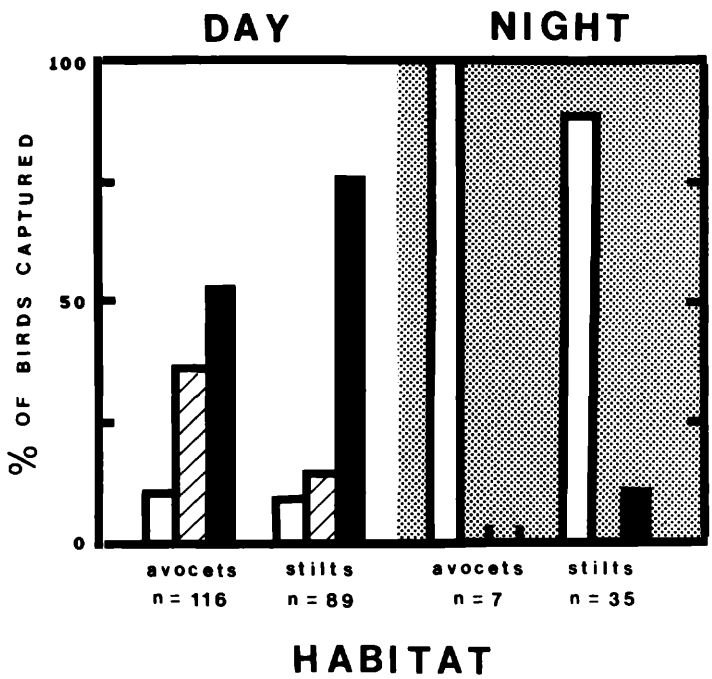

FIGURE 1. Percent of American Avocet and Black-necked Stilt chicks captured in 3 habitats during the day and at night. Open bars represent open water, shaded bars mud flats, and black bars vegetation.

open mud flats; a small percentage, usually very young chicks, crouched in shallow expanses of open water, and a few older chicks took refuge in deep water (see section on aquatic escape behavior below). At night, on the other hand, chicks were caught almost exclusively in shallow open water.

This pattern could be explained by the fact that chicks hiding in the grass would be extremely difficult to find at night (despite the fact that they are also more difficult to find in grass than on mud or water in the daytime). However, it seemed peculiar when a 1-day-old avocet brood that I caught crouching in the water at night repeatedly scrambled out to lie flat in the water each time I placed them in the grass. My subsequent capture of so many chicks at night in open water led me to consider several factors which would promote this behavior (I doubt that chicks roost in the water, as some adults do, at least until they are near fledging). The overriding factor must be that chicks are less inhibited by the danger of visual predators to move about or crouch in the open at night. Twenty-five percent (30/118) of avocet chicks captured in the daytime and 43% (3/7) of those captured at night tried to escape by running. Eleven percent (10/91) of stilt chicks captured in the daytime

and 70% (23/33) of those captured at night tried to escape by running ($\chi^2 = 39.79$, 1 df, $P < .001$). Probably chicks were both more likely to run and less likely to be discovered if hiding at night. The increased tendency to run at night could be explained by the chicks' reduced ability to see the predator, if this is the stimulus required to cause chicks to hide.

A proximate explanation of the behavior leading to a large number of captures in the water at night might be that, under cool nighttime air temperatures, chicks seek the water for warmth when disturbances prevent their parents from brooding them. Low temperatures at night tended to increase chick movement. Small chicks became chilled and chased their parents in order to be brooded; activity may also serve to generate body heat. Possibly the young do some feeding in the water at night, but their apparent inability to withstand nighttime temperatures without frequent brooding makes this an unlikely explanation for at least the first 2 weeks.

Nocturnal release from danger by visual predators permits chicks to actively escape from a disturbance center. Thus an ultimate explanation, in view of the much greater importance of olfactory predators at night, is that the behavior could be adaptive because: (1) water would not hold the chicks' scent and would therefore be a safer hiding place or escape route than solid ground or vegetation; (2) water-covered areas have fewer obstructions than vegetated areas and thus provide a faster escape route. The best strategy to elude olfactory predators searching an area at night may be to move to water and crouch (young chicks) or escape to another area (older chicks). Auditory cues are probably reduced by the loud calling and splashing of the parents.

The loud behavior of parents was much more localized around their chicks at night than during the day. This and the chicks' greater activity enabled me, as a visual predator with a flashlight, to find chicks quite readily at night.

