COMPARATIVE BEHAVIOR OF THE AMERICAN AVOCET AND THE BLACK-NECKED STILT (RECURVIROSTRIDAE)

BY

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TABLE OF CONTENTS

LIST OF FIGURES

INTRODUCTION

The American Avocet (*Recurvirostra americana*) and the Black-necked Stilt (*Himantopus himantopus mexicanus*), are usually placed in the family Recurvirostridae along with other members of their genera and members of two other genera, *Cladorhynchus* and *Ibidorhyncha*. *Recurvirostra* and *Himantopus* are generally thought to be closely related.

Both avocets and stilts are large, long-legged shorebirds which spend much of their time in shallow water where they obtain most of their food. The characters presented in the literature as diagnostic of the Recurvirostridae could have arisen by convergent evolution, all being adaptive for feeding in shallow water, and thus not necessarily reflecting phylogenetic relationships.

Little has been published about the behavior or ecology of any recurvirostrids despite the fact that all except *Ibidorhyncha* are conspicuous, social birds of open habitats. In fact, many of the scattered observations of behavior in the literature have been incorrectly interpreted because of a lack of basic life history information.

Because of the insufficiency of detailed information about the North American avocet and stilt, I studied the behavior of these species, as related to their morphology and ecology, to determine if their supposedly close relationship can be supported on other than superficial morphological grounds. Additionally, some available information has allowed me to compare these two species with other recurvirostrids to help determine the relationships of the American forms to other members of the family.

ACKNOWLEDGMENTS

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Finally, special appreciation is due my wife Jean for her encouragement and assistance throughout the study.

MATERIALS AND METHODS

This work was primarily a field study conducted in southern Alameda County, California, on properties of the Leslie Salt Company. The areas of study consisted mostly of salt evaporation ponds with their intervening dikes, salt marshes, and bay edge. There is an extensive system of access roads along the dikes of these salt ponds where observations could be made. Additional observations on feeding behavior of the avocet were made at the mud flats north of the Golden Gate Fields race track, northern Alameda County, California.

Because the study area at the Leslie Salt Company was not a "natural" one, I made a trip to the Lower Klamath Refuge and to White Lake on the California-Oregon border, Siskiyou County, California, 21–26 June 1968, to study the interactions of the birds in a more natural setting. I concentrated primarily on feeding behavior at these locations where both species, which feed in the same areas, could be readily compared.

At the study sites, I used my automobile as a blind while making behavioral observations. Some disturbance of the birds resulted each time I arrived, but usually within five minutes the birds appeared to resume normal activity. Observations were made with 7 × 35 binoculars and a 20× scope and read into a tape recorder.

Activities of both species were recorded with an 8 mm movie camera equipped with a 9–36 mm zoom lens. About 1,500 feet of film was exposed and appropriate portions analyzed to determine behavioral postures and sequences which could not be adequately studied in the field.

Avocets and stilts both breed along some of the dikes at the Leslie Salt Company, and I periodically checked nests of both species and mapped their locations.

Study skins of avocets and stilts in the Museum of Vertebrate Zoology at the University of California at Berkeley were examined and measured. I also studied 10 skins of stilts at the Museo de Historia Natural "Javier Prado" in Lima, Peru. The degree of sexual dimorphism in both species was estimated by analysis of measurements and plumages.

Where appropriate, statistical tests were made on the data obtained in this study; Bailey (1957) was consulted for parametric statistical tests, and Siegel (1956) for nonparametric tests. Statistical symbols used in this study

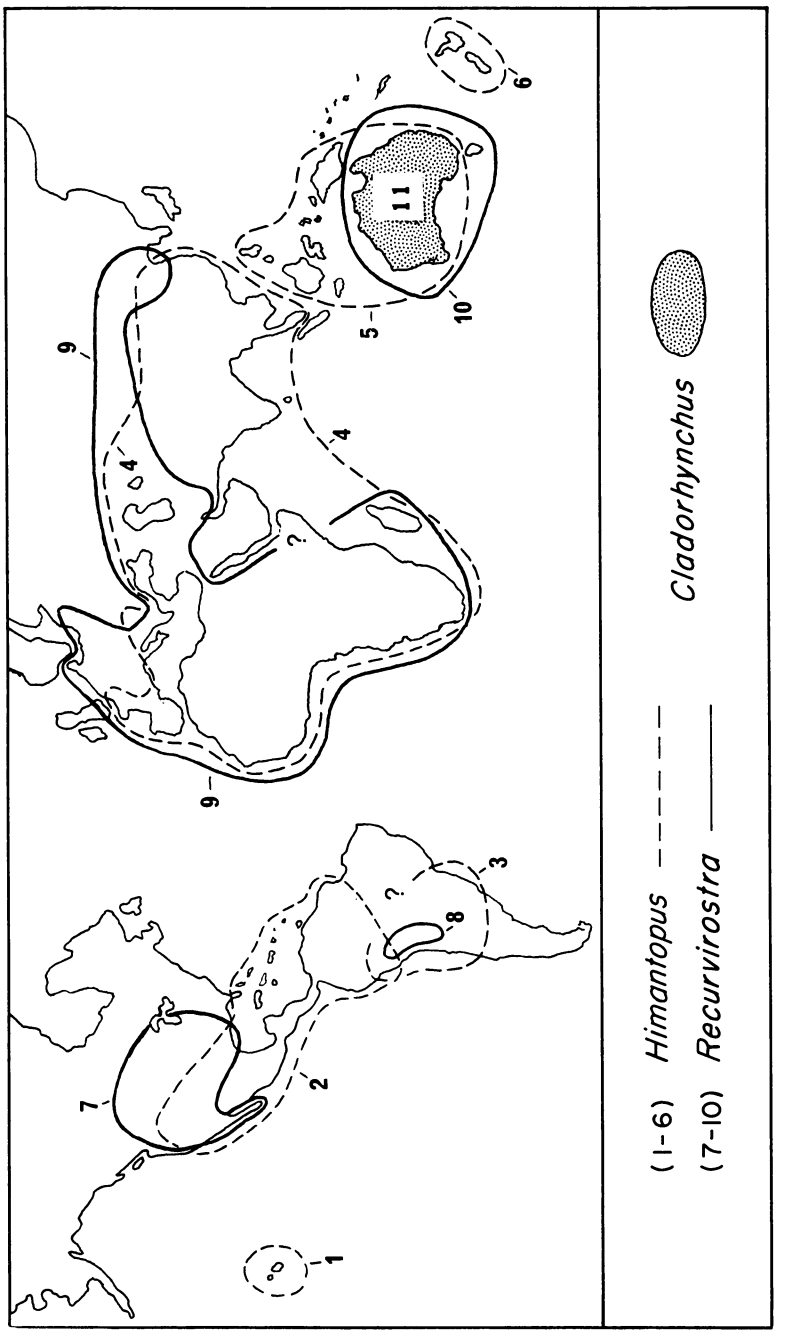

FIGURE 1. Distribution of the Recurvirostridae (modified from Larson [1957: 44, 45]). Forms are those of Peters (1934). (1) *Himantopus h. knudseni*; (2) *Himantopus h. mexicanus*; (3) *Himantopus h. melanurus*; (4) *Himantopus h. himantopus*; (5) *Himantopus h. leucocephalus*; (6) *Himantopus h. novae-zelandiae*; (7) *Recurvirostra americana*; (8) *Recurvirostra andina*; (9) *Recurvirostra avosetta*; (10) *Recurvirostra novae-hollandiae*; (11) *Cladorhynchus leucocephalus*.

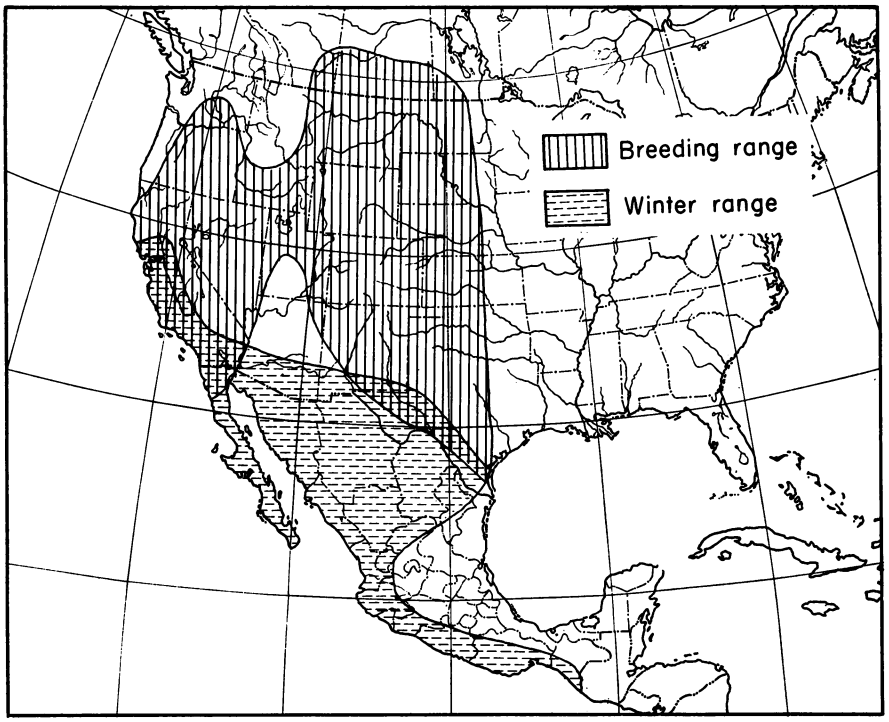

FIGURE 2. Range of *Recurvirostra americana* (modified from A.O.U. Check-list, 1957).

are those of Siegel. Results of statistical tests were considered significant when they would have occurred by chance 5 percent of the time or less ($p \leqslant .05$).

GEOGRAPHIC DISTRIBUTION

Primarily birds of tropical and temperate regions, recurvirostrids are a very widespread family with representatives on every continent except Antarctica (Figure 1). Members of the genera *Recurvirostra* and *Himantopus* are found on six continents; *Cladorhynchus* is found only in Australia. No member of the family exists in polar regions, but *Recurvirostra andina* and *Ibidorhyncha* are found above 3,000 meters elevation in the Andes and Himalayas, respectively.

The American Avocet nests in the western United States and southern Canada (Figure 2). There was once a breeding population along the east coast of the United States but none is known to breed there now (Palmer 1967: 151). The birds migrate and spend their winters in the southwestern United States, western Mexico, and Central America as far south

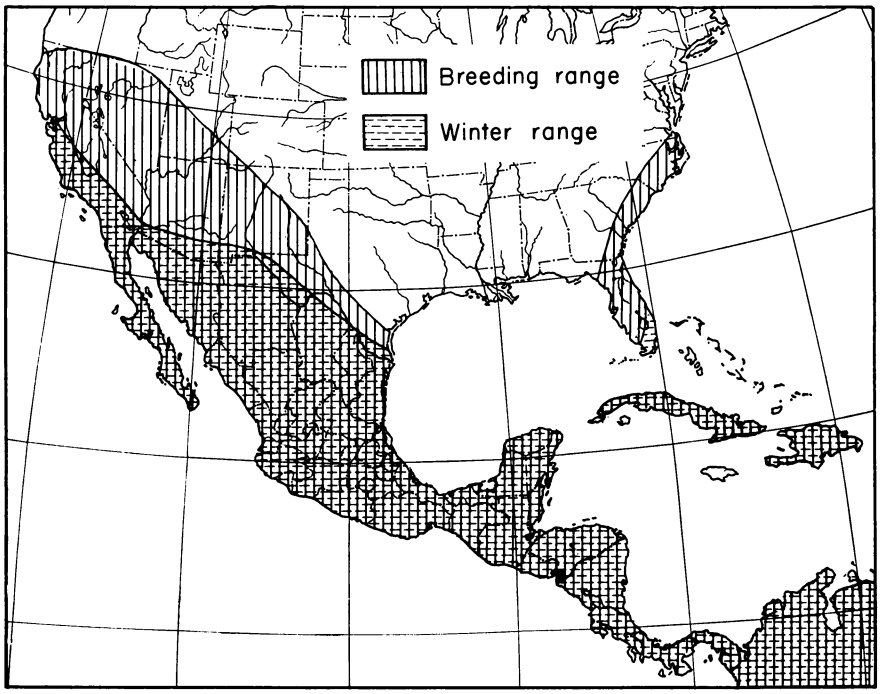

FIGURE 3. Range of *Himantopus himantopus mexicanus* (modified from A.O.U. Check-list [1957]). Southern limit not precisely known.

as Guatemala (Figure 2). Individuals are occasionally seen in winter throughout Florida, and a small flock has wintered regularly at Cape Kennedy, Florida, for the last 20 years (Christmas Bird Counts, *Audubon Field Notes*, and *American Birds*, vols. 8–27, 1954–1973; pers. obs.). I do not know whether the Cape Kennedy birds breed in the western United States or whether they come from an unknown breeding area in the eastern United States or Canada. Non-breeding avocets are regularly seen in New Jersey in the summer (Palmer 1967: 151). There is one record each for Greenland, Baffin Island, and several of the Caribbean Islands. Migrants normally arrive in the southern United States by mid-April and migration is continued until mid-May. Fall migration is from early August until October (Palmer 1967: 151).

There are two breeding populations of the Black-necked Stilt in the United States (Figure 3). The main population breeds in the western states from Oregon and Idaho southward through Mexico, Central America, and northern South America. A few stilts breed and winter along the northwestern coast of the Gulf of Mexico. In some years stilts nest as far

TABLE 1
SEXUAL DIMORPHISM OF *Himantopus himantopus mexicanus*

Measurement	Sex	N	$\bar{x}$	C.V.	F	t	$\bar{x}_m/\bar{x}_f$
Weight	♂	6	177.05[1]	12.50	1.59	1.61	1.10
	♀	12	160.31	10.97	p>.10[a]	.20>p>.10[a]	
Cube root of weight	♂		5.61				1.03
	♀		5.43				
Bill (chord)	♂	17	65.32[2]	3.93	1.35	1.98	1.03
	♀	19	63.49	4.70	p>.10	.10>p>.05	
Bill width	♂	18	5.63	5.34	1.32	0.83	1.02
	♀	21	5.54	6.21	p>.10	p>.10	
Perpendicular	♂	17	1.34	17.29	3.13	1.20	0.91
	♀	20	1.47	27.92	.05>p>.02	p>.10	
Length to perpendicular	♂	17	28.65	14.81	1.12	0.90	1.05
	♀	20	27.35	16.45	p>.10	p>.10	
Wing (chord)	♂	18	225.06	2.54	2.07	4.45	1.05
	♀	21	214.67	4.07	p>.10	p<.001	
Tail	♂	18	68.84	4.54	1.02	2.11	1.03
	♀	21	66.74	4.61	p>.10	.05>p>.02	
Tarsometatarsus	♂	18	112.99	6.03	2.59	5.23	1.09
	♀	21	103.23	4.10	.05>p>.02	p<.001	

[a] Values in F and t columns in this table in ♀ rows are probability values associated with F and t values above them.
[1] In grams.
[2] This entry and all subsequent entries in column are in millimeters.

north as Canada (AOU Checklist 1957: 210). There is also an eastern population of stilts which breeds along the Atlantic coast from New Jersey southward to Florida and some of the Caribbean Islands. In winter stilts leave the northern part of their range and move southward. The winter range of this subspecies extends as far north as the southern San Francisco Bay area. The southern populations probably do not migrate (Palmer 1967: 152). Spring migration occurs between late March and early May. Fall migration is in August and September but, in some years, it lasts into November (Palmer 1967: 152).

DESCRIPTION OF NORTH AMERICAN RECURVIROSTRIDS

The plumage stages of the American Avocet and Black-necked Stilt have been described by Palmer (1967: 150–152). Jehl (1968: 24–25) presents an even more detailed description for the downy young of these forms.

SEXUAL DIMORPHISM

Avocets and stilts are noticeably sexually dimorphic, but the form of their dimorphism is different. In the breeding season stilts can be sexed in good

TABLE 2
SEXUAL DIMORPHISM OF *Recurvirostra americana*

Measurement	Sex	N	χ	C.V.	F	$\lvert\bar{x}_m-\bar{x}_f\rvert$/S.E.	$\bar{x}_m/\bar{x}_f$
Weight	♂	16	323.38[1]	10.39	1.16	1.12[3]	1.04
	♀	17	309.78	11.64	p>.10[4]	p>.10[4]	
Cube root of weight	♂		6.86				1.01
	♀		6.76				
Bill (chord)	♂	36	95.33[2]	4.98	1.03	8.79	1.10
	♀	35	86.29	4.58	p>.10	p<.001	
Bill width	♂	45	8.72	9.41	2.25	1.81	1.03
	♀	38	8.47	6.45	p<.02	.05<p<.10	
Wing (chord)	♂	42	224.55	3.00	1.45	0.01	1.00
	♀	36	224.56	2.49	p>.10	p>.10	
Tail	♂	42	79.38	4.99	1.65	0.44	1.01
	♀	36	78.93	6.45	p>.10	p>.10	
Tarsometatarsus	♂	42	97.99	3.85	1.51	6.05	1.06
	♀	37	92.18	5.03	p>.10	p<.001	

[1] In grams.
[2] This entry and all subsequent entries in coluumn are in millimeters.
[3] Because of small sample size, *t* test was used.
[4] Values in F and $\lvert\bar{x}_m-\bar{x}_f\rvert$/S.E. columns in this table in ♀ rows are probability values associated with F and $\lvert\bar{x}_m-\bar{x}_f\rvert$/S.E. values above them.

light by plumage differences, but American Avocets have no noticeable plumage dimorphism. They also can be sexed in the field, however, by marked sexual dimorphism in bill shape. (Two specimens of each sex of *Recurvirostra andina* and *R. novae-hollandiae* that I have seen also showed sexual bill differences. I have not examined the European Avocet.)

Weight.—As a measure of absolute size, weight was used. Table 1 shows that the male stilt is approximately 1.10 times larger than the female stilt. This difference was non-significant ($t = 1.61$, $.20 > p > .10$); however, the coefficient of variability is very high, and the sample size may not have been large enough to reveal any differences. All other measures of size indicate that males are larger than females; therefore, the difference in weight between the sexes is probably real.

Table 2 indicates that the male avocet is 1.04 times heavier than the female avocet. Again, the coefficient of variability is large and the difference in weight is not significant ($t = 1.12$, $p > .20$). Other size measurements indicate that males may be slightly larger than females, but the size dimorphism is not as great as that found in the stilt.

Tail length.—Table 1 and Figure 4 show that stilts possess a slight sexual dimorphism of tail length ($t = 2.11$, $.05 > p > .02$). The tail of the male is approximately 1.03 times longer than that of the female.

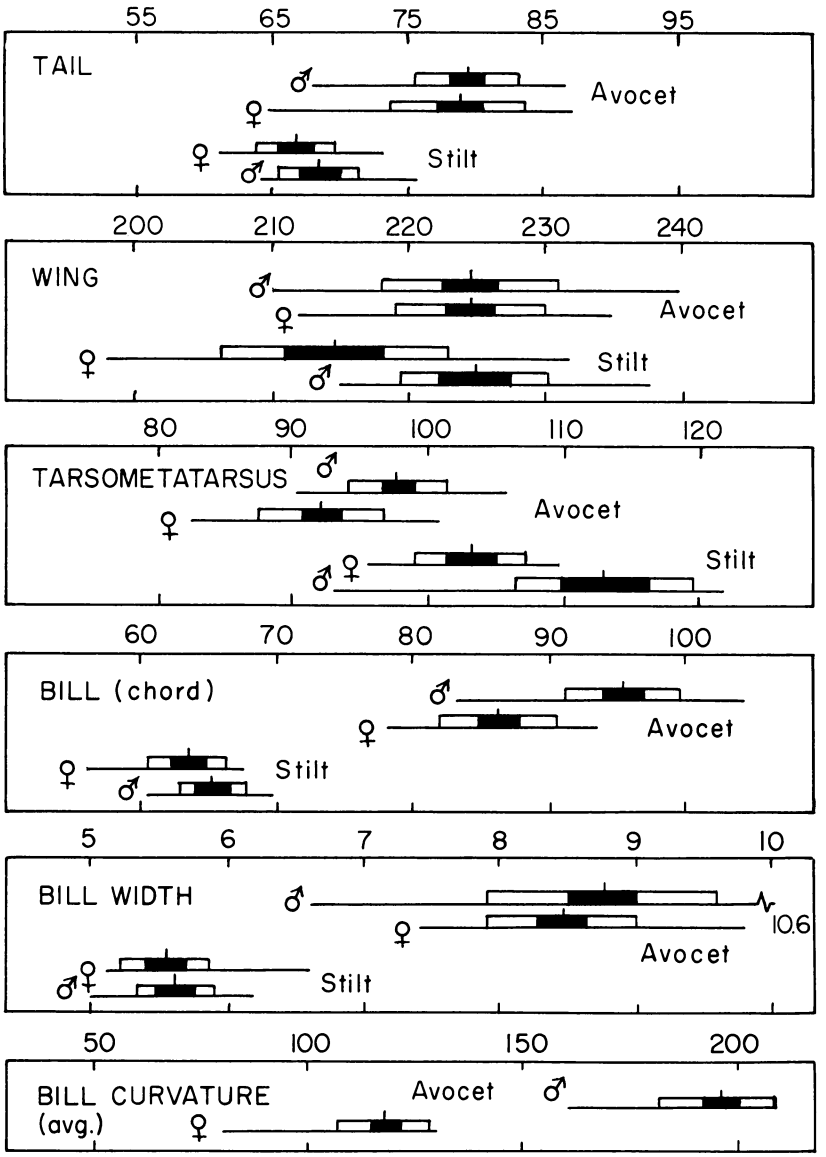

FIGURE 4. Statistical analysis (mm) of some mensural characters of *Recurvirostra americana* and *Himantopus himantopus mexicanus*. Vertical line = the mean; solid rectangle on each side of the mean = 95 percent confidence limit of the mean; this plus the open rectangle = one standard deviation. The heavy horizontal line = the observed range.

TABLE 3
RATIO OF THE MEANS OF SOME MENSURAL CHARACTERS OF THE AMERICAN AVOCET AND BLACK-NECKED STILT

Measurement	$\bar{x}$ Avocet	$\bar{x}$ Stilt	$\bar{x}$ Avocet/$\bar{x}$ Stilt
Weight [1]	316.38	165.91	1.91
Cube root of weight	6.8	5.5	1.24
Wing (chord) [2]	224.55	219.46	1.02
Tail [2]	79.17	67.71	1.17
Tarsometatarsus [2]	95.27	107.73	0.88
Bill (chord) [2]	90.87	64.36	1.41
Bill width [2]	8.61	5.58	1.54
Perpendicular/Bill (chord) [3]	6.22	2.19	2.84
Length to perpendicular/Bill (chord) [3]	56.74	43.42	1.30

[1] In grams.
[2] In millimeters.
[3] In percent.

There is no significant difference in tail lengths of male and female avocets ($|\bar{x}_m - \bar{x}_f|$/S.E. = 0.44, $p > .10$ [Table 2]).

Table 3 shows that avocets are 1.91 times heavier than stilts. To compare features (such as tail lengths) of avocets and stilts, a ratio can be calculated. These ratios are given in Table 3. If such ratios, which are taken from one-dimensional measurements, are to be compared with weight ratios (a measure of absolute size), the ratio of the cube roots of the weights must be computed. The ratio of the cube roots of the weights of avocets/stilts is 1.24. The ratio of tail lengths (avocet/stilt) is 1.17. Thus, the tail length of the stilt is relatively shorter than that of the avocet, but the difference is not pronounced.

Wing length.—Wing length was measured as the chord. Figure 4 and Table 1 show that in the American form of the Black-necked Stilt the wing of the female is markedly and significantly shorter than that of the male. A difference of this size would occur by chance less than 0.1 percent of the time. Table 1 shows that the amount of sexual dimorphism of wing length corresponds with the size dimorphism and thus the stilt sexes have wings of the expected relative sizes.

Figure 4 and Table 2 show no significant difference in wing length of male and female avocets.

Figure 4 and Table 3 also show that there is little difference in wing length of avocets and stilts. In fact, wings of male stilts do not differ significantly in length from those of avocets. Table 3 shows the ratio of avocet/stilt wing length as 1.02. Wings of stilts, therefore, are relatively longer than those of avocets.

Tarsometatarsus length.—Figure 4 and Table 1 show a significant difference between sexes of the stilt in length of tarsometatarsus ($p < .001$).

The tarsometatarsus is the stilt's most dimorphic feature. Niche diversification is a possible explanation for the dimorphic tarsometatarsus length.

Figure 4 and Table 2 show that there is a marked dimorphism of tarsometatarsus length in avocets ($p < .001$). Here, the male has the larger measurement, as would be expected from its generally larger size. Differences of leg length may be significant in niche diversification.

Figure 4 and Table 3 show that stilts have significantly longer legs than avocets, even though the avocet is the larger bird. It appears that the long legs of the stilt enlarge the shallow water area available for feeding. This phenomenon may be vital to the stilt, which neither swims nor has the variety of feeding methods employed by the avocet. The long legs of the stilt, therefore, are extreme specializations for wading.

Bill width.—There does not appear to be any significant difference between sexes of the stilt in bill width (Figure 4 and Table 1).

Figure 4 and Table 2 show that there is no significant difference in bill width of male and female avocets.

The bill is of a greater width relative to body size in the avocet than in the stilt (Table 3). This is due to the different shape of the bills of the two birds. The cross section of the avocet bill at the nares is a horizontal rectangle, whereas in the stilt it is approximately circular. The different bill shapes reflect different feeding methods of the two species. I have measured the bills both before and after drying; the variation caused by drying of the bill was minor, however, and bill-width measurements were used without adjusting for changes due to drying. This probably contributed to the rather high coefficient of variability found for bill-width measurements.

Bill chord.—Figure 4 and Table 1 show a slight but insignificant difference in bill length between the sexes in *Himantopus himantopus mexicanus.*

Figure 4 and Table 2 show that there is a marked sexual dimorphism in bill chord length in avocets ($p < .001$). Actually, the bill of the female is more curved than that of the male, so the tip of the male's bill, as shown in chord measurement, extends relatively farther from the base of the bill than does the tip of the female's bill. The error caused by bill curvature is minor, and comparisons of absolute bill lengths (culmen length) give similar results (*cf* Table 4). Bill length dimorphism may be important in niche diversification.

Table 3 and Figure 4 reveal that the bill of the avocet is relatively longer than that of the stilt. Bill lengths of avocets and stilts should not be directly compared, however (except as a measure of bill shape), because each species has a distinctive bill shape. These bill shapes reflect different feeding methods of the two species.

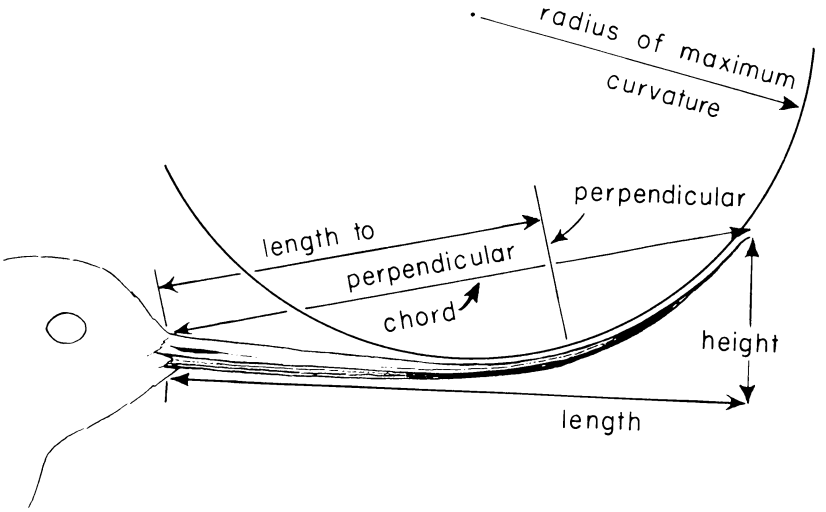

FIGURE 5. Bill measurements used to analyze bill curvature of avocets.

