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Natural History Museum of Los Angeles County • 900 Exposition Boulevard • Los Angeles, California 90007

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PLUMAGES AND MOLTS OF BROWN PELICANS

Ralph W. Schreiber,[1] Elizabeth Anne Schreiber,[1] Daniel W. Anderson,[2] and David W. Bradley[3]

ABSTRACT. Fledgling to adult plumage changes in Brown Pelicans (*Pelecanus occidentalis*) are described from extensive examination of specimens both in the field and in museums. Adults are found to have a very complex annual molt cycle that causes great changes in appearance which are generally related to the breeding cycle, although a few birds are found to breed in all stages of the cycle. Variability between individuals and geographic regions is noted in relation to breeding biology and ecology. Plumages and molts of Brown Pelicans in Florida and California do not fit exactly into either the Humphrey/Parkes (Humphrey and Parkes, 1959) or the Amadon (1966) proposed nomenclatural schemes. The Staffelmause, although originally described for the Brown Pelican (Stresemann and Stresemann, 1966), does not appear to exist in this species. A system for illustrating molt in figures is presented.

INTRODUCTION

Henry Forbes studied Brown Pelicans (*Pelecanus occidentalis*) in 1912 and 1913 in Peru and stated: "I am still unable to make up my mind what is the exact plumage sequence or how long each dress is retained. . . . Other ornithologists . . . may be induced to make and publish further observations on the subject" (Forbes, 1914). Although Palmer (1962) described the plumages of Brown Pelicans based on the material available to him, no thorough study exists on the plumages and molts of this species. Recent fieldguide descriptions of plumages are unsatisfactory or inaccurate (National Geographic Society, 1983; Peterson, 1980; Robbins et al., 1983). In this paper we attempt to fill this void.

METHODS AND MATERIALS

We have observed and recorded data on plumages and molt in Brown Pelicans since 1969, primarily in Florida, Baja California, and California, but also, to a lesser degree, in Puerto Rico, South Carolina, Louisiana, and Peru. The Schreibers recorded molt on over 900 Florida and 200 California specimens and examined virtually all specimens in American and European museum collections. Anderson has recorded molt on 175 specimens and recorded extensive field observations from Baja California and California. Dead specimens, collected from the early 1800s through 1983 with varying levels of accompanying data, were examined (Table 1).

We have eliminated from analysis all specimens whose capture data were questionable and those which remained in captivity for several weeks in a "rehabilitation" center. We believe their debilitated or dying condition, and the fact they were captured, may indicate a physiological problem that could affect plumage and molt condition and pattern. The same, of course, could be said of birds found dead in the wild. Due to the Endangered Species status of this species (U.S. Fish and Wildlife Service, 1974) we were unable to collect specimens specifically for this study. This particularly hindered our analysis of known-age birds. Plumage descriptions for known-age birds were taken from personal observation and from thousands of photographs of marked wild birds. Anderson collected 33 known-age, healthy specimens in 1980 from the Gulf of California under special permit. He also raised two pelicans in captivity. They were found to be comparable to 53 photo-documented, banded wild birds and collected specimens from the same population. We used these individuals in the detailed analysis of the sequence of plumages from juvenal to adult and individual differences. We have few specimens between 12 and 36 months of age but believe those we have accurately reflect the plumage sequence from fledgling to adult, which we describe here. The development of nestling plumage of Brown Pelicans was described by Schreiber (1976).

From museum study skins we recorded data for molt in the rectrices and outer primaries only since we could not examine the inner primaries and secondaries without damaging the specimens. We prepared our own specimens as "flat

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Table 1. *Pelecanus occidentalis* specimens examined for this study of molts and plumages.

Previously collected Museum specimens: 403 specimens
Schreiber collections,[1] Florida west coast: 415 specimens
Anderson collections,[2] California and Mexico: 64 specimens

Ages: 397 adults (45%), 168 subadults (19%), 317 birds less than 1 year old (36%)

Sexes: 397 males (45%), 362 females (41%), 123 unknown sex on label (14%)

Months collected (when known):

	Number	Percent		Number	Percent
January	76	9.2	July	89	10.8
February	90	10.9	August	59	7.2
March	68	8.3	September	41	5.0
April	75	9.1	October	38	4.6
May	94	11.4	November	48	5.8
June	56	6.8	December	75	9.1

Locations:		
	Florida east coast	104
	Florida west coast	415
	North and South Carolina	10
	Texas and Louisiana	24
	Caribbean islands	67
	Central America	23
	Peru, Chile, Ecuador	44
	Galapagos	17
	Mexico mainland	27
	California and Baja California	131
	unknown	20

[1] Housed in Los Angeles County Museum of Natural History.
[2] Housed in Division of Wildlife and Fisheries, University of California, Davis.