Avocet vs. stilt escape behavior.—Avocet and stilt chicks are quite similar at hatching, but a stilt hatchling is somewhat smaller, has relatively longer legs, unwebbed feet, and slightly darker down with black markings that are more distinct. The less aquatic stilt chick frequents vegetation, where its darker coloration and more distinct markings match the relatively dark background and shadows; while the young avocet occurs in the same places, it has a greater tendency to forage on open flats and ponds, where its paler plumage matches the washed-out background (see also Hamilton 1975:14 for habitat differences in these species). During the day I caught more stilt chicks than avocet chicks in vegetation (Fig. 1; $\chi^2 = 10.47$, 1 df, $P < .005$); conversely, I caught more avocet chicks than stilt chicks on mud flats and open water.

These habitat differences became more pronounced as the young attained their juvenal plumages—stilts tended to stay near vegetation, and avocets tended to venture into the open. Juvenile stilts have brown edging on the dorsal feathers that produces a scaly cryptic pattern,

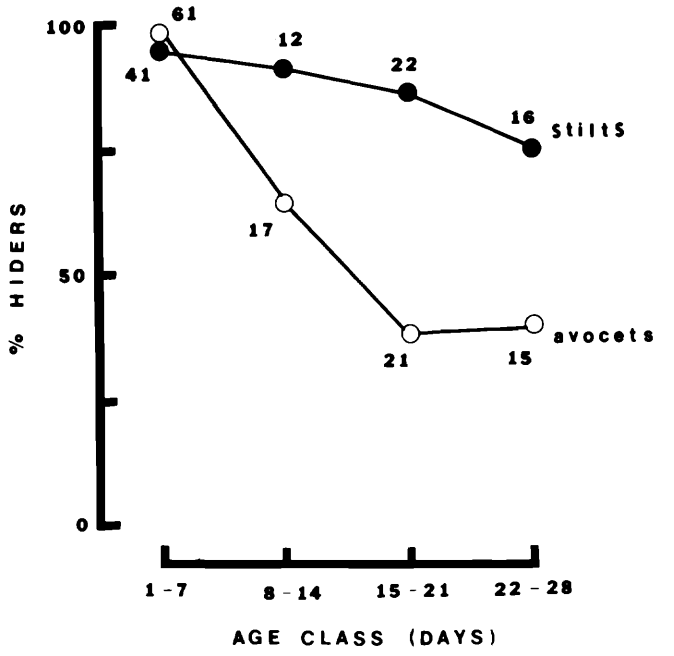

FIGURE 2. Percent of American Avocet and Black-necked Stilt chicks captured during the day that tried to escape by hiding rather than running. Sample sizes for each age class are indicated next to the circles.

whereas juvenile avocets have a black-and-white chevron pattern dorsally (like that of adults) and are relatively conspicuous when hiding in grass. Escape behavior data are consistent with this change in the relative ability of the 2 species to hide effectively. During the first week young of both species nearly always tried to hide when approached in the daytime (Fig. 2; nighttime captures are omitted because darkness and low temperatures decrease a chick's tendency to hide; see preceding section). During the second week more chicks tried to run, probably because increasing strength and speed improved their chances of escape by this method, while increasing size lowered their chances for successful hiding; the sample size is too small for valid statistical testing, but it appears that avocets ran more frequently than stilts. During the third ($\chi^2 = 8.75$, 1 df, $P < .01$) and fourth ($\chi^2 = 2.59$, 1 df, $P = .11$) weeks, i.e. when juvenal plumage was attained, avocet and stilt escape behavior diverged more strongly, with stilts tending to hide and avocets tending to run. It is not clear whether this species difference is determined by habitat selection and therefore availability of hiding places, or whether a psychological difference in hiding tendency exists.

The function of vocalizations of avocet and stilt chicks is not known, but avocet chicks were noticeably more vocal. At night calls often seemed