Analysis of Bill Curvature.—I know of no study in which the degree of bill curvature of an avian species has been analyzed. Baldwin, Oberholser, and Worley (1931: 25) gave an unwieldy method for measuring bill curvature, so I sought an easier way to measure bill curvature.

Figure 5 depicts the head and bill of an avocet-like bird with a markedly recurved bill. To find a measure of bill curvature which would be sufficiently precise to reveal small differences of bill curvature, I compared three different measurements of bill curvature: "radius of curvature," "height," and "perpendicular." Of these indices, only "radius of curvature" gives absolute values of bill curvature. "Height" and "perpendicular" measure bill curvature only in relation to some absolute measure of bill length. They are satisfactory measures of bill curvature for the purposes of this study, however.

All the measurements shown in Figure 5 were analyzed to see if any of these methods were sufficient to show sexual dimorphism in *Recurvirostra americana.*

Table 4 shows the results of a statistical analysis of sexual dimorphism for each of the bill measurements. Its last column enumerates the number of standard errors by which the means for each measurement of each sex differ and the probabilities of each result occurring by chance. All bill measurements show extreme degrees of sexual dimorphism except "length to perpendicular," which, as noted, is a measurement that does not indicate curvature but merely shows where maximum curvature occurs. The

TABLE 4
SEXUAL DIMORPHISM OF *Recurvirostra americana* BILL MEASUREMENTS

Measurement	Sex	N	$\bar{x}$ (mm.)	C.V.	F	$\lvert\bar{x}_m-\bar{x}_f\rvert$/S.E.
Perpendicular	♂	37	4.09	21.31	1.19	16.47
	♀	34	7.34	10.83	$p>.10$	$p>.001$
Length to perpendicular	♂	37	52.11	11.59	2.55	0.96
	♀	34	50.97	7.28	$p.<.01$	$p>.10$
Culmen length	♂	33	97.45	4.97	1.03	6.56
	♀	30	89.32	5.58	$p>.10$	$p<.001$
Bill (chord)	♂	36	95.33	4.58	1.02	8.79
	♀	35	86.29	4.98	$p>.10$	$p<.001$
Bill curvature (max.)	♂	39	179.2	13.14	6.01	21.72
	♀	35	90.1	10.63	$p<.001$	$p<.001$
Bill curvature (avg.)	♂	39	196.2	9.13	1.79	27.18
	♀	35	118.1	7.08	$p<.01$	$p<.001$
Height	♂	32	7.14	21.14	1.10	15.24
	♀	31	12.50	11.50	$p>.10$	$p<.001$
Length	♂	32	91.81	4.83	1.32	6.57
	♀	30	83.80	6.10	$p>.10$	$p<.001$

measures of curvature—"perpendicular," "radius of curvature," and "height" —exhibit considerable dimorphism. The best measurement (maximum value in the last column of Table 4) for showing bill curvature is "bill curvature (average)," which is an absolute measure of bill curvature and which is very simple to determine. Of the two bill length measurements—"bill chord" and "culmen length"—"bill chord" seems to be the more practicable for separating the sexes.

Figure 6 shows the average bill curvature measurements plotted against bill chord length for male and female avocets. This figure completely separates the bill shape of the adult male and female. Table 4 shows that almost all the measurements of bill curvature used were sufficient to show sexual dimorphism of bill shape, but those measurements used in Figure 6 show sexual dimorphism most clearly.

The use of "average radius of curvature" does lead to an overestimation of the average degree of bill curvature of the male avocet; this tends to decrease the difference between bill curvature measurements of male and female avocets, but the difference in amount of average bill curvature is so great that radii of bill curvature measurements serve admirably to document bill shape dimorphism of avocets. "Bill chord" measurements indicate that there is a concomitant dimorphism of bill length.

Radius of curvature.—Figure 4 shows that there is a marked difference in the radius of curvature of the bill of male and female avocets. This fea-

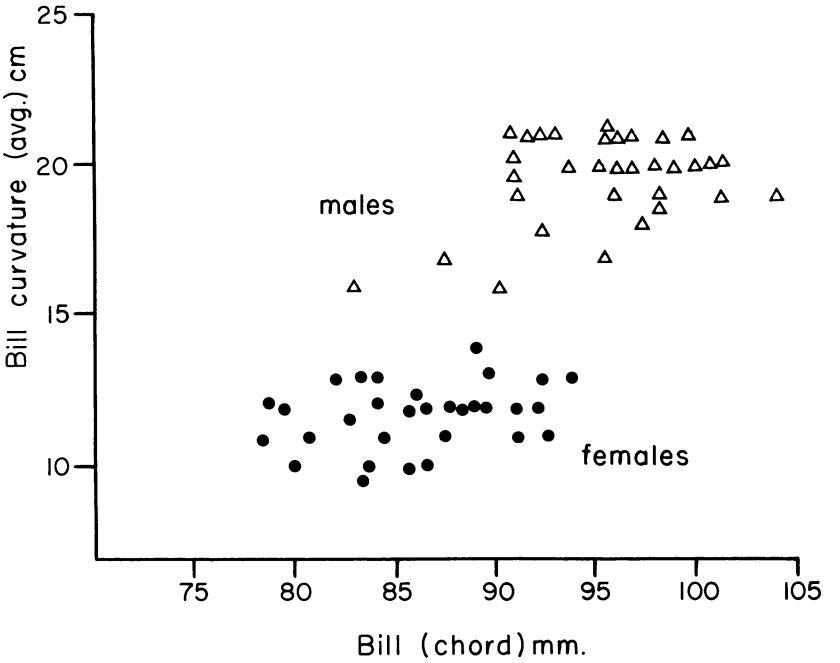

FIGURE 6. Sexual dimorphism of bill curvature of avocet adults (average bill curvature vs. bill chord).

ture was not measured in stilts, which have little noticeable curvature. The ranges shown in Figure 4 demonstrate that there is no overlap between sexes in the average radius of curvature measurements of the 74 avocets used. The difference in bill curvature between sexes is so extreme that I am able to use it for sex identification in the field with more confidence than I can sex stilts, which have dimorphic plumage (detectable only with ideal light). Bill shape dimorphism may be useful for sex identification by the birds themselves and may be the result of sexual selection. Niche diversification is another possible explanation for the evolution of sexual dimorphism in bill shape.

Perpendicular.—As a measure of bill curvature of the stilt, the "perpendicular" measurement was taken. Table 1 shows that the stilt sexes did not differ significantly in the "perpendicular" measure. However, the female had the larger measure and, in this respect, corresponded with avocets. The exceptionally large coefficient of variation was due to the fact that I had to estimate the measurement to the nearest 0.5 mm, and the measurement averages only about 1.5 mm. The same error in measurement accounts for the significantly large F value of Table 1.

HABITAT

The preferred habitats of avocets and stilts ought to differ somewhat, and the study has shown that they do. At the salt ponds of southern San Francisco Bay, stilts tended to be found in areas where some emergent vegetation existed. Stilts were frequently found in several temporary ponds caused by the flooding of grassy, lowland areas; avocets did not normally use these areas. Both species fed in salt ponds, but avocets also frequently fed on bay mud flats far from shore. Stilts confined mud flat feeding to areas near shore. Stilts displayed a greater tendency than avocets to feed in marshes.

On the northern California border, both species breed at White Lake, an area of shallow water with scattered islands and surrounded by emergent grass and sedge vegetation. At Klamath National Wildlife Refuge, about 10 miles away, only avocets were present. In the areas of Klamath National Wildlife Refuge, there was little, if any, emergent vegetation, but mats of floating algae were common.

Wetmore (1925: 17) noted that: "Stilts feed by picking up insects on muddy shore or in shallow water, and though not adverse to frequenting alkaline areas, on the whole prefer fresher water than do avocets." Palmer (1967: 151, 152), reported that habitats of avocets include saline and alkaline as well as fresh-water areas. He did not indicate that either alkaline or saline areas are suitable for stilts. Tyler (1913) indicated that avocets are always found in shallow ponds, which become stagnant in summer, and in which stilts are also present. He stated, however, that stilts nest nearby in fresh-water ponds where avocets do not occur. Wheeler (1955) emphasized that *Recurvirostra novae-hollandiae* feed at salt paddocks more than do stilts. Lane (1897) said that *R. andina* is peculiar to salt marshes of the Bolivian Andes. The literature, therefore, indicates that stilts prefer fresh-water habitats more than do avocets, which seem to be partial to saline or alkaline habitats. In order to pursue this hypothesis further, I have tabulated habitats, as reported in the literature, in which the description was sufficient to indicate type of habitat. The results are as follows: *R. americana*, fresh, 1, not fresh, 7; *H. h. mexicanus*, fresh, 14, not fresh, 3. The above data were analyzed by a Fisher Exact Probability Test, and results obtained by the above calculation would occur by chance less than 0.5 percent of the time ($p < .005$). Since I think differences in habitat correlate with differences in morphology, the results of a similar analysis for all members of the genera should yield similar results, and did so: *Recurvirostra*, fresh, 5, not fresh, 13; *Himantopus,* fresh, 30, not fresh, 5. The above data yield a χ^2 of 15.30, which would occur by chance less than 0.1 percent of the time. Thus, the literature indicates rather clearly that stilts prefer fresh-water habitats and avocets prefer alkaline or saline habitats. Very

accurate descriptions of "typical" habitats are given by Palmer (1967: 151, 152).

MAINTENANCE BEHAVIOR

Maintenance activities such as defecation, comfort movements, locomotion, and feeding occur throughout the year and are "concerned with locomotion and the general health and efficiency of the body" (Marler 1956: 8).

Defecation.—Most of the feeding of both avocets and stilts occurs in shallow water, often not far from land. When watching feeding birds, I noticed that often they would walk to land, defecate, turn around, return to water, and resume feeding. To my knowledge, this behavior has been recorded only for certain herons (Brackbill, 1966), which also habitually feed in shallow water. I have also observed this behavioral pattern in Lesser Yellowlegs (*Tringa flavipes*) and in Greater Yellowlegs (*Tringa melanoleucus*).

Table 5 shows the circumstances in which defecation occurs. The tendency to move to land for defecation is strong in both avocets and stilts. Avocets stopped feeding and moved to land to defecate in 58.1 percent (18/31) of the observations. In 84 observations of defecating stilts, the birds moved from feeding areas to land in 62 cases (73.8 percent). There is not one instance of an avocet or a stilt feeding in water and defecating in water. Feeding birds move to land to defecate by all possible means, with wading being the most prominent. Avocets moved to land by wading (walking) in 77.8 percent (14/18) of my observations, whereas stilts moved to land by wading in 87.1 percent (54/62) of my observations. Occasionally, avocets ran to land (11.1 percent [2/18]), as did stilts (3.2 percent [2/62]). Avocets flew to land in 5.6 percent (1/18) of my observations, whereas stilts flew to land in 9.7 percent (6/62) of my observations. Avocets also swam and then waded to land (5.6 percent [1/18]); adult stilts do not often swim. Therefore, it can be said that birds do move and thus expend energy in order to defecate on land. The distance travelled is not usually great, however. Avocets moved an average distance of 2 m to land, and stilts moved an average distance of 2.5 m.

Both avocets and stilts sometimes defecate when performing other activities. Birds in flight often defecate soon after taking to the air. This is the only occasion in which defecation into the water regularly occurs. Avocets defecated while flying 32.3 percent (10/31) of the time, with droppings falling into water on 90.0 percent (9/10) of these occasions. Stilts occasionally defecated when flying (4.8 percent [4/84]), with droppings always falling into water. Gulls, herons, and other species of birds often defecate after taking off (personal observation). Defecation also

TABLE 5
CIRCUMSTANCES OF DEFECATION IN AVOCETS AND STILTS

Birds moving to defecate	Land		Water		Shore line
	Avocet	Stilt	Avocet	Stilt	Stilt
Feeding bird moves to defecate					
Wading → [1]feeding	11	42	–	–	–
Wading → preening	2	1	–	–	–
Wading → resting	–	2	–	–	–
Wading → flying	–	3	–	–	–
Wading → ?	1	6	–	–	–
Running → feeding	–	2	–	–	–
Running → interacting	1	–	–	–	–
Running → ?	1	–	–	–	–
Flying → feeding	1	4	–	–	–
Flying → ?	–	2	–	–	–
Swimming and wading → ?	1	–	–	–	–
Total birds moving to defecate	18	62	–	–	–

Birds not moving to defecate	Land		Water		Shore line
	Avocet	Stilt	Avocet	Stilt	Stilt
While performing another activity					
Flying	1	1	9	3	–
Interacting	1	3	–	–	2
Alarmed	1	–	–	–	1
Total	3	4	9	3	3
Between activities (not apparently related to defecation)					
Interacting and feeding	–	6	–	–	–
Landing and feeding	–	4	–	–	–
Landing and resting	–	1	–	–	–
Resting and feeding	–	1	–	–	–
Resting and preening	1	–	–	–	–
Total	1	12	–	–	–
Total birds not moving to defecate	4	16	9	3	3
Total defecation	22	78	9	3	3

[1] Movement at left of → indicates type of locomotion; movement at right of → indicates activity following defecation.

occurred when birds were interacting; I saw this in 3.2 percent (1/31) of my observations of avocet defecation and in 6.0 percent (5/84) of my stilt defecation observations. Always with avocets the droppings fell on land; droppings of stilts usually fell on land (60.0 percent [3/5]). In 40.0 percent of the cases, droppings fell in very shallow water near the shoreline, but the defecating birds were standing on land. It is possible

that defecation occurring during interaction might be a form of displacement activity. One bit of evidence to support this, besides the fact that defecation seemed out of place in this context, was that once a stilt, which was interacting near the shoreline, walked about two feet onto land, made movements as if defecating—but with no droppings appearing—and then return to resume interaction. If defecation during interaction is a form of displacement activity, it is one of the least common forms that I have observed. Defecation also occurred when birds were alarmed. (Frequently, when birds took off and defecated into water, they had been alarmed.) I have one example of each species of an alarmed bird not flying but remaining alert and defecating—the avocet on land and the stilt on the shoreline while standing on land.

Stilts regularly seem to defecate when on land for other purposes. They therefore gain whatever advantage there is to defecating on land but without having to expend additional energy to get to land just for the purpose of defecation. These occasions usually occur when a bird shifts from one activity to another, such as from resting to feeding. A situation somewhat analogous to the latter sometimes occurs when a bird moves to land to defecate. This happens when a bird, after defecating on land, does not return to water to feed but, instead, remains on land and performs some other activity, such as preening or resting, which is normally performed on land. The energy cost of defecating on land is thereby minimized. Several examples of this energy-consuming practice for both avocets and stilts are shown in Table 5.

The tendency to move to land to defecate is the most marked on those occasions when a bird which is feeding in water goes to land, defecates, returns to water, and resumes feeding. In such an instance it is obvious that the trip to land was for defecation. Furthermore, this is a situation which would require the greatest amount of additional energy expenditure, but it nevertheless occurs quite commonly. In avocets, of the 28 observations for which I have sufficient information, 12 followed this pattern (42.9 percent), as compared with 63.2 percent (48/76) in stilts. From this, one must assume that there is some advantage to defecating on land.

One possible advantage of defecation on land would be the reduction of salt deposited into the water. This explanation seems unlikely, however, since recurvirostrids have very well-developed salt glands and often feed in very saline situations. The occurrence of toxic ingredients in waste products is unlikely to be important. Certainly occasional defecation into water during flight has been observed without any noticeable effects. Also, other species regularly defecate into water used by avocets and stilts for feeding.

Another possible explanation may involve parasites. Both avocets and stilts are regularly victimized by many internal and external parasites. I have

found numerous internal parasites in birds I collected. In one avocet, for example, I collected three tapeworms measuring 25 cm in total length and 12 flukes measuring one cm each. Most internal parasites found in recurvirostrids have complex life cycles which involve some aquatic crustacean as an intermediate host. Direct infestations without intermediate hosts may be possible. Wetmore (1925: 13) reported seeing avocets pick up tapeworm terminal segments and eat them. (He thought this might cause direct infestation, but he did not know if the species of tapeworm was one that could infest avocets.) Whether or not direct infestations are possible, parasitological infestation could probably be minimized by the simple expediency of going a short distance to the nearest land to defecate and then returning to the feeding area. If this were the only explanation and direct infestation were common, one would think that avocets, which often do not seem to feed visually, would have a greater tendency to defecate on land than do stilts, which are mostly visual feeders. This is not the case, however. Stilts have a greater tendency to defecate on land ($\chi^2 = 8.69$, $p < .005$).

An explanation for defecation on land that would probably be more advantageous to stilts than to avocets would be the prevention of the clouding of the water. Stilts have a much more limited area of food availability than do avocets, because stilts do not swim when feeding, they rarely immerse their heads when feeding, and they have shorter bills. Stilts, as strictly visual feeders, would be specifically benefitted by water as clear as possible. The clear-water explanation, in combination with the parasitological one, might explain how stilts and avocets can expend energy profitably by going to land to defecate and why stilts have a greater tendency to defecate on land than do avocets.

Table 5 shows that in only three cases could a bird have been standing in water when defecating (examples of stilts defecating on shoreline). In all cases, however, the bird was standing on land, but twice the droppings fell into water. This suggests the possibility that standing in water is in some way inhibitory to defecation in these birds.

Comfort Movements.—Comfort movements are those maintenance activities which aid in the care of the body and which are not concerned with defecation, eating, drinking, resting, or locomotion. Some of these movements differ in form from group to group and can be useful in classification. Simmons (1957), by using the method of head scratching as a character, placed the recurvirostrids near the charadriids, rather than near the scolopacids.

There are few noticeable differences in form between comfort movements in avocets and stilts. In fact, the form of many of the comfort movements is almost identical to that of gulls and other more distantly related species.

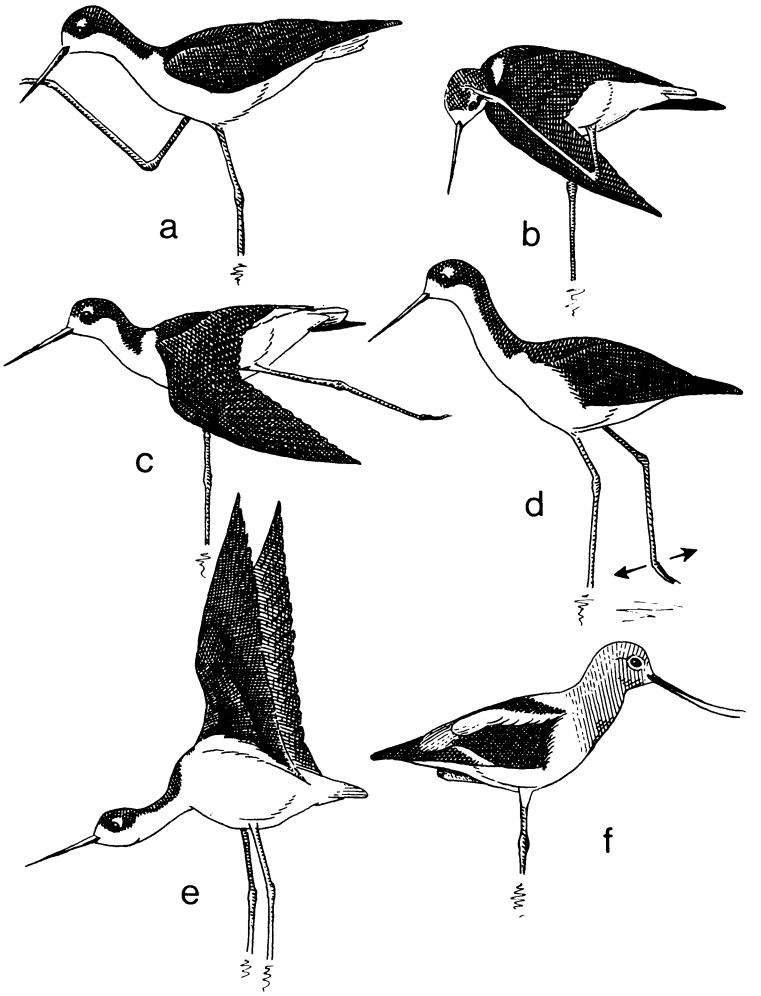

FIGURE 7. Comfort movements. "Typical" postures illustrated: (a) Direct Scratch; (b) Indirect Scratch; (c) Wing and Leg Stretch; (d) Foot Shaking; (e) Two-wing Stretch; (f) yawning.

Selection pressure for divergence of the form of comfort movements would not be expected. Any divergence of form is likely to be due to differences in morphology rather than divergence of the comfort movements *per se*. Many comfort movements of North American recurvirostrids have not previously been described or even listed.

Two-wing Stretch.—The Two-wing Stretch (Figure 7e) is a movement whereby the head is lowered and the neck is extended anteriorly below the

TABLE 6
ACTIVITIES ASSOCIATED WITH TWO-WING STRETCH

Activity	Disturbed				Not Disturbed			
	Avocet		Stilt		Avocet		Stilt	
	Prox.	Ult.[1]	Prox.	Ult.	Prox.	Ult.	Prox.	Ult.
Preceded by								
Resting	98	122	24	23	10	12	5	5
Feeding	1	1	1	2	7	7	3	4
Hop and Flap	16	–	–	–	–	–	–	–
Tightrope Display	9	7	–	–	–	–	–	–
Two-Wing Stretch	7	–	–	–	–	–	–	–
Unknown	–	1	–	–	1	1	1	1
Interacting	–	–	–	–	–	1	2	1
Scratching	1	–	–	–	–	1	–	–
Distraction Display	–	1	–	–	–	–	–	–
Alert	–	–	–	–	1	–	–	–
Bathing	–	–	–	–	1	–	–	–
Drinking	–	–	–	–	1	–	–	–
Preening	–	–	–	–	1	–	–	–
Totals	132	132	25	25	22	22	11	11
Followed by								
Flying	74	3	22	1	14	–	4	–
Unknown	1	66	–	21	2	13	3	6
Resting	26	34	2	2	1	1	–	1
Preening	11	16	–	–	3	5	–	–
Feeding	8	10	–	–	–	1	1	2
Two-Wing Stretch	7	–	–	–	–	–	–	–
Interaction	–	–	–	1	–	2	–	2
Scratching	3	–	–	–	–	–	1	–
Alert	–	–	1	–	1	–	1	–
Tightrope Display	–	3	–	–	–	–	–	–
Drinking	2	–	–	–	–	–	–	–
Hop and Flap	–	–	–	–	–	–	1	–
Wing Out	–	–	–	–	1	–	–	–
Totals	132	132	25	25	22	22	11	11

[1] Abbreviations: Prox. = proximately; Ult. = ultimately.

horizontal in a manner similar to that used by the female prior to copulation. Simultaneously, the wings are extended vertically into the air over the back and to their full extent. The feet are 5 to 8 cm apart with the plane connecting them perpendicular to the direction the bird is facing. The Two-wing Stretch is performed slowly and deliberately and usually lasts for several seconds. The movement seems to be performed in a more leisurely manner in the avocet than in the stilt. On several occasions avocets performed this activity while standing on one leg. The Two-wing Stretch regularly follows resting, and recurvirostrids commonly rest on one leg. The Two-wing Stretch was not given by birds sitting on the ground, even though

TABLE 7
COMPARISON OF TENDENCY TO PERFORM EACH COMFORT MOVEMENT
(DISTURBED VERSUS UNDISTURBED)

Movement	Avocet		Stilt	
	χ^2	p	χ^2	p
Two-Wing Stretch	170.5	.001[1]	25.9	.001[1]
Wing and Leg Stretch	1.46	.30	6.04	.02
Yawning	8.43	.01[1]	–	–
Hop and Flap	9.68	.01[1]	6.87	.01[1]
Scratching	6.93	.01[2]	16.23	.001[2]
Bathing	.598	.50	1.795	.20
Preening	157.5	.001[2]	1.85	.20
Feathers Ruffled	.0345	.90	.374	.70

[1] Performed significantly more frequently by disturbed birds.
[2] Performed significantly more frequently by undisturbed birds.

they often rested in that position. (The movement would have to be modified to be given by a sitting bird.) However, sitting birds sometimes stood and then gave the Two-wing Stretch. Birds resting on one leg often lowered the other leg before performing the Two-wing Stretch.

Makkink (1936: 7) described this movement for the European Avocet, but he neither named it nor discussed the circumstances of its occurrence.

Table 6 shows the activities which are associated with the Two-wing Stretch. This table and those given for other comfort movements are divided to show activities that precede and those that follow certain comfort movements. In these tables, I have distinguished between disturbed and undisturbed birds because of the possible correlation between disturbance and frequency of performance of certain comfort movements. (This would be expected if some of the comfort movements could also function as alarm signals, for example.) Statistical analysis of the data in Table 7 reveals that a correlation between disturbance and frequency of occurrence of some comfort movements exists. For example, the Two-wing Stretch is much more likely to be performed by disturbed avocets than by undisturbed avocets ($\chi^2 = 170.5$, $p < .0005$). Statistical analysis of Table 8 also shows that avocets were disturbed relatively more often than stilts ($\chi^2 = 4.64$, $p < .025$).

The tables also distinguish between activities proximately and activities ultimately associated with comfort movements. This distinction was desirable since several comfort movements sometimes followed one another in rapid succession, and the major activities associated with comfort movements, such as feeding or resting, would have been obscured by recording only proximate (or nearest) activity to the comfort movement. If several activities occurred successively, the activity terminating the sequence was recorded as the ultimate activity. This was usually a major activity which

TABLE 8
FREQUENCY OF COMFORT MOVEMENTS
(EXCLUSIVE OF OBSERVATION PERIODS WHEN ONLY AVOCETS WERE STUDIED)

Movement	Disturbed		Not Disturbed		Total	
	Avocet	Stilt	Avocet	Stilt	Avocet	Stilt
Two-Wing Stretch	126	25	13	11	139	36
Wing and Leg Stretch	4	2	1	21	5	23
Yawning	8	–	–	–	8	–
Hop and Flap	25	10	11	5	36	15
Scratching	13	1	39	31	52	32
Bathing	3	4	8	2	11	6
Preening	36	9	212	30	248	39
Feathers Ruffled	10	–	11	3	21	3

normally occupied a large portion of a bird's time (feeding, for example). If a major activity terminating a sequence was unrecorded, the last known activity of the sequence was used. Consequently, the frequencies for activities ultimately associated with a comfort movement are somewhat subjective, but a study of these "ultimate" frequencies is often beneficial in detecting relationships which might otherwise be overlooked.

An analysis of Table 7 shows that the Two-wing Stretch was performed relatively more frequently than other comfort movements by disturbed birds ($\chi^2 = 170.5$, $p < .0005$ for avocets; $\chi^2 = 25.9$, $p < .0005$ for stilts). Table 9 shows that disturbed avocets had no greater tendency to perform the Two-wing Stretch than disturbed stilts. Many of the observations of disturbed birds performing the Two-wing Stretch were made when I arrived at the study area each day. I often disturbed resting flocks, and frequently individuals in these flocks performed a Two-wing Stretch before flying away or resuming their rest. The Two-wing Stretch was often observed after natural disturbances, such as a rising tide or a noisy airplane, aroused sleeping birds. Thus, in addition to performing the presumed physiological function, the Two-wing Stretch could signal impending flight or indicate a state of wariness.

Disturbed avocets and stilts performed similar activities prior to the Two-wing Stretch (Table 6). Resting was the most common activity preceding the Two-wing Stretch. Avocets and stilts occasionally fed before performing a Two-wing Stretch. Avocets frequently performed the Tightrope Display (a distraction display [see p. 90]) before the Two-wing Stretch; the bird then always flew away. Hop and Flap sometimes preceded the Two-wing Stretch. Other activities performed prior to the Two-wing Stretch are shown in Table 6. On several occasions, avocets performed two consecutive Two-wing Stretches.