skins" and their usefulness for this type of study cannot be overemphasized (Norris, 1961; Clench, 1970). From flat skins and live specimens we recorded molt in all primaries, secondaries, and rectrices. We describe the shapes and colors of covert and body feathers but not details of their molts, for which we do not have extensive data. The description by Palmer (1962) of colors and shapes of feathers of Brown Pelicans is basically accurate. His comments relating the plumages to a termination of the breeding season, based on the limited data then available, were most perceptive. In our descriptions we describe first the "appearance" ["aspect" of Humphrey and Parkes (1959), or "plumage" of Amadon (1966)] and soft part colors. We did not use Dwight's (1902) terminology, which names plumages in relation to the breeding season, because the plumages of pelicans occasionally do not follow the reproductive cycle. We discuss this variability after we describe what a pelican looks like and the molt pattern as it matures to eventually undertake repeating annual cycles. We have found that the two subspecies best known to us (*Pelecanus occidentalis carolinensis* and *P. o. californicus*) follow the same fundamental patterns, although there are some distinct taxonomic differences which we discuss.

RESULTS

Adult Brown Pelicans undergo a series of changes in plumage which are best described as a regular but variable circannual sequence (Figs. 1, 2; Table 2). Juvenal plumages are dramatically different from those of adults (Fig. 2) and gradually merge into the typical definitive adult patterns during an individually varying period of 3–5 years. We first describe the annual cycle for a "typical" adult and note the variation found. We then describe the changes that occur between fledging and the adult cycle.

ADULT PLUMAGES

Annual Cycle

The annual changes in adult plumage result in birds that appear radically different at different seasons. The major annual changes in soft part colors are noted in Table 2, and in Figure 3 we illustrate the locations on the body of the parts discussed. Some of these changes in plumage and soft parts occur in 1 week or less.

In October–January most adults (birds at least 3–5 years old, on both coasts of North America) have completed a total molt and have all new feathers; the upper surface of the body is silver-gray, the belly very dark brown, the neck white, and the head mostly pale to dark yellow (Fig. 1A). At this time the adults "squeak" noticeably as they fly, probably from the fresh feathers rubbing during wing beats. The iris is dark, the eye ring and pouch are dull blue-black to dark green, and the bill is dull but begins to change to bright orange-yellow in *Pelecanus occidentalis carolinensis* (Fig. 1A) and bright pink-orange in *P. o. californicus* (Fig. 2A).

During December–March, as the normal breeding season approaches, the soft part colors intensify, the iris clears to straw white or bluish white, and the yellow head becomes darker yellow (Fig. 1B). The pouch and eye ring change to breeding colors over approximately 2 weeks. The neck molts over 2–3 weeks, from white to dark brown (Fig. 1C). This results, for a short time, in a "V-shaped yoke" on the dorsal base of the neck (Fig. 4E). In young birds (24–40 months old), the white feathers of the head do not become darker than pale yellow. However, in adults these feathers grow in pale yellow but quickly become deep yellow as the birds rub the head against the uropygial gland. Fully adult males and females do not differ in the intensity of the yellow color. Most individuals in most years begin nesting in these colors (Fig. 1C). Bill color becomes brightest 1 month to 6 weeks before pouch color is fully developed. The epidermal covering (and bright color) of the rhamphotheca sloughs off and regrows in time to have the yellow color, which serves to guide the chicks' begging, on the proximal portion of the lower mandible (Schreiber, 1977).

With the onset of incubation the soft parts begin to lose their bright colors, the iris darkens again, and the yellow feathers on the head are replaced by white feathers. In some adults brown flecks appear in the white head, giving a flecked ("salt and pepper") appearance (Fig. 1D) which lasts through