to connote discomfort, and probably functioned as a location signal and/or summons to the parents to brood the young. During the day 79% (85/108) of avocet chicks but only 39% (35/89) of stilt chicks called when captured ($\chi^2 = 30.14$, 1 df, $P < .001$). Assuming that the calls may elicit antipredator behavior from adults, this species difference can be interpreted in 2 non-mutually exclusive ways. First, avocets are more strongly colonial and more social than stilts (pers. obs., Hamilton 1975); thus calling could be adaptive if it enables a chick to evoke the aid of unrelated conspecifics. Adult avocets (and stilts) might be selected to respond to the calls of nearby unrelated chicks if doing so enhances the survival chances of their own young. Since parents guard their young closely, they are aware of threats to them, and the young stilt might often be better off to remain silent if additional help is unlikely to be near (e.g., if chick calls also sometimes attract predators). Second, silence seems more compatible with the hiding behavior of stilts than with the running behavior of avocets. All (9/9) stilts that attempted to run when captured also called, whereas only 32% (26/80) of stilts that tried to hide when captured gave calls ($\chi^2 = 12.75$, 1 df, $P < .001$). However, avocets were equally likely to call if they were hiders (76%, 62/82) or runners (88%, 23/26; $\chi^2 = 1.25$, 1 df, $P > .25$). Possibly a running stilt chick would be more likely than a hider to enter the domain of other defending parents, and thus would benefit from calling to elicit their antipredator responses. A hiding stilt chick that is vocal when captured would also be more likely than an avocet chick to attract predators to hiding places of siblings, because siblings often hide in the same general area but the probability is higher that an avocet's siblings would be running instead of hiding. Answers to these questions await detailed study of the social context of chick predator responses and explication of the effects of the chicks' calls on conspecifics.

Aquatic escape behavior.—Avocet and stilt chicks are capable swimmers, and readily take to water as soon as their down is dry. Webbed feet and shorter legs make avocets better swimmers than stilts (adult stilts rarely swim and are relatively awkward when they do). When approached by predators, chicks sometimes swim away from shore, especially if it offers little cover (pers. obs., Hamilton 1975:88). This behavior became more common in avocet chicks during their third and fourth weeks, probably because their increasing size and plumage conspicuousness rendered hiding less effective; some of these young avocets simply retreated to deeper water when I chased them, and then waited. When I reached for them they often dove (cf. Sumner 1931 for stilts, and Gibson 1971:452 for avocets), emerging again some distance away.

No chicks less than 24 h old dove, but beyond that age many did. Diving only occurred in water deeper than a chick's wading depth. Avocets and stilts propel themselves underwater mainly with shallow synchronous wingbeats, but they often kick their legs vigorously as well. Dives are to a depth of only ca. .1–.4 m. Underwater paths are usually straight, but sometimes curve as much as 90°.

Young avocets were more likely than stilts to dive, and they achieved

better underwater performances. Sixty-three percent (30/48) of avocets were divers, whereas only 32% (6/19) of stilts could be induced to dive ($\chi^2 = 4.07$, 1 df, $P < .05$). Avocet dives averaged 6.0 sec (n = 30, SD = 2.6, range = 2.3–12.8) and stilt dives averaged 4.2 sec (n = 6, SD = 1.4, range = 3.0–6.6). Avocets swam an average of 3.8 m (n = 28, SD = 1.6, range = 1.5–7.4) underwater vs. 2.2 m (n = 6, SD = 0.8, range = 1.1–3.0) for stilts. Underwater swimming speed for avocets was .64 m/sec (n = 28, SD = .13, range = .42–1.06) vs. .55 m/sec (n = 6, SD = .22, range = .37–.99) for stilts. The avocet/stilt comparisons for diving time, distance, and speed are statistically nonsignificant, but the trend suggests a greater diving proficiency in avocets.

The tendency of a chick to dive should depend largely on: (1) its diving ability, and (2) its available alternatives for escape. This may explain why the less aquatic stilt is less likely to dive. Downy chicks are poor divers, largely because they have too little wing area for propulsion; in fact they often are unable to submerge completely. Thus young chicks might be expected to dive only rarely, and to simply swim away from predators when in the water; the tendency to dive should increase with age and ability. My observations support these expectations (Fig. 3; avocet $\chi^2 = 13.83$, 3 df, $P < .005$; stilt sample too small to test statistically), assuming that different-aged chicks perceived the human threat stimulus similarly. The underwater swimming speed of avocet chicks appears to increase continuously with wing size (Fig. 4), and hence age, but underwater distance (Fig. 5) and tendency to exhibit diving (Fig. 3; $\chi^2 = 3.14$, 1 df, $P = .08$) seem to decline late in the chick stage. In view of the dissimilar selection pressures for flying in air and in water (Storer 1971:153), it might be expected that underwater ability would decrease as the paddle approaches its ultimate use as a wing. My data do not show this clearly, possibly because they are too coarse, or because the birds adjust their wing area underwater; perhaps the increasing strength of the chicks' flight muscles compensates for any decrease in efficiency of the paddle. The apparent decline in the diving response may be concomitant with a shift toward or maturation of the aerial flight response (to a human predator).