Activities performed by disturbed avocets and stilts following the Two-

TABLE 9
COMPARISON OF TENDENCY TO PERFORM EACH COMFORT MOVEMENT
(AVOCET VERSUS STILT)

Movement		Disturbed	Not Disturbed	Total
Two-Wing Stretch	χ^2	.560	4.26	.531
	$p<$	.50	.05[1]	.50
Wing and Leg Stretch	χ^2	.173	56.4	54.8
	$p<$	.70	.001[1]	.001[1]
Yawning	χ^2	.822	–	1.268
	$p<$	.50	–	.30
Hop and Flap	χ^2	1.995	.0439	.979
	$p<$	.20	.90	.50
Scratching	χ^2	.59	13.85	11.7
	$p<$	.50	.001[1]	.001[1]
Bathing	χ^2	4.74	.00413	.897
	$p<$	.05[1]	.95	.50
Preening	χ^2	.00203	56.7	23.42
	$p<$	.98	.001[2]	.001[2]
Feathers Ruffled	χ^2	1.25	.00583	1.175
	$p<$	.30	.95	.30

[1] Performed significantly more frequently by stilts than by avocets.
[2] Performed significantly more frequently by avocets than by stilts.

wing Stretch were similar (Table 6). The most common activity which proximately followed the Two-wing Stretch was flying. The reason for the large number of unknowns ultimately following the Two-wing Stretch is that after birds flew from the observation site, I seldom knew of their subsequent actions. Both avocets and stilts sometimes resumed their rest after stretching. Other activities performed after stretching include feeding, preening, stretching, scratching, and drinking. The Tightrope Display also followed the Two-wing Stretch. This occurred when a bird performing the Tightrope was closely pursued. Before flying, it often performed the Two-wing Stretch. After landing a short distance away, the bird resumed the Tightrope Display.

The frequency of each activity preceding the Two-wing Stretch in undisturbed birds is similar to that in disturbed birds, but with undisturbed birds performing a larger repertoire of activities (Table 6). Often the Two-wing Stretch is preceded by resting or feeding. Birds stretching after feeding always flew away. Stilts stretched while interacting on two occasions. Stretching during interaction may have been an example of displacement. Stretching might also have served as a signal since flight is often used in aggressive encounters by stilts, and the Two-wing Stretch is often followed by flight. Other activities preceding the Two-wing Stretch are shown in Table 6.

Activities and frequencies of occurrence performed by disturbed and undisturbed stilts following the Two-wing Stretch are essentially the same, but more variety is shown by undisturbed stilts. Undisturbed avocets usually fly away after stretching but regularly preen or resume resting. Other activities are sometimes observed (Table 6).

On 21 March 1967, a flock of seven resting avocets was observed for several hours. Each bird performed a Two-wing Stretch when it was aroused from its inactivity. Sometimes the resumption of activity was only temporary. These arousals always seemed to be caused by some mild environmental disturbance. This was the only time I watched resting birds exclusively for an extended period, and these observations suggest that birds regularly stretch after resting. In further support of this idea, when I disturbed a resting flock, the number of Two-wing Stretches observed was inversely dependent upon how quickly I approached the flock. It seemed that the birds stretched if there was time before they became alarmed enough to fly away.

Sauer and Sauer (1967: 571) discussed the function of stretching. Referring to the physiological literature, they stated that the breathing center is deactivated during rest and that the muscular contraction of stretching forces carbon dioxide to the breathing center, where it is reactivated. They also maintain that stretching aids brain circulation, which may be slightly impaired during resting. This would explain why stretching is associated with resting. However, stretching is not always associated with resting; it sometimes occurs just before flight in non-resting birds (e.g., following feeding and the Tightrope Display). Perhaps the Two-wing Stretch is also in some way preparatory for flight. The form of this display with the fully extended wings also suggests this possibility. The Two-wing Stretch could also signal impending flight to neighboring birds and thereby aid in coordinating activity cycles of social groupings.

Table 10 shows the number of birds performing a comfort movement at or near the same time. Both avocets and stilts usually perform the Two-wing Stretch singly although they may be among a large resting flock. Every case of two or more birds performing a Two-wing Stretch simultaneously was the result of a resting flock being disturbed; therefore, many birds were simultaneously placed in situations where they were likely to perform the Two-wing Stretch. Hence, I have no evidence that the sight of one bird performing the Two-wing Stretch stimulates another bird to do likewise.

The Two-wing Stretch is, therefore, about the same in form and circumstance of occurrence in the avocet and in the stilt. The only noteworthy differences between the two species are the more leisurely performances by the avocet, which could be expected because of its larger size, and the greater tendency for undisturbed stilts to perform this activity than un-

TABLE 10
FREQUENCY OF NUMBER OF BIRDS PERFORMING COMFORT MOVEMENTS AT EACH OBSERVATION

Movement		1	2	3–4	5–10	11–25	>25
Two-Wing Stretch	Avocet	40	1	6	4	–	–
	Stilt	15	1	–	1	1	–
Wing and Leg Stretch	Avocet	7	1	–	–	–	–
	Stilt	20	2	–	–	–	–
Yawning	Avocet	5	–	1	–	–	–
	Stilt	–	–	–	–	–	–
Hop and Flap	Avocet	16	3	3	4	–	–
	Stilt	5	–	–	2	–	–
Scratching	Avocet	40	–	2	–	–	–
	Stilt	28	1	–	–	–	–
Bathing	Avocet	11	5	–	1	–	–
	Stilt	5	–	–	–	–	–
Preening	Avocet	92	17	9	9	5	2
	Stilt	18	8	1	1	–	–
Feathers Ruffled	Avocet	20	2	–	–	–	–
	Stilt	3	–	–	–	–	–

disturbed avocets (Table 9). Even though this tendency was not marked, it was statistically significant.

Wing and Leg Stretch.—Another form of stretch regularly seen is the Wing and Leg Stretch. In this movement a leg is stretched backward, extended, and held almost parallel to the ground. Then the wing on the same side is partially extended and stretched backward next to the extended leg. Simultaneously, the neck is drawn in slightly, and the head is held close to the breast and below the level of the back (Figure 7c). This movement is performed in a more leisurely manner than the Two-wing Stretch and may last as long as 30 seconds. Sometimes it is done on one side and then the other.

The Wing and Leg Stretch is one of the few categories of behavior for

which I have more instances recorded for stilts than for avocets (Table 8), probably because this type of stretch is more useful to the stilt with its extremely long legs.

The Wing and Leg Stretch was described for the European Avocet by Makkink (1936: 7), but he neither named the activity nor gave the circumstances of its occurrence.

Disturbed and undisturbed avocets and stilts have been observed performing the Wing and Leg Stretch. Stilts are more likely to perform a Wing and Leg Stretch when undisturbed than when disturbed ($\chi^2 = 6.04$, $p < .01$). Disturbed or undisturbed avocets were equally likely to perform the Wing and Leg Stretch (Table 7).

Disturbed avocets and stilts often performed the Wing and Leg Stretch after resting. Avocets were observed on several occasions to perform the Hop and Flap immediately preceding the Wing and Leg Stretch. Once, after alighting, a disturbed stilt gave a Wing and Leg Stretch (Table 11). Disturbed birds are ultimately likely to resume their rest or, in some cases, to commence feeding after the Wing and Leg Stretch is performed. Preening or drinking preceded the ultimate activities on several occasions (Table 11).

Undisturbed birds are most likely to perform the Wing and Leg Stretch after feeding. Stilts occasionally performed other movements before the Wing and Leg Stretch (Table 11). On several occasions stilts performed a Wing and Leg Stretch on one side and then on the other. Undisturbed avocets and stilts performed similar activities following the Wing and Leg Stretch; often they ultimately rested or resumed feeding. Other maintenance activities were sometimes performed (Table 11).

The Wing and Leg Stretch does not appear to have any social significance. Generally, only one bird was seen to give the Wing and Leg Stretch at a time (Table 10). On the few occasions when more than one Wing and Leg Stretch was observed, stretching seemed to be performed independently by each of the birds.

The Wing and Leg Stretch should function to improve brain circulation and to reactivate the breathing center, as do yawning and the Two-wing Stretch (Sauer and Sauer 1967: 571). However, the stretching movements are not as exaggerated in the Wing and Leg Stretch and occur on only one side, so it seems unlikely that the Wing and Leg Stretch could be as effective as the Two-wing Stretch in performing these functions.

My data revealed that flying did not often follow the Wing and Leg Stretch. This would indicate that the Wing and Leg Stretch, as compared to the Two-wing Stretch, does not have the additional function of preparing a bird for flight. The Wing and Leg Stretch, however, may function to prepare a bird for the resting position. Twice, stilts walked to land, defecated, gave a Wing and Leg Stretch on one side and then the other, and

TABLE 11
ACTIVITIES ASSOCIATED WITH WING AND LEG STRETCH

	Disturbed				Not Disturbed			
	Avocet		Stilt		Avocet		Stilt	
Activity	Prox.	Ult.	Prox.	Ult.	Prox.	Ult.	Prox.	Ult.
Preceded by								
Unknown	–	–	–	–	1	1	9	9
Feeding	–	–	–	–	3	3	4	7
Resting	4	6	–	1	–	–	2	1
Defecation	–	–	–	–	–	–	2	2
Wing and Leg Stretch	–	–	–	–	–	–	3	1
Flying	–	–	1	1	–	–	–	–
Hop and Flap	2	–	–	–	–	–	–	–
Two-Wing Stretch	–	–	–	–	–	–	–	1
Interaction	–	–	–	–	–	–	1	–
Alert	–	–	1	–	–	–	–	–
TOTALS	6	6	2	2	4	4	21	21
Followed by								
Unknown	–	–	–	1	–	1	8	9
Resting	1	3	1	1	–	2	5	5
Feeding	2	3	–	–	1	1	2	4
Wing and Leg Stretch	–	–	–	–	–	–	2	2
Preening	2	–	–	–	2	–	–	–
Scratching	–	–	–	–	1	–	2	–
Flying	–	–	1	–	–	–	–	1
Two-Wing Stretch	–	–	–	–	–	–	1	–
Defecation	–	–	–	–	–	–	1	–
Drinking	1	–	–	–	–	–	–	–
TOTALS	6	6	2	2	4	4	21	21

settled to the ground to rest. Stilts do not often fold both legs when resting. Perhaps there is a connection between the performance of the Wing and Leg Stretch and the flexing of the leg(s) to the resting position. In the two cases for which I have data of a bird resting on one leg after performing a Wing and Leg Stretch, the bird stretched the leg that it subsequently flexed and held under its breast. This gives a total of six known cases in the stilt where the leg stretched was the one subsequently flexed (i.e., two for each bird resting on the ground and one each for the two resting on one leg). The probability of this happening by chance (using the binomial test) is less than .02. I have two observations of avocets in which the relationships of leg stretched to leg subsequently flexed when resting is known. In both cases the bird stretched one leg, flexed that leg, and then rested while standing on the other leg. If these results are included with the stilt results, there are eight examples of known relationship between leg stretched and leg

flexed. In all cases the leg was the same. The probability of this happening by chance is less than .004.

Several young recurvirostrids were seen stretching on one side and then on the other after resting on the ground; however, data for young birds were not included in Table 11. There was one case of an adult stilt which, after resting on the ground, stood and then only stretched on the left side. There were several cases of stilts stretching after resting on one leg, but, unfortunately, I did not record if the flexed leg was the one stretched. Stretching after resting probably serves the functions mentioned by Sauer and Sauer (1967: 571) but may also aid in restoring normal function to the previously flexed leg. However, there are many instances of birds resting when no stretch of any kind was observed. Therefore, the Wing and Leg Stretch is not necessary for any of the suggested functions.

In every case for which I have data, stilts performed the Wing and Leg Stretch on land. This is not suprising since the Wing and Leg Stretch is an asymmetrical movement which might easily result in a bird falling, and adult stilts were not observed swimming or going into deep water, thereby wetting their feathers (see p. 60). Also, unless the water was very shallow, the wing might become wet as a result of this type stretch. Avocets, on the other hand, readily swim and are often observed in deep water (see p. 60); thus, it is not suprising that avocets occasionally perform a Wing and Leg Stretch while standing in water.

One bit of evidence which indicates that the two types of stretches so far considered are similar is that, on several occasions when a flock was disturbed while resting, both types of stretches were performed—the Two-wing Stretch by some birds and the Wing and Leg Stretch by others. However, there were always many more instances of the Two-wing Stretch than the Wing and Leg Stretch. There are some differences between the circumstances of occurrence of the two stretches. The Two-wing Stretch is more likely to occur after resting and the Wing and Leg Stretch, before resting. Table 9 shows that the Wing and Leg Stretch is observed with relatively greater frequency in stilts than in avocets ($\chi^2 = 54.8$, $p < .0005$). If stretches are considered separately, stilts are much more likely to perform the Wing and Leg Stretch than avocets ($\chi^2 = 41.5$, $p < .0005$). In stilts 39 percent (23/59) of the stretches were Wing and Leg, whereas in avocets 6.1 percent (10/164) of the stretches were Wing and Leg. Since the Wing and Leg Stretch so obviosuly involves the legs, stilts perhaps perform this stretch so frequently because of their extremely long legs. There was no difference in form between avocets and stilts in the way they performed the Wing and Leg Stretch.

Other stretches.—On several occasions other types of stretches were observed. Twice, stilts were observed stretching their legs backward without

TABLE 12
ACTIVITIES ASSOCIATED WITH YAWNING

Activity	Disturbed				Not Disturbed			
	Avocet		Stilt		Avocet		Stilt	
	Prox.	Ult.	Prox.	Ult.	Prox.	Ult.	Prox.	Ult.
Preceded by								
Resting	6	8	–	–	–	–	–	–
Hop and Flap	2	–	–	–	–	–	–	–
TOTALS	8	8	–	–	–	–	–	–
Followed by								
Resting	3	6	–	–	–	–	–	–
Preening	3	–	–	–	–	–	–	–
Feeding	1	1	–	–	–	–	–	–
Unknown	1	1	–	–	–	–	–	–
TOTALS	8	8	–	–	–	–	–	–

stretching their wings. One avocet was observed stretching its wing, as in the Wing and Leg Stretch; however, the bird was sitting at the time, so the leg was not stretched. On another occasion I observed an avocet giving only a single-leg stretch, but this was immediately followed by an Indirect Scratch of the head with the leg that was stretched backward. The stretching in this instance was probably only the exaggerated first part of an Indirect Scratch; this would serve the same function as a stretch.

Yawning.—Yawning consists of opening the bill and keeping it open for several seconds. The bill tip is held open two to five centimeters for a duration of up to 15 seconds. Avocets stand erect when yawning with the neck not extended (Figure 7f). Yawning was not mentioned by Makkink (1936) as occurring in the European Avocet.

Yawning was observed on eight occasions in adult avocets and once in a one-day-old avocet chick. I did not observe stilts yawning. Table 9 shows that avocets were not more likely to yawn than stilts. This indicates that yawning was so rare that if it were as likely to occur in stilts as in avocets (or less likely), chance would account for my not having seen stilts yawn.

Avocets yawned only after being disturbed. The tendency to yawn when disturbed is statistically significant ($\chi^2 = 8.43$, $p < .005$), as shown in Table 7. In all cases avocets were ultimately resting before yawning (Table 12). Each time, they were aroused by me or by some other environmental factor. Yawning was usually followed by the resumption of resting. Preening and Hop and Flap, which followed and preceded yawning respectively, are closely associated with resting and could be expected. Once after yawning, a bird walked to water and began feeding. Yawning is seen, therefore, in

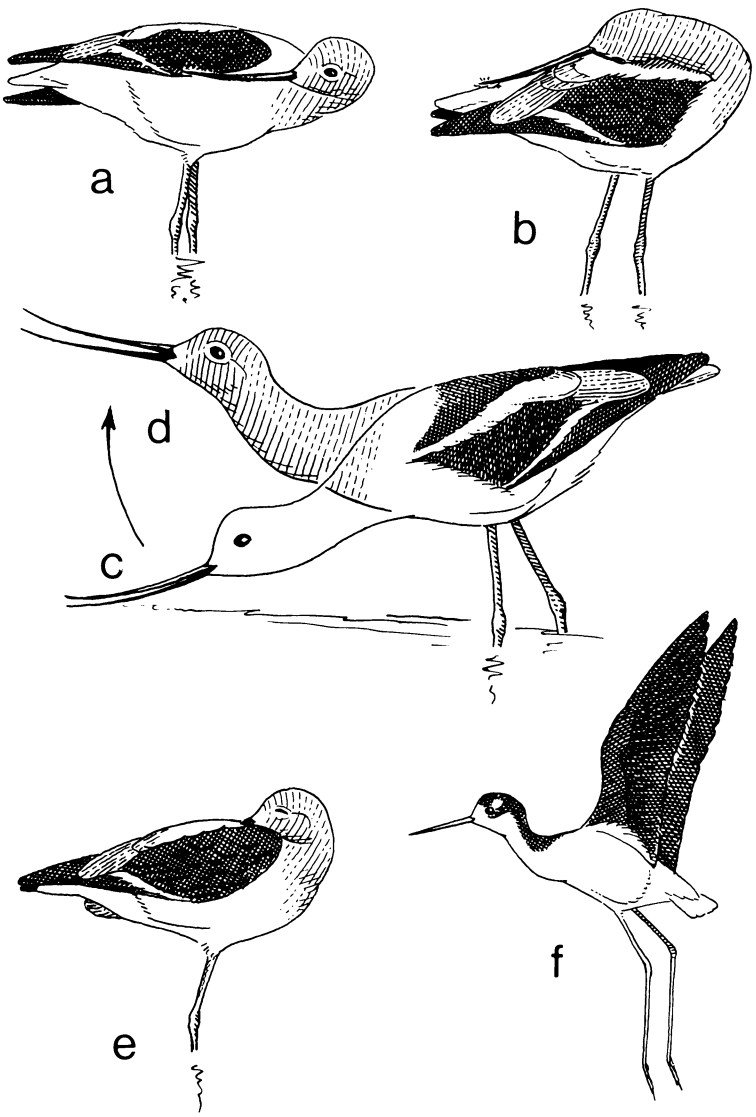

FIGURE 8. Maintenance activities. Postures illustrated (a and b) preening; (c and d) drinking; (e) sleeping; (f) Hop and Flap.

much the same situations as the Two-wing Stretch (i.e., resting birds which have been disturbed), but yawning is not associated with movement to or away from the resting location, as stretching often is.

Other birds were always near when yawning was observed, but this was

TABLE 13
ACTIVITIES ASSOCIATED WITH HOP AND FLAP

Activity	Disturbed				Not Disturbed			
	Avocet		Stilt		Avocet		Stilt	
	Prox.	Ult.	Prox.	Ult.	Prox.	Ult.	Prox.	Ult.
Preceded by								
Resting	32	40	5	5	5	5	1	1
Feeding	3	3	5	5	–	5	3	1
Flying	6	–	–	–	1	–	–	–
Bathing	1	–	–	–	4	–	–	–
Unknown	–	–	–	–	–	1	1	1
Alert	2	–	–	–	–	–	–	–
Distraction	–	1	–	–	–	–	–	–
Preening	–	–	–	–	1	–	–	–
TOTALS	44	44	10	10	11	11	5	5
Followed by								
Resting	17	35	5	5	2	6	–	–
Feeding	3	3	5	5	3	2	4	4
Flying	10	–	–	–	2	–	–	–
Unknown	–	3	–	–	–	2	1	1
Preening	1	2	–	–	3	1	–	–
Two-Wing Stretch	5	–	–	–	–	–	–	–
Feathers Ruffled	2	–	–	–	1	–	–	–
Drinking	2	–	–	–	–	–	–	–
Wing and Leg Stretch	2	–	–	–	–	–	–	–
Yawning	2	–	–	–	–	–	–	–
Distraction	–	1	–	–	–	–	–	–
TOTALS	44	44	10	10	11	11	5	5

probably due to the tendency for social resting in avocets rather than any social aspect of yawning. In only one instance was more than one bird seen to yawn at or near the same time (Table 10). This happened when a resting flock of seven avocets was disturbed by a noisy airplane.

Yawning is also supposed to have the same functions as those given previously for stretching (Sauer and Sauer 1967: 571). I have no evidence for any other possible function.

Hop and Flap.—Hop and Flap is an activity which was observed in many circumstances. Frequently, Hop and Flap was performed by a bird resting on one leg, in which case the bird hopped on one leg. This movement generally consisted of a bird hopping a short distance to the side, while simultaneously extending and flapping its wings several times (Figure 8f). Sometimes a bird performed several Hops and Flaps consecutively, but these were counted as one instance in Table 13. Hop and Flap somewhat resembled the sidewise wing-striking movements sometimes seen in aggressive

displays, but Hop and Flap was never directed at other birds and was frequently performed on one leg.

Table 13 shows the activities associated with Hop and Flap. I saw resting birds frequently Hop and Flap when disturbed. This generally appeared to be an attempt by birds to move a short distance in order to maintain their equilibrium after disturbance. On several occasions, birds that had been resting flew away while one leg was still in the resting position. These birds frequently Hopped and Flapped after alighting. Hop and Flap was also regularly observed after bathing, occurring between bathing and preening. Another occasion when Hop and Flap was sometimes seen was during feeding. On these occasions, when birds were feeding in tight flocks, one individual often Hopped and Flapped when a neighbor approached too closely. Hop and Flap was regularly followed by many of the other comfort movements and seemed to occur in the same circumstances in both avocets and stilts. There did not appear to be any social significance to Hop and Flap, although this activity was frequently performed by several birds simultaneously (Table 10), generally when a resting flock was disturbed. Both young avocets and stilts were observed performing the Hop and Flap even though their wing feathers were not developed enough to be effective in maintaining balance.

Table 7 shows that avocets ($\chi^2 = 9.68$, $p < .005$) and stilts ($\chi^2 = 6.87$, $p < .005$) are more likely to Hop and Flap when disturbed than when undisturbed. Table 9 shows that avocets and stilts do not differ in their tendency to perform the Hop and Flap relative to other comfort movements.

Scratching.—Birds use two methods of head scratching: Direct, in which the bird brings the foot directly to the head with no movement of the wing (Figure 7b); and Indirect, in which the bird lowers a wing and brings the corresponding leg over the shoulder (Figure 7a). Scratching the head probably functions to relieve the head of irritating stimuli (Simmons 1961: 37).

In the suborder Charadrii, both methods of head scratching are found; the scolopacids scratch directly and the charadriids scratch indirectly. Recurvirostrids generally scratch the head indirectly and on that basis have been placed by some with the charadriids rather than with the scolopacids (Simmons, 1957).

Although recurvirostrids generally scratch indirectly, the Black-necked Stilt and the American Avocet sometimes scratch their bills directly. Makkink (1936: 7) stated that the European Avocet scratches indirectly, but that he once saw direct scratching. The method of scratching is direct for the first few days after hatching; then it gradually shifts to indirect. This

may be a form of recapitulation, with the direct method of scratching having evolved before the indirect method. A factor which may affect the timing of the appearance of the Indirect Scratch is the fact that coordination of chicks is poor after hatching, and the more complicated method and movements of the Indirect Scratch would probably result in an inability to perform the movements or at least in losing balance and falling when trying to perform them. Chicks occasionally fall even when performing the Direct Scratch. The Indirect Scratch first appears after coordination has become well developed. It seems likely that the Direct Scratch appeared before the Indirect Scratch as the result of an evolutionary recapitulation, with the timing of the changing of scratching methods during development affected by natural selection. On the other hand, it seems unlikely that the advantages inherent in scratching the head directly (thereby minimizing the chances of a fall occurring for the first few days after hatching) are sufficient to have enabled the evolution of a distinct method of head scratching for this short period (especially since chicks regularly fall during this time anyway).

In addition to the Direct Scratches recorded for the young, both avocets and stilts were observed scratching directly when adult. In every case the bird scratched its bill when performing the Direct Scratch, and on two occasions avocets were observed scratching their bills directly while flying. It is difficult to imagine how a bird could scratch indirectly while in flight, but Makkink (1936) reported this behavior for the European Avocet. (It should be noted that English is not Makkink's native language; since his paper is written in English, his statement about the Indirect Scratch during flight may be an error due to improper use of the language.) Thus, the movements necessary for the Direct Scratch can be performed by adults. The bill of adults, however, was never observed being scratched indirectly. The type of scratching in the Charadrii is not related to the length of legs, because the (short-legged) Charadriidae and the (long-legged) Recurvirostridae scratch indirectly, and the (long-legged) Scolopacidae scratch directly.

Table 14 shows the activities associated with scratching. As a rule, a bird performs the same activity both before and after scratching. A comparison of the "Preceded by" and "Followed by" columns shows this. This is not true, however, for flight or for some of the comfort movements sometimes associated with scratching (e.g., Two-wing Stretch and Wing and Leg Stretch), since these activities are frequently performed only once and not continuously. Scratching probably occurs to alleviate some irritating stimulus. Such a stimulus is likely to be present at any time; therefore, it is not surprising that scratching is so often preceded and followed by the same activity. It is possible that the examples of scratching associated with inter-

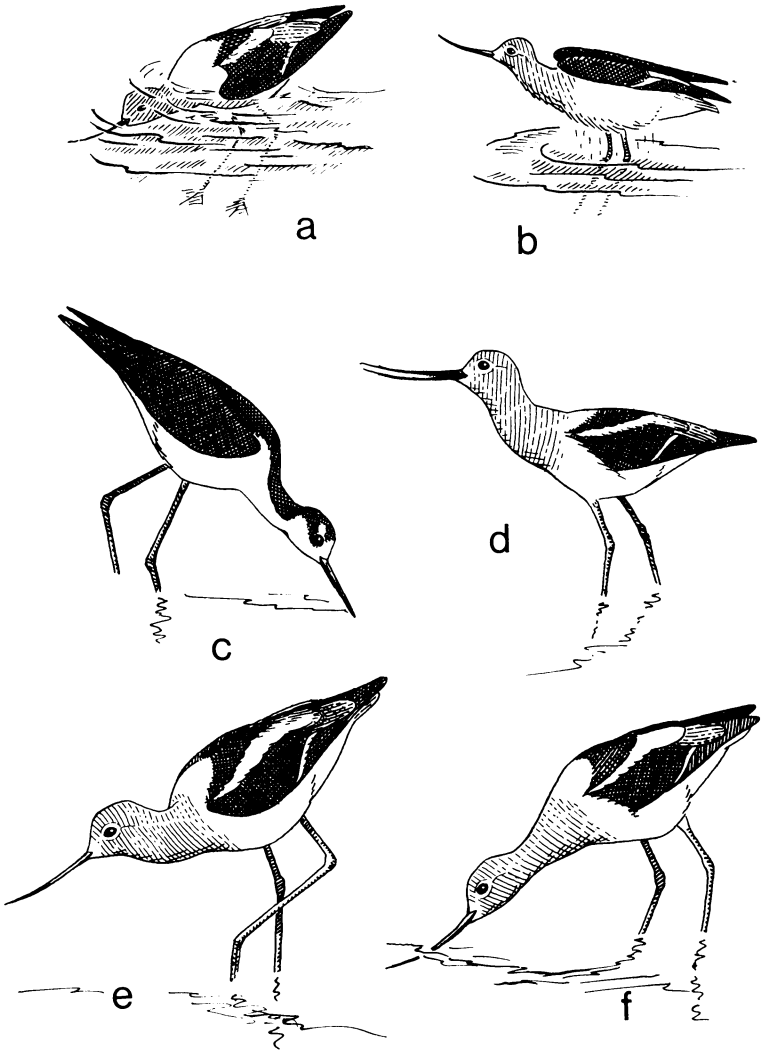

FIGURE 9. Other maintenance activities. (a and b) bathing; (c) Pecking; (d) swallowing; (e) Single Scythe between movements; (f) Single Scythe.

actions or "alert" are examples of displacement activity. Table 14 also shows that avocets and stilts scratched in similar circumstances.