Diving behavior would be effective against many kinds of predators. Even well-trained hunting dogs have great difficulty locating flightless ducks that dive in shallow water, because they concentrate their attention on the submergence point (pers. obs.). Other non-aquatic mammalian predators would probably be no less confused. Remaining on the water and diving may be a better strategy than flight against some raptors. Many prey species are reluctant to fly when a Peregrine Falcon (*Falco peregrinus*) is around (Cushing 1939:107, Meinertzhagen 1959: 152). The importance of avocets in the diet of Peregrine and Prairie (*F. mexicanus*) falcons (Porter and White 1973) suggests that diving behavior is a significant part of their antipredator repertoire. Diving should be effective against falcons (R. D. Porter pers. comm.), but it is not totally effective—Peregrines have been seen killing swimming ducks and seizing wooden decoys off the water (Cushing 1939:103; Meinertzhagen

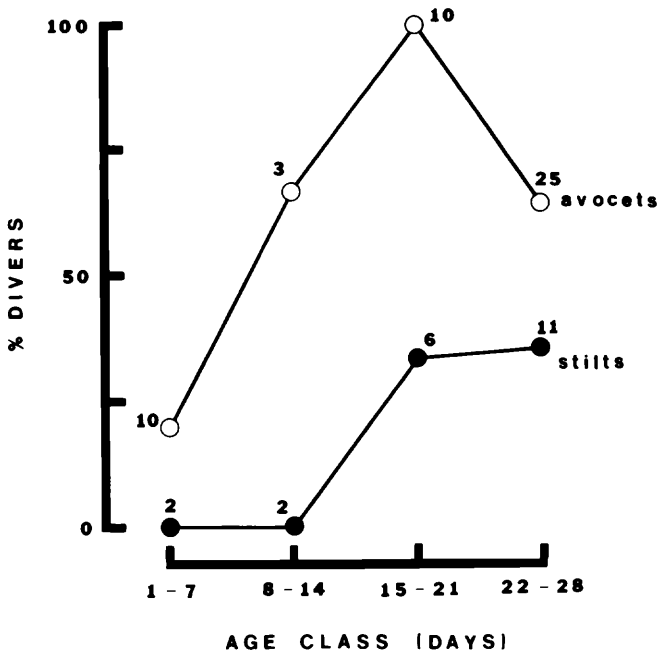

FIGURE 3. Percent of American Avocet and Black-necked Stilt chicks captured that dove when pursued closely in the water by a human. Sample sizes for each age class are indicated next to the circles.

1959:152,153), and they prey heavily on Eared Grebes (*Podiceps nigricollis*) in the Gulf of California (R. D. Porter pers. comm.).

Among the shorebirds diving behavior is seen only in an antipredator context. Several observations indicate that diving is a tactic employed successfully against aerial predators by both young (Pettingill 1976:39) and adults (Osgood 1909:36, Stone 1925, Kelso 1926, Martin and Atkeson 1958, Meinertzhagen 1959:95, 135, Nethersole-Thompson and Nethersole-Thompson 1979:182). Diving by adults is most commonly seen when they are surprised at close quarters (Sutton 1925) or are wounded (Miller 1918, Kelso 1926, Bent 1929:87), situations that are likely to be associated with raptor attacks. Thus diving is probably used by many shorebird species when the wing area of individuals is sufficient for underwater propulsion but aerial flight (the primary mode of escape) has not yet been attained, or has been lost or otherwise rendered ineffective.

SUMMARY

American Avocet and Black-necked Stilt chicks crouch or hide when danger threatens, and then rely on the aggressive and/or diversionary behavior of their parents. Chicks exhibited different escape behavior at