Perhaps a bird always uses the same leg when scratching. On one occasion I observed a bird scratch with the left leg and then with the right leg, thereby contradicting this idea. On 16 occasions of scratching where the leg used was known, the right leg was used 10 times and the left leg six. Assuming that the leg used is random, the results obtained would occur

TABLE 14
ACTIVITIES ASSOCIATED WITH SCRATCHING

	Disturbed				Not Disturbed			
	Avocet		Stilt		Avocet		Stilt	
Activity	Prox.	Ult.	Prox.	Ult.	Prox.	Ult.	Prox.	Ult.
Preceded by								
Feeding	4	7	–	–	26	27	15	19
Preening	–	–	–	–	6	6	5	2
Unknown	–	–	–	1	2	2	3	5
Resting	–	4	–	–	3	4	1	1
Scratching	–	–	–	–	3	3	–	2
Alert	5	–	1	–	1	–	–	–
Interaction	3	4	–	–	–	–	–	–
Two-Wing Stretch	3	–	–	–	–	–	–	–
Brooding near nest	–	1	–	–	–	–	1	1
Flying	–	–	–	–	–	–	2	–
Wing and Leg Stretch	–	–	–	–	–	–	2	–
Pseudocopulation	–	–	–	–	–	–	1	1
In flight	1	–	–	–	–	–	–	–
Drinking	–	–	–	–	1	–	–	–
Bathing	–	–	–	–	–	–	1	–
TOTALS	16	16	1	1	42	42	31	31
Followed by								
Feeding	4	5	–	–	25	25	18	19
Preening	–	–	–	–	7	7	2	1
Unknown	–	3	–	1	1	3	3	3
Resting	–	4	–	–	2	3	1	3
Flying	7	–	–	–	1	–	2	–
Scratching	–	–	–	–	3	3	–	2
Interacting	2	3	–	–	–	–	–	1
Brooding near nest	1	1	–	–	–	–	1	1
Alert	1	–	1	–	–	–	1	–
Two-Wing Stretch	–	–	–	–	1	1	–	–
Drinking	–	–	–	–	2	–	–	–
Pseudocopulation	–	–	–	–	–	–	1	1
Bathing	–	–	–	–	–	–	2	–
Landing	1	–	–	–	–	–	–	–
TOTALS	16	16	1	1	42	42	31	31

by chance more than 22.7 percent of the time. Therefore, the possibility of a bird population being right legged or left legged has no support in my data.

Scratching is usually a solitary activity (Table 10). On one occasion three avocets which had been disturbed from their rest scratched at about the same time; on another occasion two feeding stilts scratched at about the same time. There was no indication, however, that scratching is a social activity.

Scratching was more likely to occur when both avocets ($\chi^2 = 6.93$, $p < .005$) and stilts ($\chi^2 = 16.23$, $p < .0005$) were undisturbed (Table 7).

TABLE 15
ACTIVITIES ASSOCIATED WITH BATHING

Activity	Disturbed				Not Disturbed			
	Avocet		Stilt		Avocet		Stilt	
	Prox.	Ult.	Prox.	Ult.	Prox.	Ult.	Prox.	Ult.
Preceded by								
Feeding	–	–	–	–	10	17	–	–
Unknown	–	–	1	1	3	3	1	1
Flying	–	1	–	–	6	–	–	–
Interaction	1	2	1	1	–	–	–	–
Bathing	–	–	–	1	–	–	1	1
Preening	–	–	–	1	1	–	–	–
Copulation	–	–	–	–	–	2	–	–
Distraction Display	2	–	–	–	–	–	–	–
Scratching	–	–	2	–	–	–	–	–
Postcopulatory Display	–	–	–	–	1	–	–	–
Drinking	–	–	–	–	1	–	–	–
TOTALS	3	3	4	4	22	22	2	2
Followed by								
Preening	1	1	1	1	15	3	–	–
Unknown	–	–	1	1	2	3	2	2
Resting	–	–	–	–	–	9	–	–
Feeding	–	–	–	–	1	5	–	–
Hop and Flap	1	–	–	–	4	–	–	–
Interaction	–	1	1	–	–	1	–	–
Distraction Display	1	–	–	1	–	–	–	–
Flying	–	1	–	–	–	1	–	–
Scratching	–	–	1	–	–	–	–	–
Bathing	–	–	–	1	–	–	–	–
TOTALS	3	3	4	4	22	22	2	2

Table 9 shows that stilts have a much greater tendency to scratch than avocets. The greater relative body surface of the stilt (1.2 times that of the avocet) is not enough to account for the increased frequency of scratching by the stilt. Since scratching involves the legs, and stilts have longer legs than avocets, perhaps scratching in some way benefits the longer legs of the stilt (exercising is a possibility). The tendency for stilts to scratch more often than avocets is the main difference between the species in scratching.

Bathing.—A bathing bird (Figure 9a and b) lowers itself into the water by bending the legs until the breast is at water level. The bird then wets itself by rapidly rocking forward several times and submerging the head by bending the neck forward when the body is at its lowest position. Simultaneously, the wings are quivered slightly. Afterward, the bird stands, frequently Hops and Flaps several times, and then preens.

Bathing was observed in both fresh and salt water.

Table 15 shows the activities associated with bathing. The form of bathing was similar in avocets and stilts and did not differ noticeably from that of the European Avocet (Makkink 1936: 6–7) or from other shorebirds and gulls. My limited data for stilts bathing, which are insufficient for detailed analysis, indicate that the circumstances of occurrence of bathing in the two species are probably similar.

Bathing by undisturbed avocets was mostly preceded by feeding. Following feeding, birds proceeded to about ankle-deep water to bathe. A noticeable effort was sometimes made to reach water. In 35.3 percent (6/17) of the observations, the bird flew to reach water deep enough for bathing. After bathing, the bird frequently Hopped and Flapped several times (I think the number of instances of Hop and Flap shown in Table 13 is low since I had not categorized Hop and Flap at the time most of these observations were recorded), then preened, and frequently rested or sometimes resumed feeding.

Bathing on two occasions occurred after copulation. Both times it was the female that bathed. On one of these occasions the female also drank.

Disturbed avocets and stilts sometimes bathed during interactions. These might have been cases of displacement bathing since on these occasions the bathing movements were never complete.

Bathing frequently is performed simultaneously by two or more birds (Table 10) and at the same location. Bathing is a relatively uncommon activity, and it is unlikely that more than one bird bathing at a time would have happened by chance. Probably the sight of one bathing bird stimulates others to bathe. Bathing was also occasionally performed by young avocets and stilts.

Avocets and stilts were as likely to bathe when disturbed as when undisturbed (Table 7). However, Table 9 shows that disturbed stilts are more likely to bathe ($\chi^2 = 4.74$, $p < .0025$) than disturbed avocets. This tendency was not marked and was due to one bathing bout which had been interrupted by scratching and then resumed; this was counted as two bouts in Tables 8, 9, and 15. If the above example is counted as one bout, the results are not significant ($\chi^2 = 2.19$, $.05 < p < .10$).

Preening.—Preening consists of manipulating and arranging the feathers, usually with the bill. Frequently, oil is obtained from the uropygial gland with the bill and is manipulated into the feathers. This is especially important in avocets since they regularly swim and thus are especially benefited by waterproof feathers. While preening, birds will frequently rub the top of the head over the back and sides. This helps to spread the oil over the feathers and probably serves to preen the top of the head, which

cannot be reached with the bill. It may act to scratch the top of the head as well. A regular feature of preening in both avocets and stilts is the use of water (usually salt or brackish water). This water is picked up with the bill when preening commences and usually is worked into the breast feathers. I know of no other birds that use water when preening. Preening is much the same in both avocets and stilts, and typical poses are pictured in Figure 8c and d. Makkink (1936: 7) described a preening sequence for the European Avocet, but he called this activity "cleaning."

The Black-necked Stilt is not more likely to preen when undisturbed than when disturbed (Table 7); however, the American Avocet is much more likely to preen when not disturbed ($\chi^2 = 157.5$, $p < .0005$).

Table 16 shows that preening is an activity that is usually preceded by feeding and usually followed by resting in both avocets and stilts. The tendency to be followed by resting does not seem to be as pronounced in stilts as in avocets, but this tendency is strong in both species. This is to be expected since stilts, being smaller than avocets, have a higher metabolic rate and do not rest as often. As an indication of the tendency to rest after preening, it is often noted that, when preening at high intensities, both avocets and stilts slowly lift one leg off the ground and shake it back and forth until it becomes completely flexed in the resting position. The birds then usually start to rest. Disturbed birds do not usually preen after feeding but, instead, usually preen after being disturbed when resting; they then often fly away. The reason for this change in frequency of activities most closely associated with preening is probably not natural since I disturbed many more resting birds than feeding birds. Preening is also sometimes associated with other comfort movements. This shows the tendency of comfort movements to occur together. This tendency has not been mentioned before, but it is very pronounced.

In some of the observations of Table 16, preening could have been a displacement activity. Those observations associated with interactions (e.g., alert and distraction display) are especially likely to have been examples of displacement preening.

Preening was often observed in social situations. Copulation was often preceded by both males and females preening together. In fact, the male precopulatory display is a ritualized form of preening. Preening was most often observed after feeding, when a bird or birds would leave the feeding area, proceed to a group of resting and preening birds, and begin to preen. This shows the social nature of preening. Table 10 indicates that many birds are often observed preening simultaneously, which, again, shows the social nature of preening.

Disturbed avocets and stilts seem equally likely to preen (Table 9), but undisturbed avocets are much more likely to preen than undisturbed

TABLE 16
ACTIVITIES ASSOCIATED WITH PREENING

Activity	Disturbed				Not Disturbed			
	Avocet		Stilt		Avocet		Stilt	
	Prox.	Ult.	Prox.	Ult.	Prox.	Ult.	Prox.	Ult.
Preceded by								
Feeding	2	2	2	2	189	231	17	24
Resting	13	15	–	–	24	30	–	–
Unknown	6	9	2	3	13	34	–	2
Flying	3	–	2	–	39	–	4	–
Interaction	13	10	–	3	5	3	–	–
Bathing	1	–	1	–	15	1	1	–
Copulation	–	–	–	–	5	8	2	2
Alert	2	–	2	–	4	–	2	–
Distraction Display	–	5	–	–	–	–	-	–
Incubation	–	–	–	–	–	4	–	1
Scratching	–	–	–	–	3	–	1	1
Tossing Straws	–	–	–	–	4	–	1	–
Feathers Ruffled	–	–	–	–	4	–	–	–
Defecation	–	–	–	–	2	–	2	–
Postcopulatory Display	–	–	–	–	2	2	–	–
Hop and Flap	–	–	–	–	3	–	–	–
Two-Wing Stretch	–	–	–	–	1	1	–	–
Drinking	1	–	–	–	1	–	–	–
Wing and Leg Stretch	1	–	–	–	1	–	–	–
Preening	–	–	–	–	–	2	–	–
Approaching Nest	–	1	–	1	–	–	–	–
Precopulatory Display	–	–	–	–	1	–	–	–
TOTALS	42	42	9	9	316	316	30	30
Followed by								
Resting	8	8	–	–	229	235	9	11
Unknown	4	20	4	4	30	40	5	6
Feeding	–	1	2	2	25	34	2	5
Flying	16	1	–	–	12	1	2	6
Interaction	4	6	2	3	4	2	1	1
Alert	5	1	–	–	1	–	4	–
Scratching	–	2	–	–	4	–	3	–
Hop and Flap	–	–	–	–	4	–	1	–
Distraction Display	2	2	1	–	–	–	–	–
Incubation	–	1	–	–	–	1	1	1
Feathers Ruffled	1	–	–	–	2	–	–	–
Copulation	–	–	–	–	–	1	2	–
Precopulatory Preening	2	–	–	–	1	–	–	–
Bathing	–	–	–	–	2	–	–	–
Preening	–	–	–	–	–	2	–	–
Two-Wing Stretch	–	–	–	–	1	–	–	–
Precopulatory Display	–	–	–	–	1	–	–	–
TOTALS	42	42	9	9	316	316	30	30

stilts ($\chi^2 = 56.7$, $p < .0005$). All observations considered, avocets are much more likely to preen than stilts ($\chi^2 = 23.42$, $p < .0005$). This may be because avocets are larger than stilts and thus have more time available for preening and resting. Avocets swim, wade in deep water, and regularly immerse their heads and breasts when feeding, thereby wetting their feathers. Therefore, avocets probably need to preen more than stilts.

Feather movements.—Avocets and stilts can ruffle their feathers or sleek them. Changes in appearance resulting from these feather movements are subtle and were probably not often detected by me. Feather sleeking was only observed in certain conflict situations and was closely associated with some aggressive displays; therefore, it cannot be considered a comfort movement. The only non-generalized feather movement that I detected was ruffling of the back feathers. This behavior was not a comfort movement either, but one which served to minimize aggression. Generalized ruffling of the feathers, or Feathers Ruffled, was sometimes seen; it appeared to be a comfort movement, but it was occasionally associated with aggressive displays. In this section I am attempting to analyze only Feathers Ruffled in which a change in the aspect of the bird was detected. This change would generally be brought about and terminated by the shaking of the plumage. Observations, in which the feathers were ruffled throughout aggressive interactions, were not included in Table 17. Makkink (1936: 7) described feather shaking in the European Avocet as occurring after preening.

Feathers Ruffled.—Table 17 shows that the activities preceding Feathers Ruffled by undisturbed birds were varied, and no marked trend was observed. Some birds fed before ruffling their feathers, and several avocets ruffled their feathers after flying in from an unknown activity. Following Feathers Ruffled, undisturbed birds frequently fed or preened and then rested. Feathers Ruffled may be more closely associated with preening than is shown in Table 17, but feather ruffling associated with preening probably was not always detected.

Neither avocets nor stilts exhibited a greater tendency to perform Feathers Ruffled when disturbed than when undisturbed (Table 7). Disturbed birds also ruffled their feathers often. Frequently, resting birds, which had been disturbed, performed Feathers Ruffled and then preened. Feathers Ruffled was often observed in association with interaction, in which case it might have been a displacement activity (i.e., Feathers Ruffled in this situation was of very short duration and could be more aptly termed "feather shaking"). On several occasions displacement preening and displacement sleeping occurred in association with Feathers Ruffled.

It is probable that the degree of feather ruffling will vary from time to

TABLE 17
ACTIVITIES ASSOCIATED WITH FEATHERS RUFFLED

Activity	Disturbed				Not Disturbed			
	Avocet		Stilt		Avocet		Stilt	
	Prox.	Ult.	Prox.	Ult.	Prox.	Ult.	Prox.	Ult.
Preceded by								
Resting	4	5	–	–	–	1	–	–
Interaction	1	3	–	–	1	1	–	1
Feeding	–	–	–	–	1	3	1	2
Flying	–	–	–	–	5	1	–	–
Unknown	–	–	–	–	–	5	–	–
Defecation	1	–	–	–	2	–	1	–
Distraction Display	1	2	–	–	–	–	–	–
Preening	–	–	–	–	1	1	–	–
Hop and Flap	1	–	–	–	1	–	–	–
Alert	1	–	–	–	–	–	–	–
Displacement Preening	1	–	–	–	–	–	–	–
Two-Wing Stretch	–	–	–	–	1	–	–	–
Copulation	–	–	–	–	–	1	–	–
Postcopulatory Display	–	–	–	–	1	–	–	–
"Giraffe"	–	–	–	–	–	–	1	–
TOTALS	10	10	–	–	13	13	3	3
Followed by								
Preening	3	4	–	–	6	1	1	–
Feeding	–	1	–	–	5	5	2	2
Resting	1	1	–	–	–	5	–	1
Interaction	3	3	–	–	–	–	–	–
Flying	1	–	–	–	–	1	–	–
Unknown	–	–	–	–	1	1	–	–
Displacement Sleeping	1	–	–	–	–	–	–	–
Bathing	–	1	–	–	–	–	–	–
Two-Wing Stretch	1	–	–	–	–	–	–	–
Drinking	–	–	–	–	1	–	–	–
TOTALS	10	10	–	–	13	13	3	3

time in recurvirostrids because of demands for temperature regulation. Feathers Ruffled in this case could be considered a comfort movement, but the differences in appearance due to ruffling of feathers for temperature regulation, if they occurred, occurred so slowly and subtly that they went undetected.

Feathers Ruffled did not seem to have any social implications *per se* (Table 10), but this behavior often occurred in social situations, such as in a group of preening or resting birds.

There was no difference in form noted in ruffling between avocets and stilts, but the sample size was small and the movements were subtle, so that any differences were likely to be missed. Neither avocets nor stilts

showed a greater tendency than the other to perform Feathers Ruffled (Table 9).

Other comfort movements.—In addition to the major comfort movements, a few other comfort movements were occasionally seen.

Several times I saw avocets and stilts standing alert while shaking their bills from side to side rather violently (Bill Shaking). An avocet was once seen Bill Shaking after landing in the midst of a flock of resting birds. I do not know the significance of this activity. Makkink (1936: 9) observed this (or a similar movement) in the European Avocet and called it "nodding." He said that it was a startle movement which indicated flight intention. I never saw a bird fly after Bill Shaking. In fact, in every case, the bird ultimately rested. I did note startle movements which were quick, sudden movements of the entire body and which were often followed by flight.

Another comfort movement sometimes performed by avocets and stilts was Foot Shaking (Figure 7d). This consisted of shaking the feet rapidly as the bird walked to shore. The movements between Foot Shakings are slow and deliberate with the bird pausing at each step to shake the trailing foot rapidly. The trailing foot is always the one that is shaken. This movement probably serves to rid the feet of mud or other debris. Usually each foot will be shaken individually as the bird comes out on land. Sometimes Foot Shaking movements are made after every step for eight to ten steps. This movement is noticed especially in birds approaching a nest from water.

Another form of Leg Shaking was defined on page 38; it occurs when the leg shakes as a bird preens, thereby bringing the leg into the sleeping position. The tibiotarsus is slowly raised as the leg is shaken until the tibiotarsus is in the resting position. The tarsometatarsus still oscillates backward and forward somewhat like a pendulum until it too achieves the resting position. This seems to happen almost automatically when a bird is preening at high intensities and serves to locate the leg at the proper resting position. This form of leg shaking is, therefore, a behavior which emphasizes the close association of preening and sleeping.

Feather-arranging movements, such as the shaking of the tail or the lowering of the tail, are occasionally observed, especially after bathing or when a bird is preening. I assume that these are used only as comfort movements, but they were seen so infrequently that it is impossible to say if they may perhaps have other functions. On several occasions the flank feathers of all the birds present seemed very conspicuous. On these occasions it was extremely windy, and it is possible that the conspicuous flank feathers were the result of the wind ruffling the feathers of feeding birds. The

occasions when this was observed were similar to the occasions when ruffled back feathers were seen, and the ruffled flank feathers may have been another way of ameliorating aggression.

Resting.—Resting is a comfort movement which is difficult to define. The basic characteristic of resting is a lack of or a minimizing of activity, which probably results in minimal expenditures of energy. The most common behavior that can be included in resting is sleeping, but unfortunately, it is not always possible to determine if a bird is, in fact, sleeping. A sleeping avocet or stilt has its bill placed under its scapulars (Figure 8e); however, on some of the occasions when I was able to observe closely a bird which appeared to be sleeping, I detected that the eyes were not closed. As a result, no attempt was made to differentiate sleeping from resting. I recorded as resting (1) all birds in a sleeping position; (2) birds not in a sleeping posture but remaining stationary for more than one minute; and (3) birds that were stationary and preening at very low intensities. Birds preening at low inteneities were considered as resting because preening frequently immediately precedes and follows resting. (Preening gradually shifts to resting, and it is impossible to ascertain precisely when resting commences.) Also, resting groups with some members apparently sleeping and others preening were often observed, and when birds were mildly disturbed while resting, they frequently preened before resuming their rest. Instances when a bird was stationary and performing some other function (such as incubation or brooding) were not considered as resting, although the bird involved may have been deriving some or all of the benefits afforded by resting while performing the other activity.

Recurvirostra americana

One of the most frequent activities performed by avocets is resting. During the non-breeding season, avocets spend much of their time resting. During the breeding season, however, it was difficult to determine how frequently resting occurred, since the birds' activities were so widely scattered spatially in my study area. Furthermore, neither incubation nor brooding was included in my analysis of resting, but incubation and brooding may be the chief occasions of resting during the breeding season.

Resting avocets assume several distinct postures. For the purposes of energy expenditure, the different postures are probably roughly equivalent.

When birds are resting in water, they usually place the bill under the scapulars; the legs may be in either of two positions. In one method, the bird stands on both legs; whereas in the other, the bird stands on one leg with the other leg flexed at the ankle and knee joints and tucked under the breast (Figure 8e). In the one-leg method, the leg which will be tucked into the feathers frequently is brought slowly to the breast when the

bird is preening (the tarsometatarsus swings back and forth slowly in a parasagittal plane as the tibiotarsus is brought backward to rest against the abdomen). Sometimes preening continues while the bird stands on one leg.

Birds resting for prolonged periods will often rest standing on one leg. One-leg resting must, therefore, contribute to the survival of the species. Resting birds always face into the wind. If birds resting on one leg are watched closely, they are seen to pivot about 10 degrees to each side (somewhat like a wind-vane) on the leg on which they are standing; this wind-vane effect allows a more direct facing into the wind when the wind direction varies slightly. Even though it is not immediately apparent why birds face into the wind when resting, some possible advantages are:

1) While standing on one leg, a bird's balance is jeopardized, and it faces into the wind to prevent a potentially toppling force from being applied from the side.

2) Facing into the wind minimizes the exposed surface area of a bird, and thereby minimizes the wind's disturbance of a bird's feathers. Since a bird's feathers lie in the direction from which the wind is coming, a bird facing into the wind will merely have its feathers blown down and compressed by the force of the wind. Wind from any other direction, however, would tend to raise the feathers, probably to the irritation of the bird.

3) Birds could probably still control the degree to which the ruffled feathers are compressed by the wind and thereby regulate their temperatures; but if birds did not face into the wind, they probably could not control the degree to which the ruffled feathers are raised by the wind.

4) The minimal body area exposed when facing into the cooling wind would also be important in temperature regulation.

5) Since avocets take off into the wind, facing into the wind when resting results in a reduction of the amount of time required for take-off should escape become necessary.

Even though the above arguments show possible advantages for a bird facing into the wind, the reason for resting on one leg remains unclear; however, the "wind-vane effect" would allow a more precise facing into the wind, thereby optimizing the advantages of wind-facing.

If a bird is disturbed while resting on one leg, it might Hop and Flap several times until it is able to release the tucked leg. If the disturbance is minimal, the bird might not lower the leg at all after Hopping and Flapping, but rather it might resume resting. Sometimes a bird will fly away with one leg tucked in the sleeping position; it then alights on the free leg, eventually working its tucked leg free. Once, I observed a bird using its bill while Hopping and Flapping to pry its tucked leg free (or so it appeared).

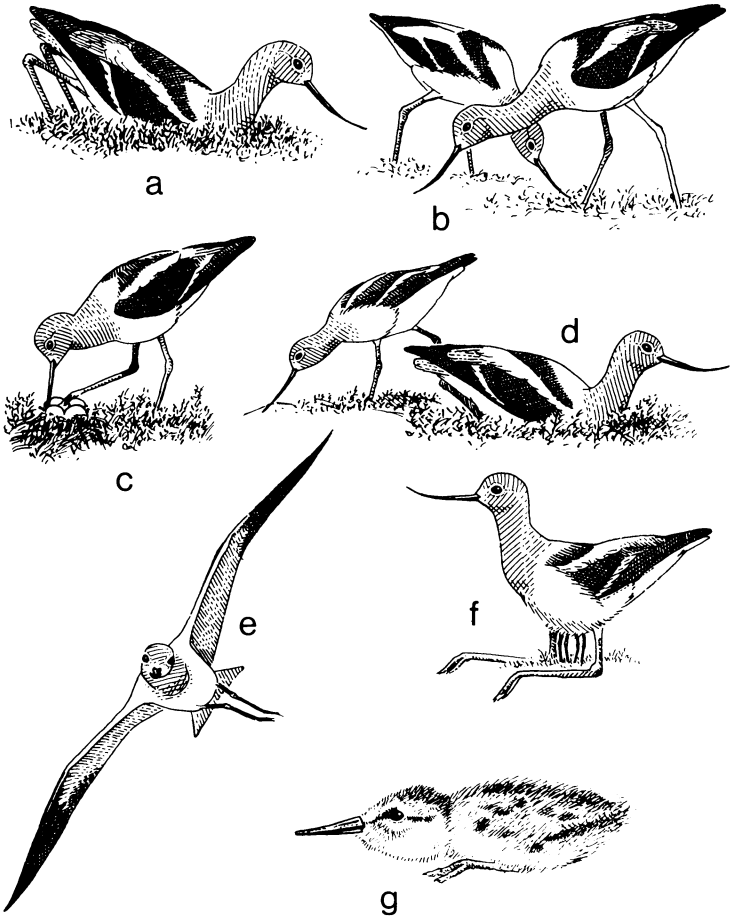

FIGURE 10. Nest-building and nesting behavior: (a) scraping nest cup; (b) pair Ground Checking; (c) Touching Eggs; (d) l. to r., Tossing Straws and incubation; (e) Dive-bombing; (f) brooding; (g) chick Crouching.

When birds rest on land, they often employ another method of resting, in which they sit on the ground with both legs tucked under their breasts. Birds sometimes rest on either one leg or on both legs while on land, but resting on the ground is more common. Avocets are especially likely to rest on the ground if the wind is strong and if there is a nearby object which can serve as a windbreak.

Occasionally, avocets have been observed resting on their tarsometatarsi (Figure 10f). This posture is also regularly observed in brooding birds and is one of the first resting methods employed by recurvirostrid chicks.

Sleeping or resting is often an activity with social significance; I have

often seen hundreds of avocets resting together in winter or during migration. After feeding, non-breeding avocets will usually join a flock of resting birds to preen and rest.

Himantopus himantopus mexicanus

Stilts, like avocets, also frequently rest—but not for as great a percentage of their time as avocets. The smaller size of the stilt, together with its probable higher metabolism, results in the need for a stilt to spend relatively more time feeding than the larger avocet.

The following data were used to compare the tendency of avocets and stilts to rest on land. To eliminate the social factor, no count was made of individuals within flocks. Therefore, a resting individual and a resting flock were each considered as one observation. Locations and numbers of observations of resting birds are as follows. Avocet: land, 97, water, 70, ?, 123. Stilt: land, 42, water, 6, ?, 34. The "?" category represents observations in which the resting location was not noted precisely. Of the observations of avocets, 42.4 percent were "?"; 41.5 percent of the stilt observations were "?". This indicates that my method of recording was not biased toward either species. The "land" and "water" columns were then analyzed by a χ^2 test and a value of 12.85 was obtained. This has a probability of occurrence of $< .001$ and indicates that stilts have a greater tendency to rest on land than do avocets—an occurrence which is to be expected because of the more extensive aquatic adaptations possessed by the avocet.

The number of observations of individuals or flocks which were resting while sitting or while on one leg are shown below. (Resting on two legs was a rare occurrence and was therefore not analyzed.) Avocet: sitting, 13, one leg, 24. Stilt: sitting, 16, one leg, 10. Analysis of the above data by χ^2 gives a value of 3.29 ($.025 < p < .05$). These results indicate that stilts are more likely to rest while sitting than are avocets. This is to be expected since resting while sitting always occurs on land, and stilts are primarily land resters. Both avocets and stilts generally rest in groups. Some social aspects of resting where the average number of birds in a resting flock is known are presented below. Avocet: land, 71.2, water, 35.9. Stilt: land, 2.3, water, 43.8. Analysis by χ^2 gives a value of 46.4 ($p < .001$), which indicates that avocets and stilts differ in flock sizes on land and in water, with avocets tending to have larger flocks on land and stilts having larger flocks in water. My data on resting stilts is minimal because most observations were made during the breeding season, a time when they were disturbed considerably by my presence. Furthermore, most of the stilts' resting time during breeding season was probably spent incubating or brooding.

TABLE 18
ACTIVITIES ASSOCIATED WITH RESTING

Activity	Disturbed				Not Disturbed			
	Avocet		Stilt		Avocet		Stilt	
	Prox.	Ult.	Prox.	Ult.	Prox.	Ult.	Prox.	Ult.
Preceded by								
Feeding	763	726	26	56	1416	1390	219	216
Preening	8	8	–	–	229	235	9	11
Flying	19	–	30	–	26	3	6	3
Hop and Flap	17	35	5	5	2	6	–	–
Two-Wing Stretch	26	34	2	2	1	1	–	1
Unknown	–	1	–	–	3	24	–	6
Interaction	–	1	–	–	6	6	7	2
Resting	–	18	–	–	–	–	–	1
Wing and Leg Stretch	1	3	1	1	–	2	5	5
Scratching	–	4	–	–	2	3	1	3
Yawning	3	6	–	–	–	–	–	–
Bathing	–	–	–	–	–	9	–	–
Feathers Ruffled	1	1	–	–	–	5	–	1
Drinking	–	1	–	–	2	3	–	–
Defecation	–	–	–	–	–	–	1	–
Precopulatory Display	–	–	–	–	–	–	1	–
TOTALS	838	838	64	64	1687	1687	249	249
Followed by								
Feeding	136	217	–	–	1594	1597	201	202
Flying	543	1	34	–	43	14	37	–
Unknown	–	396	–	31	1	19	–	36
Two Wing Stretch	98	122	24	23	10	12	5	5
Hop and Flap	32	40	5	5	5	5	1	1
Preening	13	15	–	–	24	30	–	–
Resting	–	18	–	–	–	–	–	1
Interaction	–	–	1	3	7	4	–	1
Wing and Leg Stretch	4	6	–	1	–	–	2	1
Yawning	6	8	–	–	–	–	–	–
Scratching	–	4	–	–	3	4	1	1
Feathers Ruffled	4	5	–	–	–	1	–	–
Drinking	1	6	–	–	–	1	–	–
Bathing	–	–	–	1	–	–	1	1
Distraction Display	1	–	–	–	–	–	–	–
Defecation	–	–	–	–	–	–	1	–
TOTALS	838	838	64	64	1687	1687	249	249

Flock sizes of stilts were never as large as those of avocets, but neither were stilt populations at my study area as great. Interspecific flocks of resting avocets and stilts were often observed, but in these flocks there was still the tendency for conspecifics to associate. Other species were also occasionally observed in these resting flocks of mixed species.

Activities associated with resting are given in Table 18. These activities

TABLE 19
ACTIVITIES ASSOCIATED WITH DRINKING

Activity	Disturbed				Not Disturbed			
	Avocet		Stilt		Avocet		Stilt	
	Prox.	Ult.	Prox.	Ult.	Prox.	Ult.	Prox.	Ult.
Preceded by								
Feeding	–	–	–	–	9	10	–	–
Resting	1	6	–	–	–	1	–	–
Hop and Flap	2	–	–	–	–	–	–	–
Two-Wing Stretch	2	–	–	–	–	–	–	–
Copulation	–	–	–	–	–	2	–	–
Interaction	–	–	–	–	1	–	–	–
Wing and Leg Stretch	1	–	–	–	–	–	–	–
Postcopulatory Display	–	–	–	–	1	–	–	–
Feathers Ruffled	–	–	–	–	1	–	–	–
Scratching	–	–	–	–	1	–	–	–
TOTALS	6	6	–	–	13	13	–	–
Followed by								
Feeding	5	5	–	–	7	7	–	–
Resting	–	1	–	–	2	3	–	–
Preening	1	–	–	–	1	1	–	–
Unknown	–	–	–	–	1	1	–	–
Bathing	–	–	–	–	1	–	–	–
Two-Wing Stretch	–	–	–	–	1	–	–	–
Flying	–	–	–	–	–	1	–	–
TOTALS	6	6	–	–	13	13	–	–

are primarily comfort movements (exclusive of resting), with preening and stretching especially prominent. Those observations on resting which are associated with interacting are examples of displacement sleeping.

Possibly recurvirostrids may dream while sleeping. I have observed recurvirostrids moving their bills rapidly, as when swallowing, when the bills were under their wings and their eyes were closed. Calling has also been observed being performed by birds which appeared to be sleeping.

Drinking.—When drinking, a bird lowers its head and neck as when feeding, but drinking movements are slower and more deliberate than feeding movements. When the bill is just above the water surface, it is placed into the water by movement of the entire body, which is accomplished by bending the ankle joint. The neck and body are then raised with the neck bent somewhat and the head resting along the axis of the back, but with the body angled so that the bill is higher than the back. Because of gravitational influence, water then flows into the mouth where it is swallowed. The entire act of drinking is effected in about three to five seconds (Figure 8c and d).

Avocets were occasionally seen drinking, but never stilts. Makkink (1936) did not record drinking in the European Avocet. On two occasions, I observed stilts making what looked like drinking movements, but their bills were not touching water. These were probably displacement drinking movements and may indicate that stilts do drink occasionally. Avocets usually drank salt or brackish water. Both avocets and stilts have well-developed nasal glands which should enable them to drink salt water profitably.

Table 19 depicts the activities that are associated with drinking. As with many of the comfort movements, drinking is closely associated with feeding and resting. On only two occasions was drinking not ultimately preceded by feeding or resting. On both of these occasions, drinking was preceded by copulation. In both cases, the female drank after the post-copulatory display. Once, the feathers were ruffled before the bird drank. Resting birds, when disturbed, occasionally drank. Frequently, drinking in these cases was preceded by other comfort movements, such as the Two-wing Stretch, Hop and Flap, or the Wing and Leg Stretch. Disturbed birds then usually commenced feeding; one bird preened and resumed resting. Undisturbed birds frequently resumed feeding after drinking. Several birds preened or rested. On one occasion, drinking was preceded proximately by interaction with a Killdeer (*Charadrius vociferus*). The avocet supplanted the Killdeer and then made one drinking movement. It is possible that drinking in this case might have been a displacement activity.

Of the 19 birds that were observed drinking, five made more than one drinking movement. The following tabulation shows the number of drinking movements in each bout: 1 (14 observations), 2 (3), 3 (1), 4 (1).

There sometimes seemed to be social significance to drinking. The number of birds drinking together is as follows: 1 (10 obs.), 2 (2), 5 (1). In these cases, a bird would drink; then a neighbor would drink; then perhaps the first bird would drink again. Once, five birds were drinking almost simultaneously. These birds had been resting and were disturbed by the rising tide. Since drinking occurred so infrequently, it seems unlikely that chance could account for five birds drinking almost simultaneously.

Feeding.—Because of morphological differences, avocets and stilts differ considerably in their methods of obtaining food. At my study area both species feed extensively during the winter on brine shrimp (*Artemia salina*), which are abundant in the salt evaporation ponds. Occasionally, avocets will feed at the San Francisco Bay mud flats—usually near the water's edge (sometimes several hundred meters from shore)—or on the exposed mud of adjacent salt marshes; stilts occasionally feed in the salt marshes but were never observed feeding on mud flats except close to shore. Avocets also

concentrate on the mud flats of the northern part of San Francisco Bay. The salt ponds of my study area constitute the northern extent of the winter range of stilts. When feeding in salt ponds, both species feed visually by pecking at brine shrimp that appear near the surface. Avocets have a larger area in which to feed since they often swim in parts of the ponds too deep for wading stilts. Other shorebirds, such as Willets (*Catoptrophorus semipalmatus*), Greater Yellowlegs (*Tringa flavipes*), Dunlins (*Calidris alpina*), Western Sandpipers (*Calidris mauri*), Northern Phalaropes (*Lobipes lobatus*), and Bonaparte's Gulls (*Larus philadelphia*), also feed on the abundant brine shrimp of the salt evaporation ponds. During breeding season, in addition to the numerous brine shrimp which are still available in the salt ponds, innumerable brine flies (*Ephedra* sp.) are also available as food. These flies often are so numerous that they actually darken the surface of any exposed mud. Fisher (1902: 9) reported avocets eating brine flies and their larva; Tyler (1913: 16) maintains that brine flies may be a staple of the avocet's diet during breeding season. I have observed both avocets and stilts feeding extensively on brine flies.

Avocets are especially versatile feeders; however, both species exhibit a variety of feeding methods, which are described below.

Pecking.—Pecking is the primary method used by birds which are feeding visually. It is commonly performed by both species and consists of a bird seemingly searching visually for prey while standing immobile or while walking slowly, taking one step at a time. Sighted objects are grabbed quickly with a jab of the bill; prey items may be captured either on mud or near the water's surface. Postures used vary widely but are characterized by the bird's seeming altertness and an occasional movement of the head, as if to investigate visually some potential prey. The head is not immersed as a result of the prey-capturing movement. A "typical" Pecking posture is illustrated in Figure 9c. Stilts often capture terrestrial insects (McAtee 1906; Wetmore 1925: 17–19; Danforth 1929: 364; Abbott 1931); they often use Pecking to accomplish this.

Plunging.—Another method employed by visually feeding avocets and stilts is Plunging. Plunging differs from Pecking in that the head and sometimes the neck and upper breast enter the water, whereas in Pecking only the bill (or part of the bill) enters the water. Plunging is often performed in water of greater depth than is Pecking, and it is never performed on mud; the bill never appears to reach the bottom, however. The bill of a Plunging bird is moved directly toward the prey object with no sidewise component.

The distinction between Pecking and Plunging is arbitrary. Plunging is probably merely the reaching for prey at greater depths beneath the surface than Pecking. I have considered Plunging a separate category because the

bill becomes indiscernible as the bird performs a Plunging movement, and I could not always be certain if the same movements observed in Pecking were performed in Plunging. Furthermore, a Plunging bird obtains food from a deeper layer, a factor which may be important in niche splitting between sexes or species.

Snatching.—Snatching is another method of visual feeding which is employed by both species. This method simply involves catching a flying insect with the bill. Birds were never observed to use this method exclusively. Rather, it was employed as the opportunity presented itself in conjunction with other feeding methods or even used occasionally while the birds were performing other activities. Once prey had been sighted, a bird would pursue a flying insect either by running a short distance after it or by fluttering toward it.

Bill Pursuit.—Even though only rarely observed, Bill Pursuit is a method of visual feeding employed by avocets. This feeding pattern was never observed in stilts, but I will not discount the possibility that stilts may occasionally use it. An avocet employing Bill Pursuit rapidly opens and closes its bill (to a maximum extent of about one centimeter), while simultaneously moving it erratically along the water's surface. It appears that the bill is being used to pluck from the water some rapidly moving aquatic organism; however, I never observed an object large enough to be seen captured by this method.

Filtering.—Filtering appears to be a tactile method of feeding, and like other tactile methods, it was not observed being performed by stilts. Filtering is much like Bill Pursuit, which is performed in shallow water, except that Filtering is performed on mud flats containing approximately one centimeter of water in shallow pools. The bill of a Filtering bird is opened and closed rapidly (to a maximum extent of about one centimeter), while it is simultaneously moved (apparently at random) over the mud for a duration of 3 to 5 seconds. The feeding bird then raises its head and neck several inches and swallows (Figure 9d).

Scraping.—Scraping is another tactile method performed on mud flats by avocets. In this method, the recurved tip of the lower mandible is placed on the mud directly in front of the avocet and is moved 5 to 20 cm forward in an anterior-posterior plane by extending the neck. After completion of each feeding movement, the bird raises its head and swallowing often occurs.

Single Scythe.—Single Scythe is a strictly tactile feeding method that is used either on mud or in the water and is the most common feeding method employed by avocets on mud flats; it is also commonly performed in water.

I did not observe stilts using the Single Scythe method of feeding, although Richard L. Zusi (pers. comm.) stated in 1969 that he has a film record of this movement being performed by stilts. (He also maintains that Lesser Yellowlegs often perform the Single Scythe movement. Urner [1933] also reported Lesser Yellowlegs "sideswiping.") A bird performing the Single Scythe progresses one step at a time, pausing after each step. The bill and neck are normally held in line with the back, and the back is held at a slight angle (5 to 10 degrees) below the horizontal (Figure 9e and f). As the bird pauses between steps, it places the recurved tip of the bill flat on the substrate to one side of the midline and immediately moves the bill tip very rapidly to the opposite side of the body (a distance of perhaps 25 cm) with the distal part of the bill scraping the bottom. The bill is opened less than one centimeter during the Single Scythe movement. After a Single Scythe, the head and bill are raised, at which time swallowing frequently occurs. Then the bird takes another step, and the process is repeated on the other side. Normally, the Single Scythe movement is started on the side opposite the lead foot of the feeding bird, which alternately walks and pauses.

Multiple Scythe.—Multiple Scythe feeding movements are similar to Single Scythe feeding movements except the bill is not raised after each movement but instead is returned to the other side and perhaps back again without pause (always in contact with the substrate). The first scythe movement of the Multiple Scythe was always the most extensive; subsequent movements always traversed shorter distances. Multiple Scythe feeding movements were performed only rarely by avocets.

Dabble Scythe.—The Dabble Scythe movement is performed in deep water (water too deep for wading) and, with that exception, the bill movement is identical to the Single Scythe movement. The feeding bird immerses its head and breast into the water by tipping on the transverse axis from a swimming or breast-wading position and brings the bill to the bottom. The upended position of the bird is maintained by a backward kick of the feet; the tibiotarsi often break the surface during the Dabble Scythe movement. This feeding method is termed the Dabble Scythe because of the resemblance of a bird performing it to the dabbling of ducks (e.g., *Anas platyrhynchos*). Ross (1924) reported avocets feeding by this method.

Urner (1933) and Black (1941) reported that avocets probe into the mud. I did not observe this behavior. Furthermore, I do not believe that the thin, flexible bill tip of the avocets, often with a small hook at the tip, would be suitable for such probing.

Niche diversification.—Since avocets and stilts often occur in the same habitats and feed in the same areas, how is the available food partitioned?

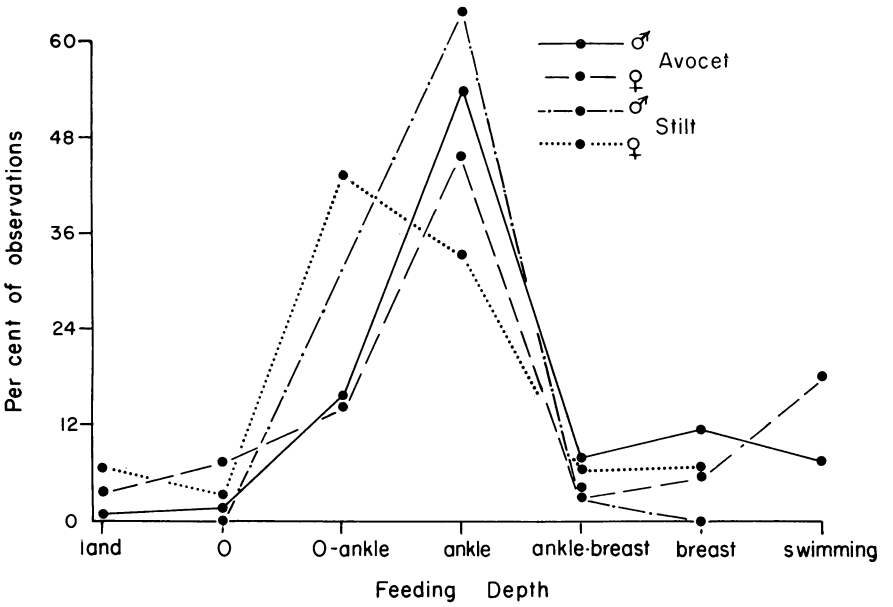

FIGURE 11. Approximate feeding depth of avocets and stilts at White Lake, Siskiyou County, California. Depth increases from left to right. (Anatomical landmarks were used to estimate depth. Thus, "O-ankle" is water that reaches between the feet and the ankle of the feeding bird.)

In addition, are there behavioral adaptations that would allow differential niche utilization of the sexes? (See Selander, 1966.)

Food seemed to be superabundant on my study area; therefore, competition and methods to avoid competition were difficult to study. During the breeding season, when the chicks had hatched and the food supply theoretically should have been more critical, both avocets and stilts often fed in marshes, where it was very difficult to make feeding observations. Furthermore, my study area was not a "natural" one, since it consisted of man-made salt-evaporation ponds with "superabundant" food. In order to gain information on the feeding behavior and ecology of the avocet and stilt in a more natural setting, I visited White Lake in Siskiyou County, California, 21–26 June 1968, where both species breed. This is a fresh-water lake with numerous small grass- and sedge-covered islands which are used for nest sites. The lake itself is surrounded by grass and sedge vegetation and contained extensive mats of algae. In addition to avocets and stilts, Wilson's Phalaropes (*Steganopus tricolor*), Canada Geese (*Branta canadensis*), Western Grebes (*Aechmophorus occidentalis*), and several species of ducks also breed at the lake. There did not appear to be any brine shrimp in the water,

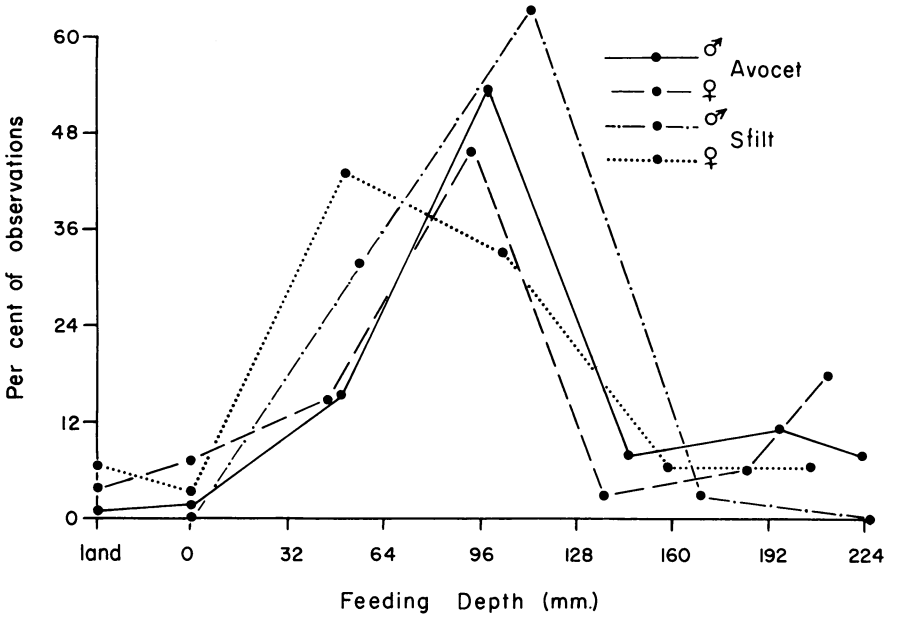

FIGURE 12. Approximate depth of water, in millimeters, at which avocets and stilts feed in White Lake, Siskiyou County, California.

and there seemed to be much less available food than at the San Francisco Bay salt ponds. In other words, this location appeared to be suitable for determining if there are indeed behavioral differences between the sexes and between the species that would allow the niches of each subgroup to be diversified and therefore result in higher populations of animals.

One possible way for different classes (such as sexes or species) to divide a niche is for each to feed in a different area. Figure 11 shows the results of data I gathered at White Lake as to feeding locations of avocets and stilts. I used anatomical landmarks of the wading birds to record the depth of water in which they were feeding; consequently, Figure 11 is slightly misleading because of differences in leg measurements between the sexes and between the species. Therefore, Figure 12 was prepared to demonstrate accurately the depth of water in which birds were feeding (taking into account differences in leg measurement). This modification of Figure 11 immediately separates the species, because the longer legs of male stilts enable them to feed in somewhat deeper water than avocets. Stilt females displayed a tendency to feed in shallower water than did stilt males or avocets. In order to determine the significance of these results, I tested some of them statistically using the χ^2 test.

The following data show the number of observations of birds feeding in

"ankle"-deep water or at other depths: here ankle deep means water which is approximately at the depth of the birds' ankles (joint between tibiotarsus and tarsometatarsus).

	Avocet		Stilt	
	♂	♀	♂	♀
"Ankle"	72	37	16	10
Other	62	44	9	20

These data yield a χ^2 of 3.99 ($.02 < p < .05$) for stilts, which indicate that male stilts do have a greater tendency to feed in "ankle"-deep water than female stilts. Therefore, we already see one mechanism for niche splitting (i.e., feeding at different water depths). The above data yield a χ^2 of 1.00 ($p > .30$) for avocets, which indicate that the avocet sexes show no difference in the tendency to feed in "ankle"-deep water.

Figure 11 indicates that the stilt sexes may differ in their tendency to feed in water less than ankle deep. The pertinent data are as follows:

	♂	♀
Less than ankle deep	8	13
Other	17	17

These data yield a χ^2 of 0.34 ($p > .50$), which do not support the hypothesis of a sexual difference in the tendency to feed in water "less than ankle" deep.

Since male stilts do have a greater tendency to feed in "ankle" deep water than females, do male stilts then have a greater tendency to feed in "ankle" deep water than avocets? The pertinent data are presented below:

	Avocet	♂ Stilt
"Ankle"	109	16
Other	106	9

These data yield a χ^2 of 1.10 ($p > .10$ for the one-tailed test), which indicate that there is no greater tendency for male stilts to feed in "ankle"-deep water than for avocets. However, the longer legs of male stilts enable them to feed in deeper water than avocets, although both concentrate their feeding activities in water that is "ankle" deep.

Figure 11 indicates also that there may be a greater tendency for female stilts to feed "less than ankle" deep than for avocets. The following data are useful in indicating that female stilts do have a greater tendency than avocets to feed in water less than ankle deep:

	Avocet	♀ Stilt
Less than ankle deep	33	13
Other	182	17

Analysis of these data reveals a χ^2 of 122 ($p < .0005$ for the one-tailed test).

In summary, stilts split their niche by feeding in slightly different depths of water, but avocets did not show the tendency to feed at different depths. Stilts differed from avocets with regard to feeding depths because of the tendency of female stilts to feed in water less than ankle deep, which is more shallow than that normally used by avocets. Male stilts primarily feed in water ankle deep, as do avocets, but male stilts' longer legs enable them to feed in deeper water.

Niches can be split in other ways than by dividing the feeding depth; e.g., the different sexes or species may use different feeding methods. The only feeding methods observed being performed by avocets and stilts at White Lake were Pecking and Plunging. The number of observations are as follows:

	Avocet			Stilt		
	♂	♀	Total	♂	♀	Total
Pecking	211	135	346	42	165	207
Plunging	377	158	535	8	12	20

The stilt sex data yield a χ^2 of 3.06 ($.10 > p > .05$), which is not significant; but the stilt's niche is already divided to a degree by the sexes feeding at different depths. The avocet sex data from the above table yield a χ^2 of 8.10 ($.01 > p > .001$), which indicates that male avocets have a significantly greater tendency to use the plunging feeding method than female avocets. This then is one way that avocets divide their niche.

In order to determine if avocets use feeding methods different from those of stilts, the above data were analyzed by species. The pertinent data yield a χ^2 of 192 ($p < .001$), which indicate that avocets have a much greater tendency to perform plunging movements than stilts. As a result, the two species possess different niches which allow resources to be divided between them with less competition. The longer bill of the avocet probably serves to accentuate the differences found in feeding methods.

Therefore, both avocets and stilts do have behavioral differences which allow the food sources of the environment to be divided between the sexes and between the species with a lessening of competition. Stilts divide resources between the sexes by feeding at different water depths (this niche division is accentuated by the dimorphic leg length of stilts); avocets divide resources between the sexes by using different feeding methods (which again is accentuated by sexual dimorphism—this time, bill length). Competition is reduced between the species because stilts feed at different water depths than avocets, and avocets feed deeper below the surface than stilts. This interspecific niche splitting is also accentuated by morphological dif-

ferences since avocets, which feed deeper below the surface, have longer bills than stilts; male stilts feed in deeper water than avocets because of the male stilt's relatively longer legs.

There are, of course, many other competitors for food resources than those discussed above. I have made no attempt to analyze precisely the mechanisms that allow avocets and stilts to co-exist with this competition. Incidental observations indicate, however, that the long legs of both species enable them to feed in somewhat deeper water than many of their avian competitors. Avocets' and stilts' long bills also enable them to feed deeper below the surface than such deep-water competitors as phalaropes or gulls. Normally, no other vertebrate species were observed feeding in close proximity to avocets and stilts.

LOCOMOTION

Flight.—Flight is one of the ways in which avocets and stilts differ the most markedly, a circumstance which correlates with one of the most striking morphological differences between avocets and stilts—wing length. The sample means of specimens that I have measured indicate that stilts have relatively longer wings than avocets. The results are as follows:

	Avocet		Stilt	
	♂	♀	♂	♀
Wing (chord)	224.55	224.56	225.06	214.67
Weight^{-3}	6.8	6.7	5.7	5.5
Wing/Weight^{-3}	33.0	33.3	39.7	39.1

Thus, the stilt wing (chord) is relatively longer (approximately $39/33 \approx 1.2$ times) than the avocet wing. The avocet shows no sexual dimorphism of wing length, and all the sexual dimorphism of stilt wings corresponds with the larger size of male stilts.

Even though neither species can be considered a long-distance migrant, Figures 2 and 3 indicate that the avocet travels farther than does the stilt. Consequently, one would expect the avocet to have relatively longer and more pointed wings than the stilt (Averill 1920: 578; Meinertzhagen 1951: 82–83), but the reverse is true. Further, the relatively larger size of the avocet, with its corresponding decrease of relative surface, suggests that the avocet should have relatively longer wings. Stilts have a variety of clearly delineated flight types, whereas avocets basically have only one. The relatively long wings of stilts may be due to the fact that several displays involve hovering, in which long, pointed (hummingbird-like) wings are probably important.

Even in normal flight, avocets and stilts assume different postures. Both birds fly with their legs trailing straight behind, but the neck of each species

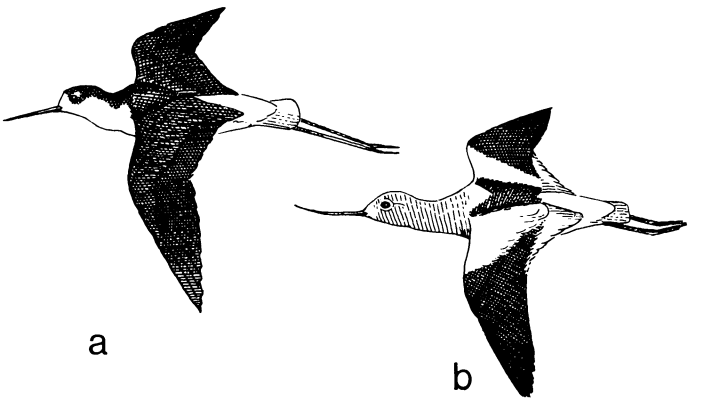

FIGURE 13. Normal flight postures of (a) the stilt and (b) the avocet.

is held in a distinctive manner (Figure 13). Basically, avocets fly with their necks extended in a manner similar to that of cranes (but not as extreme), whereas stilts fold their necks slightly in a manner somewhat analogous to that of herons (but not as extreme). These differences in neck position may be due to variations in wing shape or to variations in relative size of extremities; the neck position may be important in keeping the center of gravity under the wings. Despite the fact that differences in neck posture during flight are obvious though subtle, to my knowledge this has never been reported in the literature.

In the normal flights of avocets and stilts, the legs are brought up to the flight position soon after take-off and are lowered just before the bird alights. In some types of display flights of stilts, the legs are dangled. Occasionally, immediately after my arrival at the study area, I would see birds flying with only one leg trailing (the other leg was held flexed next to the abdomen); I believe this was due to birds taking to the air from the one-leg resting position after being disturbed by my presence. Birds flying with the one leg trailing always landed on that leg; then they generally Hopped and Flapped several times, after which the other leg would frequently be lowered. I contend that this behavior results from the birds' inability to lower the flexed leg rapidly or easily from the resting position. Once, a stilt was observed flying with neither leg extended. This, too, occurred immediately after my arrival and was, I believe, due to my disturbing a bird which had been resting while sitting; the bird had probably taken off before extending either leg. Before alighting, this legless-appearing bird hovered for about 20 seconds, seemingly trying to lower its legs, and finally alighted very clumsily with its legs still in a flexed position. Im-

mediately after alighting, it straightened its legs while staggering to the standing position.