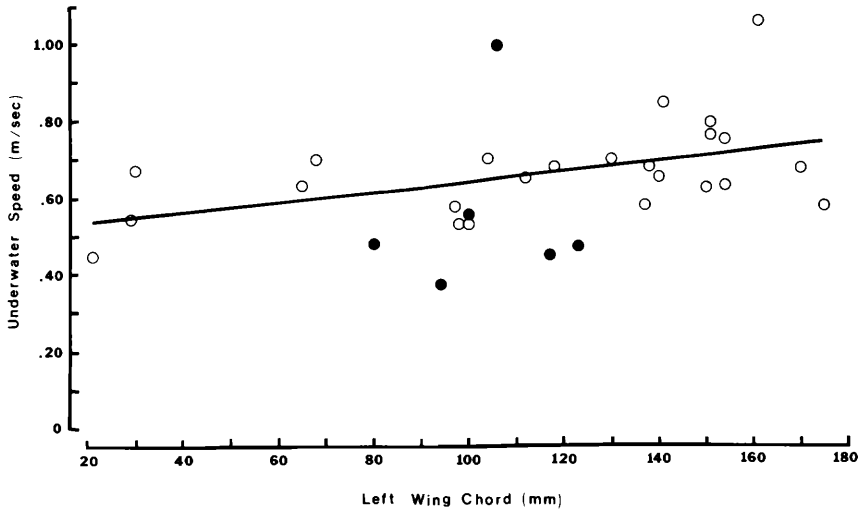

FIGURE 4. Underwater swimming speed of American Avocet (open circles) and Black-necked Stilt (solid circles) chicks as a function of wing size. Linear regression equation for the avocet data is: y = .5112 + .0013 (x). Correlation coefficient r = .48; t = 2.55, 22 df, $P < .05$.

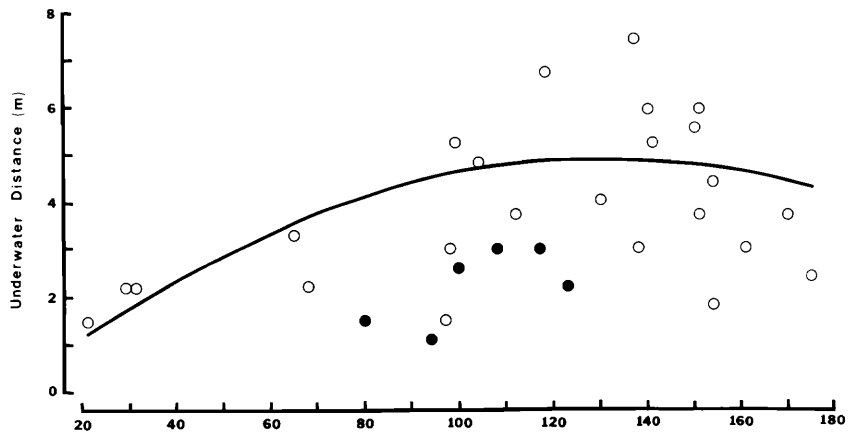

FIGURE 5. Underwater swimming distance of American Avocet (open circles) and Black-necked Stilt (solid circles) chicks as a function of wing size. Curve fitted for avocet data by step-up polynomial computer program to the equation: y = −.2934 + .0787 (x) − .0003 (x^2). Correlation coefficient r = .54; t = 3.03, 22 df, $P < .01$.

night than in the daytime. At night, release from danger by visual predators may allow chicks to actively escape from a disturbance center. Other factors, such as low temperature and inability to see the predator increase the activity of chicks at night when a disturbance prevents parents from brooding them. An apparent tendency to "hide" in shallow water or to cross stretches of water at night may represent a strategy to avoid scent-oriented nocturnal predators, and merits further study.

During their first week, avocet and stilt chicks nearly always attempted to hide when approached, whereas in subsequent weeks many tried to run away. During weeks 2, 3, and 4, avocet and stilt escape behavior diverged, with stilts tending to hide and avocets tending to run. This species' difference may be related to the greater tendency of avocet chicks to forage in open areas, and to their less cryptic juvenal plumage, both of which render hiding less effective. Avocet chicks were more vocal than stilt chicks when captured, but the explanation is not clear.

Avocet and stilt chicks can swim 1–2 h after hatching. After the first 24 h many chicks dive when pursued in the water. Chicks propel themselves underwater with their wings. Thus underwater swimming ability was positively correlated with wing size and age. Avocet chicks were more likely to dive, and they swam farther, faster, and stayed underwater longer than stilt chicks. Diving is probably effective in eluding many kinds of predators.

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NOTES AND NEWS

Bird Evolution Symposium.—The Zoology Department of Ohio Wesleyan University will host a symposium, "Evolution of birds: processes and products." The symposium will be held Friday, 15 April 1983, beginning at 9:30 A.M. and continuing throughout the day. Speakers will include: Alan Feduccia, Richard F. Johnston, George F. Barrowclough, William R. Dawson, and Glen E. Woolfenden. Meals will be arranged in conjunction with the symposium. Overnight accommodations can be arranged. For further information please contact: Edward H. Burtt, Jr., Department of Zoology, Ohio Wesleyan University, Delaware, OH 43015 (614-369-4431, ext. 400).