Avocets and stilts usually flap their wings continuously during normal flight with a wing-beat of approximately 43.5 beats/minute for avocets and 40.8 beats/minute for stilts ($t = 2.73$, $p > .20$); gliding does sometimes occur. The body of each species is held at an angle of about 5 degrees above the horizontal during level flight, and the wings of both species traverse arcs of about 90 degrees (each wing moves from 60 to 150 degrees from the vertical). When gliding, the wings are held approximately horizontal.

At times other than during the breeding season, both species frequently fly in flocks (the largest flock observed numbered about 5,000 avocets); rapid changes of direction with complicated maneuvers are common in these recurvirostrid flocks, as in many shorebirds.

As is true of other birds, avocets and stilts both take off and alight into the wind. As birds at my study area were rather inactive on 2 and 4 March 1966, I concentrated entirely on the directions of their taking off and landing for a total period of 2½ hours. Wind varied from about 5 to 20 knots during this period. The following tabulation shows the number of birds taking off and alighting into the wind. (No bird was observed not taking off or alighting into the wind.)

	Avocets		Stilts		Other Shorebirds	
Taking off	4	$p = .004$	10	$p << .001$	81	$p << .001$
Alighting	5	$p = .001$	15	$p << .001$	65	$p << .001$

The above probabilities are based on the assumption that I could correctly estimate if birds were taking off or alighting into the wind within 45 degrees in either direction. (I am confident that my error was considerably less than 45 degrees.) Thus, the probability of a bird taking off or landing into the wind was 90 degrees/360 degrees = .25. Using this figure, probabilities in the above tabulation were obtained.

When taking off, both species customarily use their legs to obtain the necessary spring. A "typical" posture is shown in Figure 14a.

When alighting, both species increase the angle of their backs above the horizontal slightly before touching down. This puts the birds into a stall, thus causing them to drop lightly to earth. Avocets show no hesitancy in alighting in water; stilts tend to alight on land. If alighting in water, stilts (instead of stalling as described above) hover with their legs dangling and lower themselves gingerly into the water. I have not observed stilts, which hesitate to swim, alight in water too deep for wading; but avocets, which are proficient swimmers, often land in deep water.

As noted, avocets use only the normal type of flight, which they some-

times modify slightly; they do not seem to possess any specialized display flights. Stilts, however, have at least four types of display flights; in three of these displays, the birds dangle their brightly colored red legs. Display flights of stilts mainly consist of exaggerated wing-flapping with very slow progress. In fact, stilts are able to hover and even to fly diagonally sidewise or backwards.

The most conspicuous display flight of stilts occurs occasionally in late winter. It involves hovering 5 to 10 meters in the air. The bird then sometimes lowers itself to near the surface of the water but immediately returns to the original height. Frequently, the displaying bird flies very slowly a distance of 10 to 25 m and hovers at another location. This up-and-down movement and slow flight of the display reminded me of the flight of a butterfly, and I termed this display the Butterfly Flight. The displaying bird flies with its neck somewhat more contracted than in normal flight; the tail is spread; and the long red legs are dangled. The body of the displaying bird is held at an angle of about 45 degrees above the horizontal. When hovering, the angle of the body is increased. A "typical" Butterfly Flight posture is shown in Figure 14f.

The function of the Butterfly Flight was not determined. However, the form of the display, which resembles territorial flights of other birds, suggests that it has a territorial function—an hypothesis which is supported by the conspicuous position of the red legs.

Other types of specialized stilt flights are discussed in subsequent sections (see pp. 64, 68, and 90).

Walking, Running, and Wading.—Most of the locomotion of both species occurs on the ground or in the water where the birds walk, run, or wade. Walking or wading is the usual locomotive pattern for moving short distances. Running was normally observed during interactions. The legs are moved alternately when walking, running, or wading. The exact postures used are determined by the other activities which are simultaneously being performed.

Forms of movement are basically similar in the two species, but the steps taken are longer in the longer-legged stilt.

Swimming.—Figure 14b shows the "typical" posture of a swimming avocet. When swimming, a bird holds its breast low in the water; the tail is held high; and the head is nodded almost imperceptibly. Urner (1933) commented on the "stern high" posture, saying that it was distinctive. Makkink (1936: 6) reported that the European Avocet "swims gracefully without conspicuous head movement." During my study, I accumulated about 1,700 records of adult avocets swimming; but I only observed an adult stilt swimming once (a stilt, in an attempt to land on

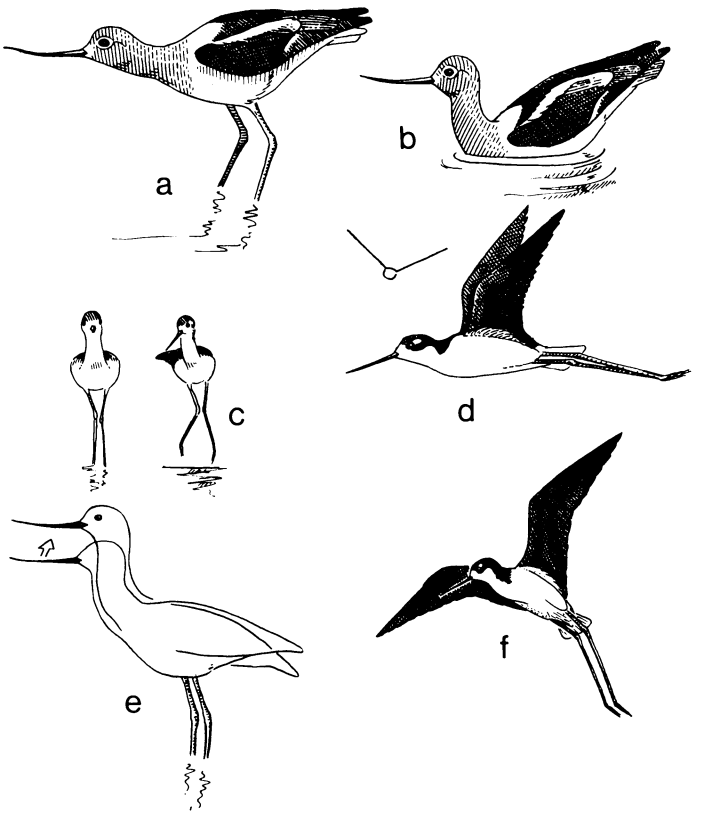

FIGURE 14. Miscellaneous behavioral patterns: (a) taking off; (b) swimming; (c) interspecific interaction; (d) Dihedral Wing Flight; (e) Head Bobbing; (f) Butterfly Flight.

a floating plank, missed the plank and landed in the water instead, after which it swam to the plank—a distance of about 30 cm—and struggled onto it).

Mortimer (1890: 338) described a wounded stilt swimming rather clumsily across a river, but he stated that ordinarily stilts probably never swim. Bent (1927: 52) maintains that stilts can swim and dive if necessary but that they are very awkward performing these activities. Cahn (1922: 175) reported a stilt landing in water and swimming away.

The avocet, with its webbed toes, is well adapted for swimming. The toes of stilts are only slightly webbed; moreover, their extremely long legs make efficient swimming very difficult. Most birds which swim have moderately short legs; the avocet has relatively long legs for a bird which routinely swims.

On the other hand, the young of both species regularly swim; I often observed avocet and stilt chicks swim away from shore as I approached. Their legs are a suitable length for swimming, and the feet of chicks (being relatively much larger than the feet of adults) are effective as paddles. Sumner (1931) reported a young stilt (approximately one-third grown) swimming and diving under water. When swimming under water, this stilt flapped its wings strongly and synchronously while kicking its legs; but the young stilt made little progress under water.

Feeding is the most common activity performed by swimming avocets. Occasionally, interacting birds will land in the water, and one will swim in pursuit of the other. As reported by Wolfe (1931: 56), avocets which are disturbed near the nest will sometimes land in water and swim away. Urner (1933) reported avocets returning to deep water and swimming as they were pursued by a Peregrine Falcon (*Falco peregrinus*).

SOCIAL BEHAVIOR

Intraspecific Interactions.—I have arbitrarily categorized agonistic intraspecific interactions as mild (in which no physical contact occurs between individuals) and violent (in which physical contact between individuals does occur). There are many similarities between the two, but mild interactions usually are of a shorter duration and are characterized by each participant assuming a different posture. The duration of the violent intraspecific interaction is longer, and each participant may alternately use the same posture.

The Upright posture, which is used by both species during these interactions, is characterized by the birds standing immobile with the angle of their backs about 10 degrees above the horizontal and with their necks extended and their heads raised high (Figure 15a); this posture is often held for several seconds before other postures are assumed. Frequently, when several birds are interacting, both will assume an Upright posture. As one bird approaches another, one or both birds will assume an Upright posture. This behavior does not appear to differ in detail between avocets and stilts.

During intraspecific interactions, the orientation of the bodies of interacting birds is very important to them (as well as to the observer who attempts to understand the actions of the birds). If birds face each other, this indicates aggression or a tendency to attack. Facing away (or looking away) indicates appeasement. When either facing toward or facing away, interacting birds use an Upright posture; they will frequently stand parallel to each other (approximately .5 m apart), and their heads may either be facing the same direction or opposite directions. The bodies parallel relationship between combatants is probably advantageous to both species since both commonly use their wings when fighting; this position would enable

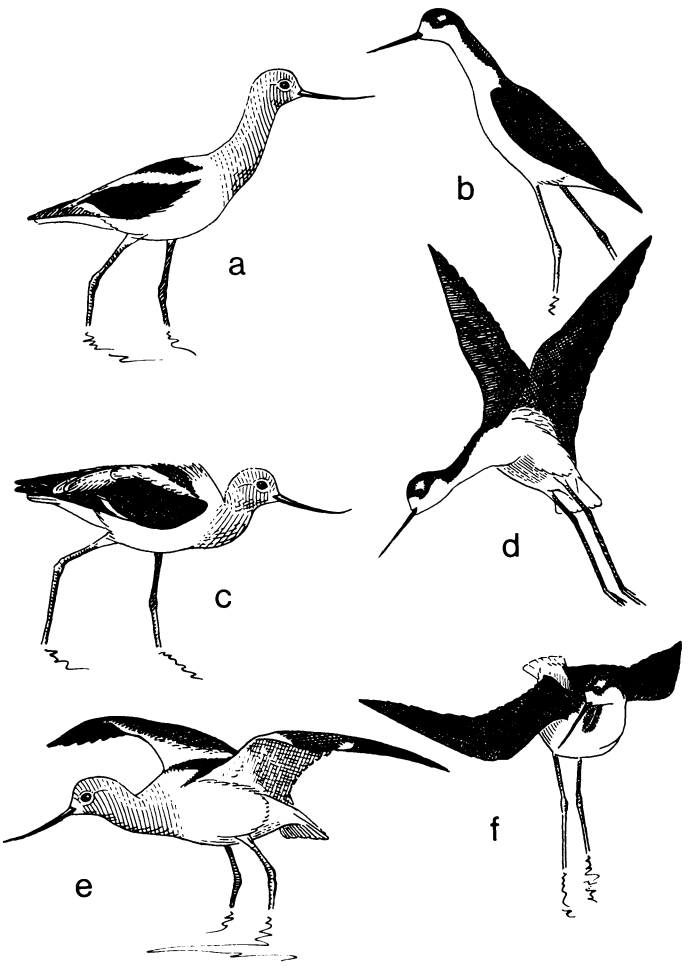

FIGURE 15. Postures used in aggressive interactions and distraction displays: (a) Upright; (b) Giraffe; (c) Crouch-Run; (d) Legs and Head Down flight; (e) Tightrope (distraction display); (f) Wing-flagging (distraction display).

either interacting individual to strike with its wings. Attack or retreat are equally possible from the bodies parallel position. The Upright posture may be modified somewhat by having the wings slightly raised from the body. (Often flank feathers cover the margins of the wings, but when birds stand with their bodies parallel, the wings will be lifted clear of these feathers.)

Mild intraspecific interactions are often concluded by one or both birds performing displacement pecking. A bird performing displacement pecking

will turn away from its opponent while making pecking movements into the water. It then walks away while continuing to make pecking movements, as if feeding.

Other postures are sometimes observed in intraspecific interactions. One that is commonly performed by stilts is the Giraffe posture. (This posture has been observed in avocets only on rare occasions.) In the Giraffe posture, the bird holds its back at a very high angle (approximately +50 degrees); the neck is extended but bent forward from the upright position. The position of the neck and back form an angle greater than 180 degrees (in an Upright posture this angle would be less than 180 degrees). The feathers are extremely sleeked, and the bird looks very slim indeed. This posture (Figure 15b) was termed Giraffe because of the performer's striking resemblance to a giraffe (*Giraffa giraffa*). Generally when a bird performs this display, it walks slowly and deliberately toward another bird, facing its opponent directly. At no time was the Giraffe posture used simultaneously by two or more interacting birds. This display appears to serve as a threat to peck the opponent and represents a likely explanation as to why the Giraffe display is performed much more frequently by stilts, with their comparatively sturdy bill, than it is by avocets. The Giraffe display was also frequently used in interspecific interactions.

Another posture sometimes used during mild intraspecific interactions is the Crouch-Run. In this posture, the neck is held retracted; the back is held at an angle below the horizontal; and the midback feathers are often ruffled (Figure 15c). This posture too is directed at another bird, and as the name implies, it is accompanied by movement toward the other bird, either by walking or by running (usually the latter). The Crouch-Run seems to be used primarily by an aggressive bird which is trying to lessen the distance between itself and an opponent. The Crouch-Run probably shows an attack tendency without indicating how the attack will occur.

As noted, mild intraspecific interactions occur while a bird is stationary or while it is running or walking on land or in water. Furthermore, mild intraspecific interactions sometimes occur in flight. Frequently, one bird will pursue another, which is also in flight, often attempting to strike the opponent with its bill.

Stilts will frequently perform an aggressive Head and Legs Down flight, in which one bird takes off and hovers .5 m or less above an opponent. In this type of flight, the neck is held extended and below the horizontal somewhat similar to the position assumed in the Two-wing Stretch (see p. 18). The legs are not brought up to the normal flight position but are left dangling (Figure 14d). On several occasions the legs were seen to touch the back of the opponent; the aggressive bird, however, did not appear to strike its opponent with its feet but rather appeared to be attempting

to land on the opponent's back. Avocets were not observed to perform the Head and Legs Down flight.

Individual distance.—Because of their social nature, both avocets and stilts regularly come within close proximity to others of their species. Warm-blooded vertebrates, generally, do not allow other individuals to approach closer than a certain minimum distance (the individual distance). On some occasions, I have watched both avocets and stilts feeding from boards which extended into deep water; individual birds were always in a linear arrangement on these boards and distance between individuals could always be easily estimated. As a rule, birds of neither species would approach closer than about .5 m to another bird. However, as feeding progressed, birds would approach closer than .5 m and thereby encroach on the individual distance of its neighbor, and an Upright posture would be assumed by both birds. One would then turn and walk away, thereby increasing the distance between individuals and terminating the interaction.

On several occasions, both avocets and stilts fed in exceptionally tight flocks with birds about .3 m from each other (thus closer than the individual distance discussed above). Few interactions occurred between birds in these tight feeding flocks; however, an occasional individual would Hop and Flap to the edge of the flock if approached too closely by a neighbor. The disturbed individual would then almost immediately rejoin the flock.

Sometimes flocks of resting birds are very compact; on several occasions I observed birds which, after entering these resting flocks, approached resting birds so closely that physical contact resulted when the resting bird moved. This contact did not seem to cause any reaction by either bird; therefore, both avocets and stilts are quite tolerant at times (other than during copulation and brooding) of a close approach.

Supplanting.—Supplanting is a form of mild intraspecific interaction in which an aggressive bird flies or runs to the position of another bird. If the non-aggressor fails to defend his position and flies or runs away, supplanting has been effected, and the relinquished position will be assumed by the supplantor. If, however, the non-aggressor does not respond and remains in the immediate area, ground pursuit by the aggressive bird (in which the Crouch-Run is used) may result. Both avocets and stilts frequently engage in supplanting interactions during late winter and early spring.

Violent intraspecific interactions.—Violent intraspecific interactions involve actual physical contact with an opponent. The wings, the bill, or the feet are used as weapons by an attacking bird. Although these interactions are sometimes prolonged, an injury was never observed to result. Violent

interactions are quite similar in many respects to mild interactions, but neither participant in a violent interaction initially shows any indications of appeasement; rather, both birds demonstrate a definite tendency to attack. The most common posture observed during violent intraspecific interactions is the Upright posture, in which the bodies of interacting birds are parallel and approximately .3 to .5 m apart. From the parallel position, one bird will often flutter at the other and will try to deliver a blow with a wing or with the feet. The attacked bird may duck or flutter out of the way. These actions persist for several minutes until one of the interacting birds turns and walks away while performing displacement pecking. The aggressive bird usually does not follow the bird performing the displacement pecking.

The position of the body during violent intraspecific interactions is very important, as each interacting bird seems to try to attain a favorable position relative to its opponent. This results in constant movement as the interacting birds circle each other in maneuvers which produce elaborate footwork, reminding one of a boxer.

The attack or escape tendency of interacting birds is demonstrated by their leaning toward or leaning away from their opponent respectively. This leaning is sometimes very exaggerated, and "typical" postures are shown in Figure 14c.

Sometimes when one bird turns and walks away while performing displacement pecking movements, the interaction will not be terminated—in which case the retreating bird is pursued by its more aggressive opponent, which frequently flies at and seems to attempt to land on the retreater's back. Sometimes violent kicks are administered by the pursuing bird in this situation, and non-aggressors have been observed to duck completely under water to avoid the blows of the landing pursuer. On one occasion, a pursuing avocet made a violent, side-sweeping motion of the head (similar to that used in feeding but more exaggerated) toward its opponent, which managed to flutter out of the way before contact was made.

Violent intraspecific interactions occur most frequently at the time of the prenuptial molt. During late winter and early spring, when intraspecific interactions are common, the majority of feeding recurvirostrids have their interscapular feathers raised, an action which seems to alleviate aggression. (Interacting birds rarely have raised scapulars.)

Territory.—Violent intraspecific interactions are those which an observer would expect to witness in territorial encounters. Most of these interactions, however, occur in winter and may be associated with pairing. Although many Violent Intraspecific Interactions were observed later in the year, I was unable to determine how many were associated with territorial

behavior. The birds observed in this study were not marked for individual recognition and consequently I could not tell whether the same birds were always involved in interactions at any particular area. On occasions when I observed one bird or a pair of birds for several hours during the breeding season, I observed that they defended an area for a portion of the time. Often, however, the area previously defended was subsequently occupied by several other pairs; the resident pair had usually, but not always, departed on these occasions. These territorial-like interactions usually occurred at feeding areas or near the young. Gibson (1971: 21–24, unpubl. Ph.D. thesis, Oregon State Univ.) in a study of color-banded avocets maintains that they are territorial but the area defended varies with the stage of the breeding cycle, as follows: (1) prior to egg-laying, territories were centered around feeding areas; (2) during incubation, secondary feeding sites were centered or established near the nests and both feeding areas were defended; (3) after the eggs hatched, the territory became chick-centered and mobile. In general, my findings support those of Gibson. My observations, however, indicate: (1) that a defended area may subsequently be occupied by other birds; (2) that there are no displays associated exclusively with territorial advertisement or defense in avocets; (3) that territories are rather small (the defended areas that I observed were approximately one to two hectares). The defended area changed during the nesting season, as pointed out by Gibson. The territorial behavior I observed can be explained by an increase in aggressiveness toward intruders by paired birds and the tendency for members of a pair to return to the same localities regularly. I do not know whether the birds always returned to the same feeding sites at my study area, but Gibson's observations indicate that the birds on his study area did.

Some avocet nests were located as close together as two m on my study area, but there were few interactions between neighboring birds. The nests were closer together on my study area than on Gibson's, and it is possible that the super-abundance of food at the salt evaporation ponds where my study was conducted increased the social tendencies of the avocets and decreased their territorial tendencies. But at White Lake, California, an area with an apparent lesser amount of available food, avocets seemed more territorial and their nests were farther apart than at the salt evaporation ponds.

Stilts, on the other hand, were more territorial than avocets. This may have been due to the smaller food supply available to them. Stilts perform several aerial displays which seem to function in territory advertisement and defense, and those birds nesting in the marshes of my study area maintained extensive territories near their nests. Stilts were noticeably more intraspecifically aggressive near their nests than were avocets.

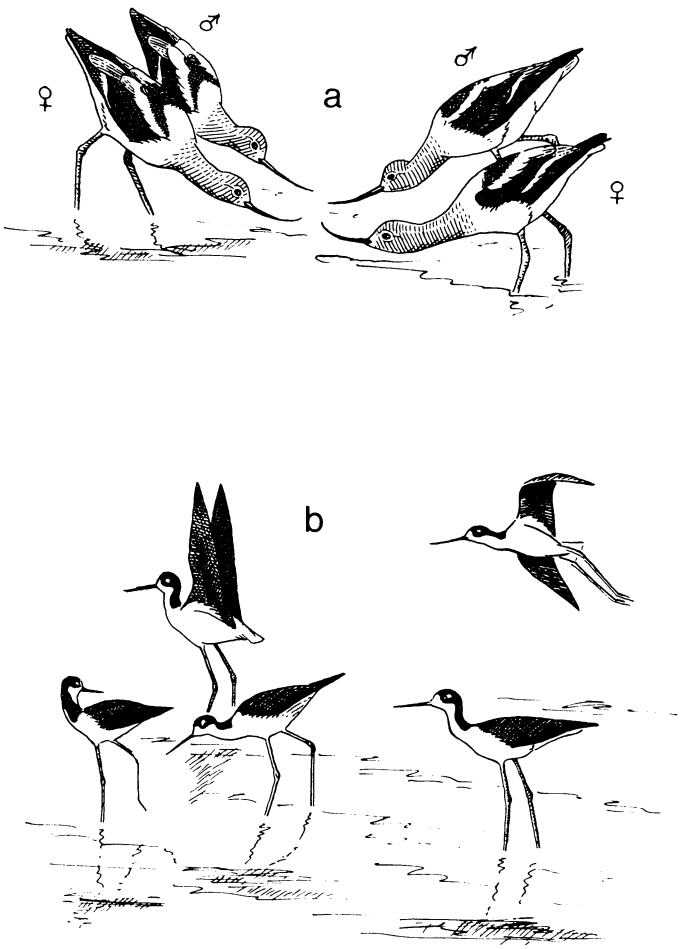

FIGURE 16. Intraspecific group interactions: (a) Group Circle display of avocets and (b) Mob display of stilts.

Intraspecific Group Interactions.—Intraspecific group interactions are those highly social activities which require for their performance more than two individuals. These interactions are somewhat ritualized and involve special postures; furthermore, these interactions seem to attract conspecifics from near and far. Once an interaction has begun, even though certain stylized movements are performed, fighting may result and eventually the group disbands and disperses. Both avocets and stilts perform group interactions, but interactions differ greatly in detail between the species.

Intraspecific group interactions of stilts occur in late winter before the

onset of the nesting season. In these interactions, three or four birds congregate in shallow water, emitting loud vocalizations (frequently many of the interacting stilts—usually females—have their interscapular feathers raised). Sounds emitted by the interacting stilts attract other nearby stilts, which run or fly to join the interacting party. During the interaction, one or more birds can often be seen flying over the interacting group, using a distinctive flight. Stilts, when performing this flight, take off; they fly to a height of about one to five m; then they fly slowly with their legs dangling over the immediate vicinity of the non-flying members of the interacting group. After about 30 seconds, the bird or birds will alight, usually near other birds which duck to avoid being hit. Frequently, when taking off and alighting, interacting stilts will fly diagonally backwards; in fact, backward flight is usual in this type of interaction. Non-flying birds do not assume any special postures but mostly remain alert with neighboring birds sometimes interacting individually as they would during mild intraspecific interactions. Postures of the participating birds in this group display are varied, but all interacting birds often seem to be facing in the same direction (Figure 16b). I call this interaction the Mob display. For no apparent reason, the Mob display appears to break up spontaneously.

Intraspecific group interactions performed by avocets are similar to those of stilts in that they, too, are accompanied by loud vocalizations which attract nearby birds. They differ in that (1) interactions occur at the time of nesting and are not observed during the winter; (2) paired birds are obviously involved; (3) no flight occurs in connection with the interactions; and (4) ritualized postures are employed on the ground.

Positions of interacting avocets are somewhat ritualized with members of the pair close together and facing other pairs. Thus, the birds form a roughly circular pattern with the heads of interacting birds facing inward. Often the group circles haltingly one way and then the other. Interacting birds hold their backs below the horizontal at an angle of about –25 degrees; the neck is somewhat extended and lower than the back, and the bill is held parallel to the water just above the surface. "Typical" postures used by avocets during an intraspecific group interaction are shown in Figure 16a. I call this interaction the Group Circle display.

After several minutes, an avocet group interaction will normally evolve to a violent intraspecific interaction between pairs; then the group disbands and disperses. Makkink (1936: 17–18) reported an apparently identical group social display which is performed by the European Avocet, which he called "grouping." Makkink maintains that incubating birds will join this type of interaction, even leaving their nests ungarded; however, I was unable to collaborate his observation.

Other Social Interactions.—There are several other types of social interactions which have not yet been thoroughly discussed. As noted, both avocets and stilts regularly rest in flocks. Birds, if feeding independently, will join a resting group after completing a feeding bout. Resting flocks of both species are often quite large, and I have observed avocet flocks consisting of about 5,000 individuals. The stilt flocks seen, on the other hand, were much smaller, but stilt populations at my study area were smaller. Sometimes interspecific resting flocks were observed, but even then birds tended to associate with members of their own species within these flocks.

Often feeding birds, especially avocets, were observed in loosely organized flocks. Occasionally these flocks were very dense and seemed to form in response to some locally superabundant organism. Sometimes feeding avocets, usually when the Single Scythe feeding method was used, tended to organize themselves into loose-feeding flocks. On these occasions birds tended to feed parallel to one another and progress in the same direction. These loose feeding flocks, which contained up to several hundred individuals, were not highly organized and remained in existence for only a few minutes before separating. Often when individual feeding avocets were observed, I noticed that they would follow another feeding avocet for a short time. It was the coalescing of these transitory groups that resulted in the large feeding groups.

Bathing frequently appears to be social, as do drinking and preening. After pairing, members of the pair generally associate almost exclusively with each other and remain together until their offspring are fully grown.

Interspecific Interactions.—Both avocets and stilts interact with other species, sometimes aggressively and sometimes non-aggressively. I have observed Wilson's Phalaropes (*Steganopus tricolor*) feeding in the vicinity of avocets. Each Wilson's Phalarope present was feeding near an avocet (as many as four phalaropes were associated with one avocet) and, in fact, seemed to be feeding on the material which avocets raised from the bottom as they fed with their customary scraping motions. Williams (1953) described the same form of commensalism between 50 avocets and 400 Wilson's Phalaropes, where each avocet was accompanied by several phalaropes. One avocet had 46 phalaropes associated with it.

The most frequent interspecific interactions observed were those between avocets and stilts. These interactions were generally not prolonged, because the smaller stilt normally retreated when confronted by the larger avocet.

Aggression was sometimes observed between avocets or stilts and other species. Small sandpipers, when feeding along the same shore as avocets and stilts, will always, if forced to pass near, pass posteriorly—an action which probably tends to alleviate aggression. Interspecific interactions were

rare and when encounters occurred, they were generally very brief. Avocets and stilts have been observed interacting with Willets, dowitchers, Lesser Yellowlegs, Greater Yellowlegs, Wilson's Phalaropes, and Northern Phalaropes.

On several occasions during late winter, prolonged interspecific encounters ensued as a result of Lesser Yellowlegs feeding in the vicinity of stilts. The yellowlegs merely retreated, however, as they were pursued by stilts. Lesser Yellowlegs in these instances seemed to serve as a supernormal releaser for aggression in stilts. Stilts would not tolerate yellowlegs nearby and would chase them for greater distances than they would any other species, even their own.

Both avocets and stilts often reacted to predators. During the non-breeding season, the general reaction would be mass flight, which was observed in response to Marsh Hawks (*Circus cyaneus*) and Red-tailed Hawks (*Buteo jamaicensis*); no reaction was observed in response to Turkey Vultures (*Cathartes aura*). During the breeding season, reactions to hawks were different; some of the breeding birds would fly to the level of the hawk and fly at it, calling excitedly. On several occasions, avocets were observed to strike Marsh Hawks with their bills.

Both species avoided man and would generally fly from the area when approached (except when performing distraction displays—see p. 90). Once several avocets were observed near a group of small boys who were throwing rocks toward them. The avocets reacted by calling excitedly, while standing near where the rocks were landing, and leaning away; the birds finally walked from the area but did not fly. Nesting birds would fly toward a man and perform distraction displays. If the young had hatched, avocets would perform Dive-bombing Displays in the direction of the intruder. Only occasional reactions toward other ground predators were witnessed (see p. 84).

There was no noticeable reaction to gulls during the non-breeding season. During the breeding season, however, reaction was marked. Generally, incubating birds will remain on the nest when a gull approaches; non-incubating birds attempt to drive gulls from the area by flying to the height of the gulls, chasing them, and calling as they would when pursing a hawk. Both avocets and stilts gave this reaction. If a gull continued to approach, which was not usual, avocets then gave a special call as they proceeded to attack it. The behavior of gulls with regard to avocets and stilts also changed during breeding season. At this time gulls could often be seen flying back and forth over the nesting dikes, seemingly in search of eggs or young; this behavior was not observed during the non-breeding season.

Sexual Interactions

Pairing.—The apparent absence of specialized pairing displays of avocets and stilts prompted Huxley (1925) to report that the European Avocet performs no courtship display. Pairing, however, does occur and seems to be the result of the intraspecific interactions discussed previously. Some authors report pairing as occurring during migration and before arrival at the breeding site (e.g., Wolfe 1931: 50; Brown 1948). Others (e.g., Brooks 1909) reported pairing at the breeding grounds. Makkink (1936: 39–41) maintains that the European Avocet pairs both during the latter part of migration and immediately after arrival at the breeding grounds. Pairing occurred in late winter at my study area, but I could not ascertain if the paired birds remained to breed or subsequently migrated to breed in another area.

Pairing seems to be the result of the persistent association of a female with a male, notwithstanding the initial rebuffing by the male. During the female's attempt to associate with the male, she is able to minimize the distance between herself and the male by assuming a non-aggressive posture, such as displacement pecking, and by not looking directly at the male. Many prolonged interactions occur during the pairing process, but finally the male no longer attacks the female, and instead freely associates with her. Thus, pairing has been accomplished. Both avocets and stilts pair in this manner.

For pairing to occur as described above, sexual dimorphism must be discernible to the interacting birds. Stilts have dimorphic plumage, which is probably an aid to pairing; I believe that the dimorphic bill shape of avocets is useful in their pairing. Of course, I cannot discount dimorphic behavior, but the only sexually dimorphic behavior I observed was related to copulation, which occurred after pairing. Both sexes acted aggressively during intraspecific interaction and, in fact, the most aggressive individual I observed was a female. Makkink (1936: 45–46) emphasized that most of the behavior of the European Avocet was not sexually dimorphic but that nevertheless the European Avocet seemed to be able to distinguish between the sexes. Makkink (*loc. cit.*) assumed that there was some dimorphism present which he was not able to detect. He argued:

> Therefore I come to the conclusion that the idea of Heinroth, according to which the birds become only aware of their sexual identity by the way of their conduct, does not hold for the Avocet and that the birds must be able to distinguish each others' sex already in the beginning of their meeting. It may be that this occurs by means of taxonomical, phonetic, mimic or other characters which are too subtile [subtle] for our discrimination.

From photographs I believe that the European Avocet, like the American Avocet, has a sexually dimorphic bill shape. Perhaps the vocalizations of

the European Avocet are sexually dimorphic, as also appears to be true of the American Avocet.

Precopulatory Displays.—Precopulatory displays occur immediately before copulation and are performed by birds which seem to be already paired. Sexual preening is a slightly ritualized preening of the breast, generally with water. A bird dips its bill into the water, raises its head high by extending the neck upward, lowers the bill, and preens its breast. Pairs of breeding birds often are observed together sexually preening for short periods of time. The other precopulatory displays are also frequently preceded by sexual preening; in fact, the precopulatory display of the male is actually an exaggerated and frenzied form of sexual preening. The female, when sexually preening, tends to extend her bill farther anteriorly to dip her bill into the water than does the male; when picking up water, the female often assumes a posture which resembles the female precopulatory posture. The sexual preening of the female thus often shifts into the female precopulatory display.

The copulation sequence is initiated when the female assumes a stylized posture, the Neck Extended posture, which consists of standing with the legs firmly planted about 5 to 10 cm apart and the feet parallel; the body is held at an angle lower than the horizontal (approximately −15 degrees) with the neck fully extended and held low over the water; and the bill is held about 2 cm above the water and parallel to it (Figure 17a). The female holds this posture until copulation has been completed or aborted. When the male moves, the female moves to maintain the proper orientation; her head is located slightly to the front and side of the male. She keeps her head and neck low over the water when moving, however.

The precopulatory display of the female influences the male to increase the intensity of his sexual preening. This preening is very stylized and is always conducted at a fixed position relative to the female; the male stands about 20 to 30 cm from the female and approximately opposite her "shoulder." Occasionally, the male will move from one side of the female to the other, always passing behind her. The female will move to maintain proper orientation or to prevent the male from passing in front of her. During the course of the precopulatory interaction, the male may pass behind the female five or more times.

The preening male holds its neck extended, with the distal part and the head bent downward as the bill preens the breast on the side facing the female (Figure 17b). I call this posture Upright Breast Preening. Water is used in sexual preening, and the bill goes to the water with increasing frequency as the interaction intensifies. The bill is shaken when it is placed in the water, and this bill dipping becomes more violent as the interaction

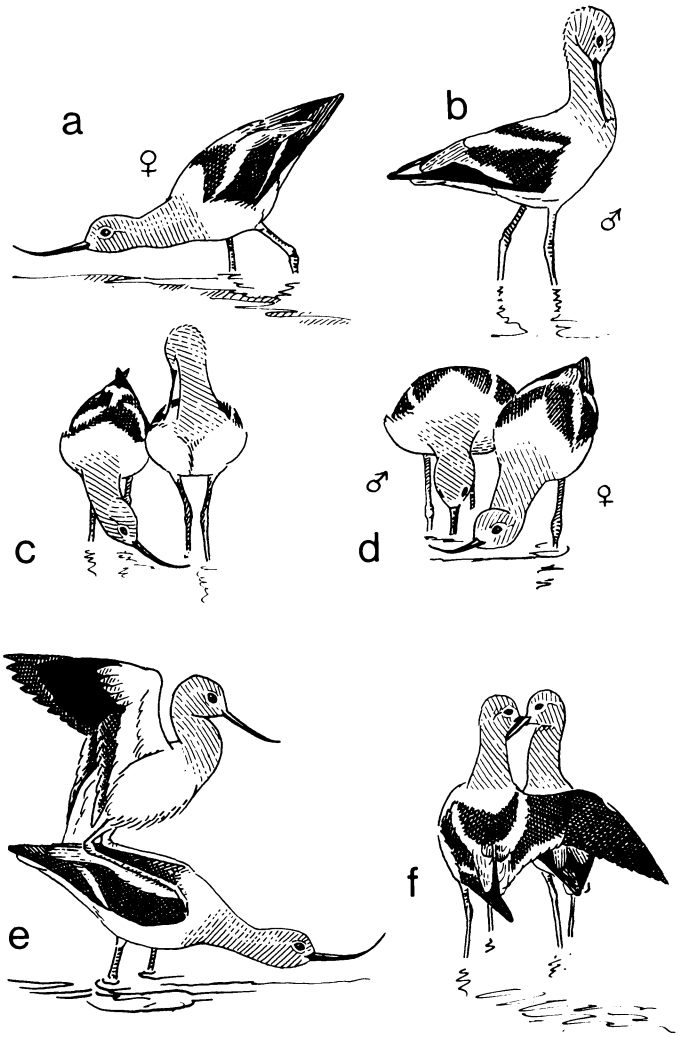

FIGURE 17. Copulatory behavior. Postures illustrated: (a) female, Neck Extended (precopulatory); (b) male, Upright Breast Preening (precopulatory); (c) l. to r., female, Neck Extended and male, Upright Breast Preening (precopulatory); (d) l. to r., male Bill Dipping and female, Neck Extended (precopulatory); (e) copulation; (f) Bills-crossed Run (postcopulatory).

progresses; prior to the male mounting the female, water may be splashed three or four meters into the air, and the noise made by the male's bill splashing the water is quite audible to an observer 30 m away. A precopulatory preening male is always oriented somewhat parallel to the female (Figure 17c

and d), but with his breast directed slightly toward the female; Bill Dipping always occurs near the female's feet.

Perhaps the visual effect of precopulatory preening is accentuated by the chestnut color of the head, neck, and breast of avocets. (This chestnut color might also serve to accentuate the female's precopulatory display.) The pinkish tinge of the breast of male stilts in breeding plumage, especially in conjunction with their red legs, might also function to increase the effectiveness of the male's precopulatory display. The black patterns on the head and neck of stilts might also help to accentuate the precopulatory displays; such a function is not probable, however, since the head and neck pattern of the stilt races is very variable and indeed it varies somewhat with individuals. The adult Australian Avocet has a dark head in all plumages; if the bright chestnut plumage aids breeding, one would expect the Australian Avocet to breed at any time of the year. (The harsh climate of much of the breeding range of the Australian species might cause such opportunistic breeding.) Bryant (1947) referred to a breeding date of 23 July 1946, which is the austral winter; he also reported breeding in September, 1946. Cain (1938) reported Australian Avocets breeding in February, 1937. Therefore, it does appear that the Australian Avocet breeds at various times of year and that its chestnut head color may be important in breeding.

Precopulatory displays of the European Avocet seem to be identical to those of the American Avocet and the Black-necked Stilt (Makkink 1936: 12–13).

Copulation.—The precopulatory ceremony often lasts for several minutes before copulation occurs. At the height of his precopulatory frenzy, the male mounts the female by fluttering onto her back; he flexes his legs (thereby lowering himself onto the female) and slides backward until cloacal contact is attained. During coition, the male holds his wings over his back and moves them in a way which helps to maintain his balance. To facilitate cloacal contact, the female moves her tail to the side; during copulation, she also moves her head slowly from side to side (about 30 degrees) in a scythe-like motion—all the while maintaining the precopulatory posture (Figure 17a). Finally, after intromission, the male slides off the female.

Makkink (1936: 15) commented on the fact that copulation by European Avocets is usually successful but said that this not always true in all species of birds. He maintains that birds which do not always copulate successfully do not have elaborate precopulatory ceremonies and that the elaborate and ritualized precopulatory ceremony employed by avocets insures the success of copulation. However, male avocets, while performing frenzied precopulatory preening movements, were observed on several occasions (Makkink 1936: 47; pers. obs.) to leave the female to supplant a nearby bird

(perhaps 10 m away). Precopulatory activities were not always resumed after these interruptions, nor did copulation always subsequently occur.

Postcopulatory Display.—After the male dismounts, the pair then crosses bills and runs forward together, with the bills of the pair still crossed (Figure 17f) for a distance of 2 to 10 m—sometimes with a wing of the male spread over the back of the female. I call this behavior the Bills-crossed Run. The wrists were sometimes slightly extended as the birds ran, and thus the tips of the wings "drooped" slightly. The birds then separate diagonally, leaning away from each other as they run several additional meters before stopping. Members of the pair, after separating, frequently independently perform comfort movements, such as drinking or bathing. Preening is often observed at this time.

The above descriptions apply to the avocet as, during the course of my study, I saw copulation only once in stilts, but the stilt copulation did not differ noticeably from copulations of avocets. An aborted stilt copulation was also observed, and it too appeared to be of the same form as an avocet copulation. Benson (1950) described the copulation of the nominate stilt race *himantopus* whose copulation behavior corresponds with that of *mexicanus*. However, Burrows (1948) described the "copulation" of *leucocephalus* (*novae-zelandiae sensu* Peters, 1934), as being quite different. I think Burrows' description was not that of a copulation but rather one of an aggressive interaction. Copulatory activities of the European Avocet, as described by Makkink (1936: 12–17), were essentially the same as those I observed for the American Avocet.

Copulation with Inanimate Objects.—Avocets and stilts were sometimes seen "copulating" with inanimate objects. This behavior was observed early in the year (before the onset of the breeding season) and, in the case of stilts, sometimes occurred frequently. Generally, these movements were made in relation to some object of approximately the size of a female (e.g., a brick or a piece of driftwood). Birds, whose sexes I was unable to identify because of poor lighting conditions, would make Bill-dipping movements close to the object. "Precopulatory preening" was considerably reduced and was hardly recognizable with the bill only touching the breast occasionally. After three or four Bill-dipping movements, the "copulating" bird would hop upon the object and lower itself to the level of the object with its wings raised in the manner used in actual copulation. Generally, the mounting bird did not appear to lower itself as far as in normal copulation or actually to make contact with the object. This pattern might be repeated for 20 or 30 times at approximately 30-second intervals. No "post-copulatory" performance was observed. Movements were never as elaborate as in an actual copulation, and the entire performance merely suggested an

"outline" of copulatory behavior. Makkink (1936: 15–16) reported three such copulations, which he called "eruptive copulations," performed by European Avocets.

NESTING BEHAVIOR

Nest Location.—Locations of the nests for the main colonies studied in 1966 and 1967 are shown in Figure 18. Scattered nests were found on other dikes but were not plotted in the figure. With few exceptions, nests were located on dikes from 2 to 10 m in width. (There were no other sites above water in the main part of my study area except for some salt-water marshes.) The dikes had been constructed by dredging the bottom of salt ponds and piling the bottom material above the water by the dredge. Because of this construction technique, recently constructed dikes were very rough and uneven and had cross sections different from the older dikes, which had weathered to relative smoothness; there was generally less rise above water surface in the middle of older dikes. Little vegetation was found on the nesting dikes; new dikes had no vegetation whatsoever, and older dikes had only occasional clumps of *Salicornia.* Forster's Terns (*Sterna forsteri*), Caspian Terns (*Hydroprogne caspia*), and Snowy Plovers (*Charadrius alexandrinus*) also regularly used these dikes for nesting. However, neither avocets nor stilts were ever observed nesting in association with these species.

Both avocets and stilts nested in loose interspecific colonies at my study area. Only recurvirostrids occurred in these colonies. Gibson (1920: 62) reported that *H. h. melanurus* also nests in colonies. Nicholson (1929) also reported that *H. h. melanurus* was colonial. Nicholson (1929) reported colonies of *H. h. mexicanus* in Florida. Sibson and McKenzie (1943: 51) recorded colonial nesting in *H. h. novae-zelandiae.* Rockwell (1912) recorded colonial nesting in the American Avocet. Extreme examples of colonial nesting were found in the Banded Stilt, where Howe and Ross (1931) reported a colony of about 27,000 pairs with nests about 5 m apart. On my study area, many dikes were completely devoid of avocet and stilt nests, and other dikes held loose colonies. Nests were found as close together as 2 m. It was impossible to always determine the maximum distance between nests in the colonies, because there were isolated nests on the perimeters; consequently, I was not able to delimit the colony boundaries precisely. Within a given colony (or what I called a colony), the greatest distance found between nests was 42 m. (Thirty-one nests were found in that colony.) The mean distance between nests in an arbitrarily delimited colony was 21.9 m. In 1966, within the main colony studied, avocet nests were randomly distributed with a variance/mean of .907 ($\chi^2 = 0.96$). On the other hand, within these colonies, stilt nests were more regularly dis-

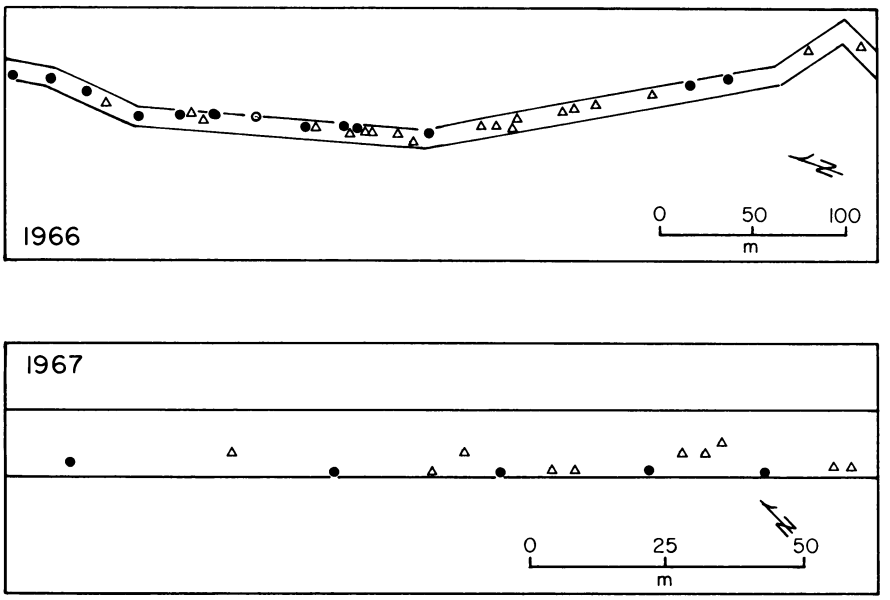

FIGURE 18. Distribution of avocet and stilt nests on main nesting dikes studied in 1966 and 1967. Open triangles = avocet nests; black circles = stilt nests.

tributed. Variance/mean was .539 ($\chi^2 = 5.78$, $p < .01$). In 1967, the results were similar, but the colony size was not large enough to be analyzed by χ^2. However, inspection of Figure 24 reveals the same trends, that is, stilt nests are spaced regularly and avocet nests more randomly. Variance/mean for stilts was .556. Data from the 1966 nests were analyzed using the "Moses test of extreme reactions." The distance between nests of each species was divided by the mean distance between nests in the main part of the colony. This calculation gave a percent deviation from the mean for each nest. These percent deviation figures were then analyzed with the Moses test. Theoretically, if the nests of one species were spaced statistically more regularly than the nests of the other species, the Moses test should reveal this difference in nest distribution. The test yielded a p of .024, and thus confirmed that nests of one species were more regularly spaced than nests of the other species in the 1966 colony; nests of stilts were more regularly spaced than nests of avocets.

The 1966 nest dike shown in Figure 18 was not used in 1967, nor was the 1967 nest dike used in 1966. In 1966, the 1967 nest dike was not in existence. In 1967, there was no apparent reason why the dike used in 1966 could not be re-used. However, this dike was farther from the bay than the dike which was selected. Since both species regularly feed in the

bay or in its adjacent *Salicornia* marsh, it seems that both species tend to nest as close as possible to accessible feeding areas. Furthermore, on 18 May 1966, many nests were destroyed by a ground predator—probably a striped skunk (*Mephitis mephitis*). The birds abandoned the 1967 nest site in 1968, and some nested again on the dikes used in 1966. A likely explanation for this abandonment was that prior to the 1968 nesting season, the top of the 1967 dike had been leveled and was being used as a road. Even so, there were suitable sites for nesting along both sides of the road, but the occasional traffic was probably sufficient to prevent nesting there. At my study area, nests were never re-used a second season, nor was an exact nest site employed more than once. This seems to indicate that site fidelity was not important for either species. Carnaby (1946) reported that Banded Stilts nested at Grace Lake (Australia) in 1930 and did not re-nest there until 1945. This is an exceptional example of lack of site fidelity of recurvirostrids. Another fact which illustrates the lack of site fidelity is the periodic invasion of breeding stilts in northern Europe (Stenzel, 1958; Petonke, 1959).

Inspection of Figure 18 shows that in 1967, stilt nests tended to be nearer the water than avocet nests. Distances from water were analyzed by a Mann-Whitney U Test. A U-value of 21 ($.025 < p < .05$) resulted. The distances of nests from water in 1966 were similarly analyzed, but no significant difference between avocet and stilt nests was found. Figure 18 shows the positions of nests relative to the water's edge. The probable reason for the yearly variation in the tendency to nest close to water was that the dikes used each year were of different configurations. The dike used in 1966 was an older dike with a low profile, but the dike used in 1967 was a new dike with a high profile which rose rapidly from the water; therefore, the height above water was probably more significant in nest location than the distance from water. This height was not measured, and since the surface of the dikes was very irregular, it is impossible to calculate the height above water using the distance of the nest from water. Stilt nests were often located just an inch or so above the water level; in fact, several of the stilt nests often had water in the bottom of them.

Figure 18 reveals a strong tendency for all nests of both avocets and stilts to be located on the same side of the dike. I checked these data for statistical significance (using a binomial test) by dividing each dike in half and counting nests on each half of the dike. Nests located in the middle of the dike were excluded. The following probabilities were obtained:

	1966	1967
Avocet	$p<.001$	$p=.011$
Stilt	$p<.001$	$p=.031$
Total	$p<.001$	$p=.001$

There are several possible reasons for this tendency to nest on only one side of the dike. On most afternoons during the breeding season, the wind blew quite strongly (often about 20 knots). The wind was usually northerly, and Figure 18 shows that in both years the nests were located on the leeward side of the dike. Furthermore, the main feeding areas were to the west, and consequently nests are constructed on the side of the dike facing the feeding areas. Human disturbance might also be a factor in nest placement. The 1966 dikes were placed in a position which would reveal the approach of humans, but the 1967 nest sites were shielded from human approach by the dike. It is impossible to determine precisely the importance in nest-site selection of each of the above factors or to say which is the single most important factor. On one nesting dike, not shown, which was situated perpendicular to the feeding areas, nests were placed on the leeward side of the dike, indicating that the wind probably does influence placement of nests. On this dike, the nests were located on the side of the dike away from human approach. It is impossible to say whether wind or human disturbance was the more important factor at that dike. One might think that some of the nests located near the center (the top) of the dike might be influenced by the wind. However, almost all nests were constructed downwind of some small environmental obstruction, which probably served as a windbreak. Therefore, most nests are protected somewhat from the wind's influence.

One important feature of the social nesting of both avocets and stilts is the communal distraction display. Both species would fly out from the nesting location at the approach of an intruder (in this case, me). The birds would then settle on the ground several hundred meters from the nest sites, and each bird would perform distraction displays. Often 10 to 20 birds of each species were seen performing these distraction displays. When I first observed these displays, it appeared that I was in the midst of a nesting colony. I darted from place to place looking for nests but found none. When the nesting areas were finally located, I was surprised to find the number of distraction displays greatly reduced. Generally, no distraction displays were observed, but when they were observed, only birds whose nests I approached displayed. The diminution of display activity was more than habituation to my presence, because when I left the nesting colonies, the number of distraction displays again increased. Natural selection favors evolution of group distraction displays for the protection of these semi-colonial nesters, which is attested to by the effectiveness of communal distraction displays in diverting my attention from the nesting colonies.

Avocets and stilts generally nest in rather open areas; if near vegetation, they nest at the edge of vegetation in a spot that affords a view of 360 degrees. They tend to nest as close to feeding areas as available nesting sites will allow. The lack of site fidelity is probably due to the fact that

both species often use ephemeral water sources as feeding sites and therefore have evolved an adaptability for nesting site selection which would allow them to use ephemeral sources.

Nest Building.—Nest-building activities were not observed at my study area. I did, however, witness nest-building behavior by avocets during a June, 1968, trip to Lower Klamath Refuge. Every instance of nest building that I saw occurred after copulation; several copulations occurred which were not followed by nest-building activities, however. Since nest-building activities occurred at different locations from those of copulation on my study area (at least the nests were found in a different area), it was impossible to ascertain if nest-building activities regularly followed copulation. Figure 10a shows "typical" postures observed during nest building. When making the nest scrape, the bird holds its breast very low in contact with the ground and its back at an angle of about –30 degrees to the ground. The nest cup is formed by a rotation of the breast as the bird pushes with its feet, first on one side and then on the other. Makkink (1936: 33–38) described nest-building behavior for the European Avocet. He emphasized that the scrape is made with the bend of the wings. I did not, however, observe this. My observations indicate that the breast is used in forming the nest scrape. Brown (1949: 8) reported that the European Avocet holds its wings loosely and makes the scrape with its breast—thus agreeing with my observations. Brown also stated that these activities occur after copulation and that both sexes performed these actions. Both sexes of the American Avocet also performed nest-scraping movements (usually after the members of the pair have simultaneously investigated the ground—Ground Checking). Birds hold their bills near their feet as they perform these searching movements, and their backs are held at angles of approximately –15 degrees (Figure 10b). Members of the pair remain close together during this activity. On several occasions, pairs of birds were observed to perform nest-building movements at the same location, with interactions occurring between the pairs. The interacting birds emitted a distinctive vocalization when this occurred. I have not observed birds bringing nesting material to their nests, but after the preceding actions were observed, birds were seen picking up objects from the ground and tossing them over their backs. The birds were facing away from the nest scrape while tossing this material, an orientation which resulted in the material being propelled toward the presumed nest site. "Typical" posture for this behavior is shown in Figure 10d. This tossing of material was indistinguishable from the display that occurs at nest relief. Some nesting material is added to the nest by incubating birds, generally either at the commencement or at the termination of the incubation period.

Empty nest cups have frequently been found—many in areas not used for nesting. These areas are suitable for resting, however, and birds have been observed on several occasions resting in them. Perhaps birds regularly use these empty cups as resting sites. The cups are never substantially built and are usually devoid of nesting material.

I did not observe the Black-necked Stilt performing nest-building activities; however, the postures used during nest relief are the same for stilts as for avocets, and since nest-building activities resemble the nest-relief activities, it is probable that nest-building activities are also similar. As do avocets, stilts also occasionally add material to their nests while incubating. There are some generalized descriptions in the literature of nest building by stilts. These descriptions are not detailed enough to compare with the nest-building habits of the avocet, but generally describe the augmentation of nests at the time of flooding (see p. 83).

Nests.—Recurvirostrids' best-known features are perhaps their nests and their eggs. There are many excellent photographs and descriptions of both nests and eggs of avocets and stilts in the literature. Nests are located on the ground and vary from simple scrapes, with almost no material added, to large mounds of stems and twigs (up to 40 cm high). There was only one of these massive nests on my study area, but numerous references to them are found in the literature (Bryant 1914: 226; Wetmore 1925: 12; Wolfe 1931: 51–52; Wheeler 1955: 285; von Frisch 1961; Palmer 1967: 151–152). Nests are lined with a variety of materials including pebbles, shells, stems, twigs, feathers, dry mud chips, and bones. When feathers are used, they are generally primaries obtained from dried carcasses and not the soft downy feathers which line many birds' nests; recurvirostrid nests are not lined with soft materials. The variety of material used in lining a nest seems to correlate with the type of material available on the nesting dike, and even though nesting dikes are rather barren, various materials suitable for nests are scattered about the dikes. Mud chips are often abundant, especially on freshly dredged dikes; fragments of shells are also common. On some of the older dikes, there are dried bird carcasses from which avocets and stilts obtain bones and/or primary feathers for nesting material. Nests found in areas which contained pebbles were generally lined with pebbles, and nests found near *Salicornia* were generally lined with *Salicornia* stems. As a rule, both avocets and stilts line their nests with whatever material is most readily available. Generally, nests are considerably more substantial where nesting material is locally available than where nesting material is scarce.

Incubating birds often picked up nearby material and placed it in the perimeter of the nest. This behavior was especially prominent at the times

of nest relief. Nesting material was accumulated in the vicinity of the nest as a result of the nest-relief display of the departing bird (tossing small objects over the back as the bird walked from the nest—see p. 82).

There are many examples in the literature of avocets and stilts building up nests under their eggs in response to rising water (Dawson 1923: 1203, 1212–1213; Wetmore 1925: 12; Jewett 1929: 215; Sibson and McKenzie 1943; Palmer 1967: 152). Makkink (1936: 35–36) reported the same behavior for the European Avocet. Owan (1927) reported a Snipe (*Capella gallinago gallinago*) and a Moorhen (*Gallinula chloropus chloropus*) in England raising their nests in response to flooding, and Haverschmidt (1927) reported Black-tailed Godwits (*Limosa l. limosa*) augmenting their nests as waters rose. On my study area the only raised nest found was a stilt nest about 20 cm high. It was constructed of *Salicornia* stems and was located on a patch of exposed mud in a *Salicornia* marsh. During periods of very high tide, the added height of this nest was essential for keeping the eggs above water. Unfortunately, I did not find this nest early enough to determine if it was originally constructed 20 cm high, or whether it was built lower and later heightened to correspond with the level of the water.

Incubation Behavior.—The incubation period of neither the avocet nor the stilt is known, and I made no serious attempt during my study to determine it precisely. My study does, however, reveal some pertinent facts regarding the incubation period. The incubation period for laboratory-incubated avocet eggs was 24 days (four eggs), whereas data from the field indicate an incubation period for avocets of 23 to 25 days (six eggs). The incubation period in the laboratory for stilts was 25 days (two eggs). I did not determine the stilt incubation period in the field. Derscheid (1939) gave a laboratory-incubation period for undeveloped candled eggs as 21 days and 22 hours for the European Avocet. Pocock (1907: 259) gave an incubation period of 24 days for the European Avocet. Lint (1959) listed the incubation period for a hybrid stilt (*H. h. melanurus* and *H. h. mexicanus*) as 25 days. Sibson and McKenzie (1943: 53) reported an incubation period for the *H. h. novae-zelandiae* as 25 to 26 days. McGilp and Morgan (1931: 45) stated that 28 days is the period of incubation for the Banded Stilt.

I did not observe the start of incubation at any nest; however, on no occasion was an incomplete clutch warm to the touch. (Complete clutches were usually warm to the touch.) From this I conclude that incubation probably is not begun until the clutch is finished (or nearly finished). Pocock (1907: 259) stated that the European Avocet began incubating one day before the last egg was laid (one nest). Yeates (1941: 44) reported that the Black-necked Stilt *H. h. himantopus* started incubation when

the last egg of one nest was laid and when the penultimate egg of another nest was laid. Eggs were generally laid every day by both avocets and stilts, but occasionally stilts laid eggs every other day.

Both male and female avocets and stilts share in incubation duties. Lint (1959) described the incubation at the San Diego Zoo of a nest containing a cross between *H. h. melanurus* and *H. h. mexicanus*. He stated that the male incubated during the day and the female at night. However, my observations of incubation indicate that the sexes took turns incubating during the daytime. I was unable to see the nests during the night, but generally the female was on the nest at the time of my last observation of the day. In the morning, the first nest relief I observed was usually of a male relieving a female. Thus, I conclude that females probably do incubate throughout the night. The following data show the number of minutes which nests were incubated versus the time they were unincubated.

	Avocet	Stilt
Covered	3449	1185
Uncovered	155	65

(In the above tabulation, only data recorded when nests of both species were being studied simultaneously are included.) A χ^2 test showed that avocets and stilts do not leave their eggs uncovered a significantly different period of time ($\chi^2 = 1.51$, df $= 1$, $.2 > p > .3$). The eggs were uncovered 4.3 percent of the time in avocet nests and 4.6 percent of the time in stilt nests. Eggs were generally uncovered as a result of some environmental disturbance, such as a motor vehicle passing on a nearby road or a ground squirrel running along the dike. Thus, incubating avocets and stilts do not differ significantly in their tendency to leave the nest in response to environmental disturbance.

Typically, one bird incubates the eggs for an appropriate period of time (averaging 77 minutes); then the incubating bird is relieved by its partner. One day, a male avocet did all the incubating of one nest except for occasional periods of about 15 minutes each when it left, presumably to feed. I was very surprised the next day to discover both the male and the female performing incubation duties at that nest. The average time (in minutes) of an incubation bout is as follows:

	♂	N	♀	N	Total	N
Avocet	87.6	26	64.3	18	81.1	44
Stilt	64.6	11	82.0	10	72.9	21

There is little variation in the average length of incubation bouts, but there is an opposing trend in the sexes of avocets and stilts; male avocets and female stilts tend to have longer bouts than their mates. These differences

are not statistically significant when analyzed by a χ^2 test. However, if avocets are compared with stilts, a χ^2 value of 4.93 is obtained ($.05 > p > .02$). In other words, there is a greater tendency for female stilts to incubate in the daytime than there is for female avocets. The slightly cryptic plumage possessed by the female stilt would be a benefit to a diurnal incubation. To check these results, I reworked the above data to show the total time spent in incubation by each sex. The results, in minutes, are as follows:

	♂	♀
Avocet	2218	1231
Stilt	686	733

A χ^2 test of these results gives a value of 115.5 ($p < .001$). Thus, the tendency of female stilts to incubate during the day relatively more than female avocets is confirmed.

At nest relief the non-incubating bird typically flies in and alights in the water near the nest. (Often a bird approaching a nest will shake its foot behind when emerging from the water. This Foot Shaking was described as a maintenance activity on page 42.) As the relieving bird settles on the nest, its mate walks directly away from the nest toward the water with its back to the nest and its head down in a manner similar to that used in settling on the eggs (Figure 10c and d). The departing bird will regularly pick up small objects from the ground and toss them over its back in the direction of the nest. This tossing of straws was observed in the European Avocet (Makkink 1936: 48). Often departing birds performed this Straw-tossing activity for more than a minute. After reaching water, the non-incubating bird then usually flies away to feed.

Incubating birds have several responses to predators. If a gull is flying over, an incubating bird will remain immobile on the nest; some non-incubators fly to the height of the gull and pursue it, sometimes giving a characteristic call. A bird's reaction to ground predators, such as man, is generally to leave the nest (usually before the intruder has approached the bird on the nest, and probably before the incubating bird is seen by the intruder), fly to the vicinity of the intruder, and perform a variety of distraction displays. Both avocets and stilts react in this manner, although the forms of the distraction displays are different (see pp. 90–92). Once a Beechey ground squirrel (*Citellus beecheyi*), walking along the nesting dike, stopped near an avocet nest. After several minutes, the incubating avocet arose and approached the ground squirrel, calling continuously until the squirrel left the vicinity. Brown (1948) reported a similar encounter between a male European Avocet and a sleeping Sheld-duck (*Tadorna tadorna*) 3 m from the avocet nest. The avocet harassed the much larger

Sheld-duck until the duck moved further from the nest. Small mammals and birds observed on the nesting dikes have been largely ignored by incubating birds.

Hatching.—Several days before hatching occurs, soft peeps can be heard from within the eggs. Approximately a day later, the eggs become pipped; then within a day or so, the young are hatched. Hatching of the young seems to elicit a protective behavior in parent birds. From the time of the hatching of the first chick onward, when avocet parents are with their young and are approached by a ground predator, parents will fly directly at the predator, calling continuously. At the last possible moment, the adult bird will swoop upward and thus avoid hitting the predator. I call this behavior the Dive-bombing Display (Figure 10e). Oftentimes the call of Dive-bombing avocets will change in timbre at the point of closest approach to the predator. When approached by a ground predator, an adult stilt with young will circle overhead and call. I did not, however, observe stilts flying directly at predators. At this time, stilts may give calls which appear to be homologous to calls given by Dive-bombing avocets. Dive-bombing (or a similar display) is performed by the European Avocet (Makkink 1936: 55–56; Brown and Lynn-Allen 1948). Bryant (1947) also reported that Dive-bombing is performed extensively by the Australian Avocet (317 consecutive dives and more than 1,000 total in 5.5 hours). Stokes (1953) reported Dive-bombing in *H. himantopus leucocephalus.* Stokes was actually struck by a wing of a Dive-bombing stilt. This display appears to function to intimidate a ground predator, but the smaller stilt is not so effective at intimidation as the larger avocet. A similar (probably homologous) behavior to the Dive-bombing Display is performed by the Pomarine Jaeger (*Stercorarius pomarinus*), the Forster's Tern, and the Caspian Tern (pers. obs.) in similar situations. Other large shorebirds also perform this display (Jehl, pers. comm. 1968). Perhaps this behavior originated with the ancestors of the Charadriiformes and has been retained by the larger species.

I have never observed egg shells in the nests of avocets or stilts either during the hatching process or after hatching. I once found two open egg shells in shallow water near the nesting dike. Obviously, the adults remove egg shells as soon after hatching as possible. Makkink (1936: 53) reported that the European Avocet removed egg shells from the nest, took them to the nearest water, and submerged them. Both the eggs and the young of avocets and stilts are protectively colored, and I had difficulty finding them. The light inner shells of the eggs are very conspicuous, however. Chicks usually remain in the nest for no longer than 24 hours. Egg shells must be conspicuous to potential predators (they are quite conspicuous

to me) for avocets and stilts to have evolved and/or maintained a behavior that would be of benefit for such a short period of time in the annual cycle.

Soon after hatching, the chicks scamper out of the nest but return periodically to be brooded. After the entire brood has hatched, the young are led as a group from the nest by the adults. Chicks of both avocets and stilts are at first quite shaky on their feet but manipulate their wobbly legs surprisingly well. Within two hours or less, coordination of the young has improved substantially. On 16 May 1967, I observed a stilt nest where all four young were hatched at 15:00, but the young were not led from the nest at that time, even though they were very active and ventured to a distance of about 3 m from the nest. The young were brooded in the nest throughout the night, and about 08:00 the following morning, the parents led the young from the nest site.

Young recurvirostrids are not generally found along the sparsely vegetated nesting dikes, where scant cover occurs, but are found instead in *Salicornia* marshes or along older dikes, which provide considerable vegetation for cover. The young are led to the *Salicornia* marshes and vegetated dikes by the adults.

Brooding.—Brooding is accomplished by the same posture used in incubation (Figure 10d), or by birds resting on their tibiotarsi with the young standing beneath them (Figure 10f). Both methods are used by the American Avocet and the Black-necked Stilt, and there is no noticeable difference between the brooding behavior of the two species. European Avocets (Makkink 1936: 56) also rest on their tibiotarsi when brooding young. The incubation posture was only used to brood the very young and was only observed at the nest site. Young are regularly brooded during their first few days by both sexes. I do not know the age of the young when brooding is terminated, but I never observed chicks being brooded after they were about one week old. Gilliard (1958: 168) stated that the American Avocet broods its young for 11 days.

Care of Young.—After the young are hatched, they are often brooded at different times by each of the parent birds. Even before chicks are dry, they begin to toddle away from the nest, and soon after the brood has hatched, the young can no longer be found in the vicinity of the nest. On 9 May 1966, I checked a stilt nest, which had previously contained four eggs, and discovered that only one pipped egg remained. This nest was located on an island of about 75 square meters, which also contained three avocet nests. The island was mostly bare, but there were two patches of *Salicornia*, with an area of approximately two square meters each. I searched diligently for the hatched young and was able, after about 10 minutes, to locate one chick crouched low on the ground next to one of the *Salicornia*

patches. Five minutes later, another chick was found in the same *Salicornia* patch. Several times earlier, I had searched in this patch but had failed to detect any young. The fourth chick, which was presumably still on the island, was not found. Generally, no young were seen near the nest more than a day after hatching occurred. I am certain of this because, even though chicks were very difficult to find, the parent birds performed certain characteristic behavioral patterns when I approached their young. This protective behavior of parents was observed near the nest only for a day after hatching. Where, then were the young? Young are always hard to find; I was often not able to locate chicks even though the behavior of the parent birds indicated that young were nearby. However, in areas of extensive *Salicornia*, adult avocets constantly perform Dive-bombing Displays at intruders (Figure 10e), a behavior which indicates the presence of young. Stilts usually fly in circles overhead calling continuously. Young were occasionally seen along the margins of some of the salt ponds in areas grown over with *Salicornia*, but they did not seem to remain long in these areas.

Once the young have stopped moving and go to cover, they are very difficult to locate. On two different days, as I approached the nesting area, I observed several young stilts scampering for cover in a *Salicornia* marsh. I remained at the marsh for about five hours each day, but on neither day did I again see a young stilt in this marsh. Young habitually crouch motionless when alarmed, with their legs folded and the head resting on the ground (Figure 10g). The protectively colored young are very difficult to find when crouched. Normally, their only conspicuous feature is their shadow, which is minimized by the crouching. Both young avocets and stilts also occasionally swim away from the shore when approached by predators. Swimming normally occurred when a brood was disturbed along a shoreline with little cover. The young were very conspicuous in the open water, but I never saw them being attacked, which was probably due to the adults' close attendance.

How do the young get from the nest to the feeding areas? I have watched young chicks follow the parents, much as young ducklings will follow the hen, but recurvirostrid chicks were frequently observed following adults at greater distances (three to ten m). The vocalizations given by adults when chicks were following were not noticeably different from those which occurred at other times. However, many of these vocalizations were not loud and not clearly audible to me; there may have also been subtle differences which I did not detect. One extremely revealing observation was made at White Lake, California, on 21 June 1968. As I was filming distraction displays of an avocet, I detected the avocet's nest about 20 m from the highway. The adult bird alternated performance of distraction displays with

flying in circles and calling. Soon I noticed that whenever there was no adult at the nest, one chick would repeatedly leave the vicinity of the nest and start swimming directly away from the nesting island. One of the parent birds (usually the male) would then land between the errant chick and the nest, calling excitedly. (This call was not noticeably different from any other call usually given by an excited adult.) Generally, within two seconds after an adult had landed, the chick would turn 180 degrees and swim toward the adult, which then moved toward the nest. Upon reaching land, the chick would normally clamber toward the nest. This occurred with the same result at least 10 times. Once a parent bird did not land between the chick and the nest but in water at the side of the island. Again the chick swam toward the parent. The chick, as it followed the adult, swam entirely around the island before returning to the nest. It appeared to be less than a day old, but it must have traveled about 40 to 50 m. On 26 June 1968, at Goose Lake, California, I caught an avocet chick which had been crouching along the shore. This chick, which was 7 to 10 days old, was measured and released, and took off running across the alkali flat directly away from me at the point of release. Soon an adult bird, which had been performing a Tightrope Display nearby, flew after the chick and landed between it and the shore, calling excitedly like the parent calling the newly hatched chick to the nest (as described above). But the chick frantically continued to run. When the chick was 10 to 15 m away, the adult again flew or ran toward the chick and landed between it and the shore, repeating the earlier performance, but with the chick continuing to ignore it. The adult approached the chick five or six times to no avail, and when last seen the chick was still fleeing with the adult still in pursuit.

Several times adult avocets were seen caring for as many as six young, but never did I find a nest which contained six eggs. Frequencies of number of young tended by one pair of adults are:

	1	2	3	4	5	6
Avocet	5	8	5	5	2	4
Stilt	6	6	7	2	0	0

Upon close examination, the "broods" of six young usually contained two size classes and therefore probably two age classes. I saw mixed broods of avocets so often that I must conclude that brood intermingling by avocets is common. Further evidence of this was obtained on 28 June, 1966, when a group of five young of two sizes were attended by one pair of adult avocets, and about 50 m away, a single young was with another pair. The previous day, one pair of adults had been observed with a combined brood of six young at the same location. This brood had obviously been sub-

divided sometime between 27 and 28 June. Only once did I observe stilts with a mixed brood when two adults were seen with two young about two weeks and one about one week old. However, stilts in my study were less numerous than avocets, and perhaps stilts also regularly tend combined broods. Intermingling of broods probably results from lack of territorial behavior of the parents and their inability to distinguish their young. Furthermore, young are taken to the same areas by many pairs of parents, thereby increasing the likelihood of intermingling. Often adults associated with young would fight with other adults, and it sometimes appeared that two or more adults were vying for the same brood. Several times adults seized young from one of these large broods by actually extending the bill around the neck of a chick. The hold would almost immediately be released, however, when a nearby adult approached and chased the aggressive bird away. In my study, the young were never seen being carried away. Makkink (1936: 57–59) reported European Avocets grabbing chicks.

Distraction Displays.—Distraction displays are directed toward an intruder (usually man) during the time of nesting. These displays are quite conspicuous and would tend to draw the attention of an intruder toward the displaying bird and away from a nest or from young. Commonly the displaying bird moves away from the intruder, with the intensity of the display decreasing as the bird is approached; however, if the intruder retreats, the displaying bird is likely to follow and increase the intensity of the display.

Both avocets and stilts have large repertories of distraction displays which are commonly given in the nesting season. These displays differ markedly in the two species, however. Both have a type of distraction display in which the wings are extended and held conspicuously away from the body. I have termed the extended-wing display performed by the avocet the Tightrope Display, because the wings are maximally extended more or less symmetrically as they would be in flight. The tail is widely spread and sometimes depressed; often the neck is contracted and the head is held close to the body (Figure 15e), as the displaying bird faces the intruder and repeats almost continuously a low, nasal call. It often walks slowly toward the intruder, tipping its wings from side to side without fluttering them—a movement resembling that of a tightrope walker. The Tightrope Display is performed during the nesting season by both male and female avocets when either the nesting colony, the nest site, or the young are approached.

Stilts perform a display similar to the Tightrope Display under the same circumstances. I have termed the stilt display Wing-flagging, as the wings are less extended than in the Tightrope Display and are continually ab-

ducted and adducted. Furthermore, a Wing-flagging stilt is likely to extend only one wing at a time, which results in extreme asymmetry of the movement (Figure 15f). Wing-flagging stilts often alternate performing this display while sitting and standing, and some displaying stilts oscillate regularly between the sitting and standing position. A vocalization similar to that given by Tightroping avocets is emitted by Wing-flagging stilts. Wing-flagging is performed at the times of nesting and care of young.

Distraction displays by mixed flocks of avocets and stilts are so constant and vigorous away from nesting sites that a naive observer is likely to assume that eggs or young are nearby. I spent hours looking for nests before I discovered that distraction displays were not necessarily given at or near an active nest.

Both species also have distraction displays which resemble incubation. Displaying individuals crouch on the ground, as if incubating eggs, but in areas devoid of nests. It is obvious that incubation is not occurring, however. Displaying birds exhibit extreme mobility, and their constant sitting-rising-moving to another location to "incubate" might remind one of a mechanical toy (jack-in-the-box). Further, these incubation-like distraction displays frequently alternate with the wing displays noted earlier, also an indication that actual incubation is not occurring. In addition, distracting birds frequently perform a Crouch-run or a Crouch-walk when changing locations and performing these incubation distraction displays; prior to normal incubation the nest is approached cautiously by adults in an Upright posture. Incubation-like distraction displays are similar in both species, but stilts are much more restless than avocets and consequently move from place to place more frequently.

Aerial distraction displays are also observed. Both species give fluttery flight displays in the vicinity of the nest; avocets frequently land in water and swim with the head close to the body, whereas stilts hover above water with their legs dangling. Distinctive calls are given during these displays. Stilts will frequently perform a Dihedral Wing Flight Display, seemingly as a distraction display since it is often both preceded by and followed by Wing-flagging. In the Dihedral Wing Flight, a bird flies in large circles; the displaying bird holds its legs in a normal position and alternates several normal wing beats with gliding, as the wings are held at a dihedral (but in a manner somewhat more exaggerated than that of Turkey Vultures [Figure 14d]).

In the nesting area, only birds whose nests are approached perform distraction displays—but never very near the nest. Dive-bombing Displays of avocets, which are performed near nests containing eggs that are hatching or near nests that still have young in the vicinity, were the only displays

observed in immediate proximity to the nest. (The Dive-bombing Display, however, did not appear to be a distraction display, but rather a threat.)

INTENTION MOVEMENTS

Intention movements signify the impending performance of an activity. The most common recurvirostrid intention movement is probably Head Bobbing, which is performed by both avocets and stilts and is generally given from an Upright posture. Head Bobbing simply consists of a very rapid extending of the neck, resulting in the head being raised about two to five cm; a slight bending of the ankles also occurs (Figure 14e). In both species, Head Bobbing is identical in detail and is frequently performed when a bird is disturbed; it often indicates flight intention. After alighting, birds (especially isolated birds) will usually Head Bob for several minutes until they seem to feel relaxed in their new environment.

Near the nest, Head Bobbing is accentuated by much ankle bending. This is probably a result of the same combination of tendencies present in Head Bobbing, together with the tendency to settle to the ground to incubate. This display is only performed when birds are alarmed near their nests and seems to provoke almost equal tendencies to incubate and to fly away. Birds performing this display will alternate in going to the nest, incubating five to ten seconds, and flying away while calling excitedly.

Sometimes pecking movements are made without the customary activities such as swallowing or preening following them. This type of pecking probably indicates intention to feed or preen and is generally performed prior to the start of an appropriate activity, such as feeding or preening. These pecking intention movements are especially common between feeding and preening.

Interacting birds will often quickly adduct their folded wings about an inch and immediately abduct them to the normal non-flying position. This movement seems to indicate an intention to strike an opponent with the wings and/or to fly away.

DISPLACEMENT ACTIVITIES

Thorpe (1963: 29) wrote: "Displacement is the performance of a behaviour pattern out of the particular functional context of behaviour to which normally related." Marler and Hamilton (1966: 185) added that displacement activity "often seems to occur in the absence of the customary eliciting stimuli."

During this study, avocets and stilts performed displacement activities many times. Displacement pecking was the most frequent displacement activity observed; it was often performed at the termination of agonistic interactions when the less aggressive bird turned and walked away, period-

ically making displacement pecking movements. Displacement sleeping, nest-building, bathing, drinking, and preening were also observed.

SUMMARY AND CONCLUSIONS

Recurvirostra americana and *Himantopus h. mexicanus*, two closely related species, are adapted for feeding in shallow water and along margins of ponds and lakes. The preferred habitats of the two species differ; avocets usually breed on the borders of alkaline or saline lakes, whereas stilts breed along the edges of fresh-water ponds. There are many morphological and behavioral differences between the species which correlate with habitat differences and probably reflect differences in the evolutionary history of the two forms.

The fresh-water habitats preferred by stilts often have grassy margins and sometimes are quite ephemeral. Stilts are less social than avocets, probably because the available feeding areas are usually small, and food is not superabundant in typical stilt habitats. Stilts feed by pecking insects, fish, and small crustaceans from shallow water or by catching insects which they flush from the bordering grasses and sedges. The long legs of the stilt extend the area available for feeding; their dimorphic size and the tendency for each sex to feed in different areas aids niche diversification. As an aid in maintaining territories and communicating in an environment somewhat obstructed by grasses and sedges, several types of aerial displays are used. Stilts' long red legs are displayed in these flights as the displaying bird hovers in one spot; their long wings facilitate the performance of these aerial displays. When nests are located in loose colonies, they are spaced somewhat regularly. Each nest is located in or near the water. The small size of the stilt makes active nest defense ineffectual; a mass distraction display performed at locations distant from the nest site serves as nest protection. The female stilt is more cryptically colored than the male and spends more time incubating the eggs. The bright plumage of the male probably facilitates territorial defense.

The alkaline or saline habitats preferred by avocets often have barren margins of mud flats. The recurved bill of the avocet is suitable for scraping food from these mud flats and the adjacent shallow water. The niche is divided between sexes through the tendency of each sex to use different feeding methods. Because of the open nature of their habitats, aerial displays are non-essential; consequently, avocets do not perform these displays, and relatively short wings have evolved in this species. Food probably is more abundant than in the areas in which stilts breed. Avocets are the more social of the two species and usually nest in colonies; often their nests are very close together. They fly out from these nest sites, which are often isolated islands, to communal feeding areas. Dimorphic

bill shape is apparently sufficient for sex recognition in the absence of plumage dimorphism. Lack of plumage dimorphism facilitates social coordination. Males and females with their similar plumages, spend equal time incubating the eggs. The avocet, because of its relatively large size, is likely to defend its nests and young by direct attack.

Avocets and stilts do not defecate in the water when feeding. I regularly observed feeding birds wade to shore, defecate, return to water, and resume feeding. This behavior has also been observed in some herons, Greater Yellowlegs, and Lesser Yellowlegs. Avoidance of defecating in the water probably serves to minimize parasitic infestations and probably helps to keep the water transparent, thus aiding in the sighting of prey items.

Comfort movements of both avocets and stilts are quite similar; the forms of the movements are usually indistinguishable. However, there is some tendency for one species to perform certain comfort movements more frequently than the other species (see Table 9). For example, stilts scratch and Wing and Leg Stretch more often than avocets. One reason perhaps that stilts scratch more often is their smaller size which results in their relatively larger body surface. However, scratching is so frequent in stilts, relative to avocets, that the body surface factor alone would not explain the difference. The frequency with which comfort movements involving extensive maneuvering of a leg (e.g., scratching and Wing and Leg Stretch) occur in stilts in conjunction with their long legs, suggests that both activities may, in some way, aid in the functioning of the legs. Since stilts preen significantly less frequently than avocets, perhaps irritating stimuli which are soothed by preening in avocets are soothed by scratching in stilts. Preening may be more frequently performed by avocets, since they commonly employ feeding methods which submerge their heads; avocets thus may require more preening. Furthermore, avocets spend a lesser proportion of their time feeding than stilts (probably because of the larger size of the avocet and a concomitant decrease in metabolism). Consequently, avocets have more time available for preening and other activities.

The characters which distinguish the Recurvirostridae are not morphologically conservative. Storer (1960: 75) characterized the family as: "Medium-sized, long billed, very long-legged birds with bold color patterns." These characters, however, may represent nothing more than adaptations for wading and living in shallow water. Because of the non-conservative nature of the characters which are used to distinguish the recurvirostrids, some workers consider the Recurvirostridae only a subfamily; others do not even consider them a natural grouping. My study of the behavior of two recurvirostrid species should help to reveal whether they are, in fact, closely related or whether they have been erroneously placed in one family because of convergent adaptations.

A comparison of the behavior of these species with others in the family Recurvirostridae should also help to ascertain relationships. However, I have found only one detailed study (Makkink, 1936) of the behavior of any other recurvirostrid species, other accounts being fragmentary and some seemingly incorrect. Such behavioral comparisons as I was able to make revealed a similarity of behavior among all recurvirostrid species with the behavior of *Recurvirostra avosetta* and *Recurvirostra americana* being almost identical and that of *Himantopus h. mexicanus* differing as follows: (1) the variety of flight types, (2) the forms of the distraction displays, (3) the feeding methods employed, (4) the group displays, and (5) the fact that adult stilts do not swim. The frequencies with which much of the behavior of the two species occurred also differed. (Comparison of frequencies was not made between *R. avosetta* and *R. americana.*) Many of the differences between *Recurvirostra* and *Himantopus* seem to correlate with differences in morphology and differences in habitat of the two species. Thus, the behavioral differences agree with the morphological differences used by taxonomists to differentiate the genera and the behavioral similarities indicate that the species are related at least at the Family level. The fragmentary references which exist to the behavior of the other forms of the genera *Recurvirostra* and *Himantopus* indicate that the behavior of these forms probably corresponds closely to that of the American forms of the same genus and thus confirms the present classification.

Little is known about the behavior of *Cladorhynchus*, but there are some interesting nesting adaptations (Jones, 1945) which distinguish it from other members of the Recurvirostridae. This, together with obvious morphological differences, seems to indicate that for the present *Cladorhynchus* should be maintained as a separate genus.

The Ibisbill (*Ibidorhyncha struthersii*) is also normally included in the Recurvirostridae but Jehl (1968: 32) thought that there is insufficient evidence to warrant placement of the Ibisbill with the Recurvirostridae. The fragmentary description of Ibisbill behavior (see La Touche, 1921; Ludlow, 1928) that I have found revealed no similarities to avocet or stilt behavior. The little that is known about Ibisbill behavior is thus in agreement with Jehl's contention that there is no apparent reason for placing it in the Recurvirostridae.

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