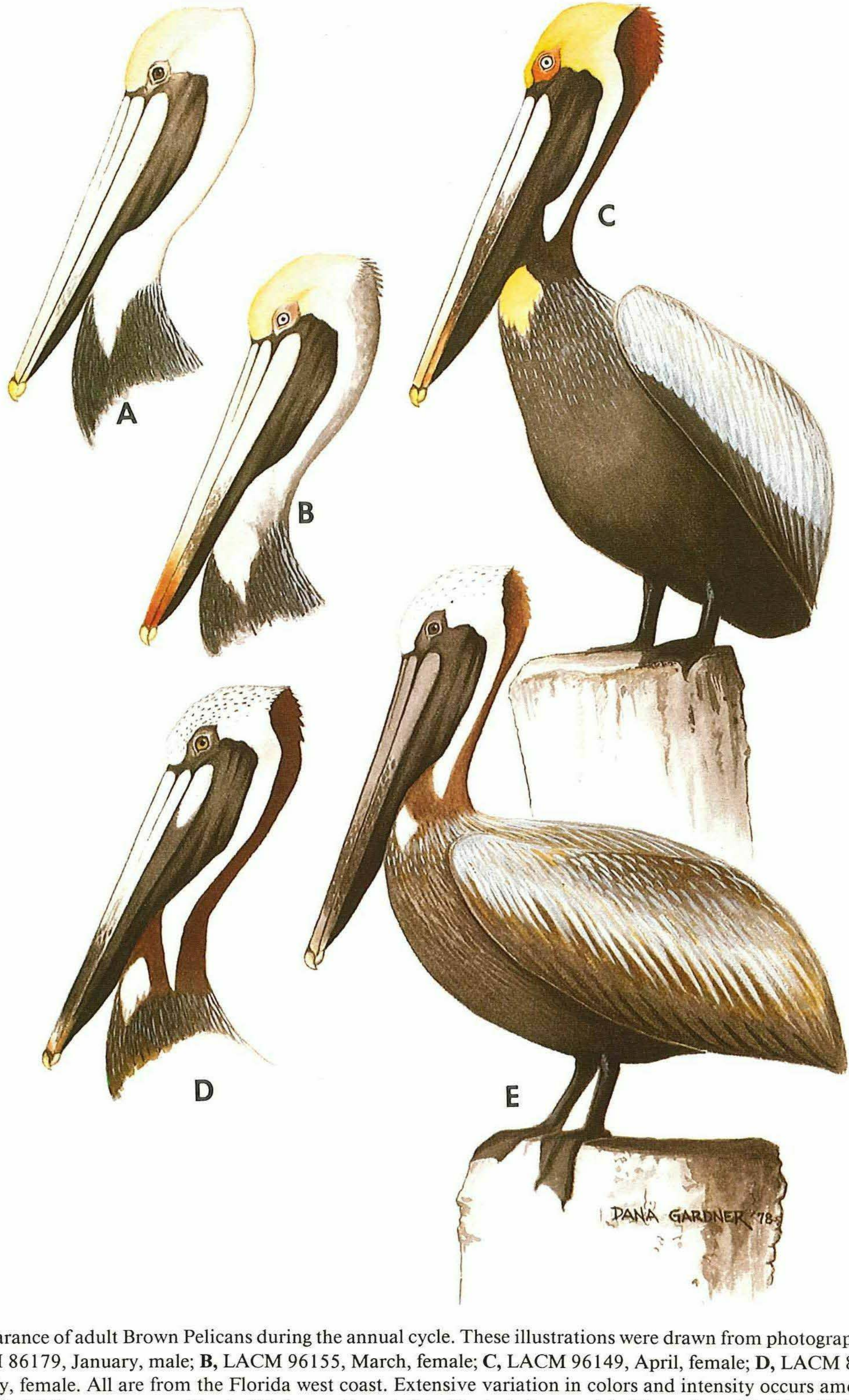

Figure 1. The appearance of adult Brown Pelicans during the annual cycle. These illustrations were drawn from photographs and the following specimens: **A,** LACM 86179, January, male; **B,** LACM 96155, March, female; **C,** LACM 96149, April, female; **D,** LACM 86111, June, female; **E,** LACM 86114, July, female. All are from the Florida west coast. Extensive variation in colors and intensity occurs among individuals, and soft parts are especially labile on a seasonal basis. We have attempted to illustrate here and in Figure 2 readily identifiable examples.

Table 2. Color descriptions* of soft parts and head and neck feathers of adult Brown Pelicans. These overall changes are brought about by various combinations of hormonal influences, feather wear and fading, feather replacements, and perhaps also pigment changes. See Figure 3 for locations of body parts by numbers.

Body part	Season: / Activity:	Appearance: Winter / Pre-breeding	Spring / Breeding	Late summer / Post-breeding
1. Nail		buff yellow	bright buff yellow	buff yellow
2. Upper mandible (distal)		buff yellow over pinkish orange	buff yellow-orange-red over bluish pearl gray	buff yellow, some orange, over pearl gray
3. Upper mandible (proximal)		pinkish orange	bluish pearl gray, pinkish	gray
4. Lower mandible**		pinkish orange	bluish pearl gray	gray
5. Gular pouch (proximal):				
Western North America		reddish orange	bright poppy red	yellow-gray, faded
Eastern North America		green-gray	blackish metallic green	gray-green
6. Gular pouch (distal)		dark gray-green	blue-black-green	dark green
7. Forehead		pale yellow	deep yellow-orange	salt and pepper***
8. Lower crown		pale yellow	deep yellow-orange	salt and pepper***
9. Upper crown		pale yellow	deep yellow-orange	salt and pepper***
10. Crest		white	dark brown	reddish brown
11. Occiput and nape		white	dark brown	medium brown
12. Lower neck		white	dark brown	medium brown
13. Back		silver-gray	silver-gray	dull brown
14. Wing coverts		silver-gray	silver-gray	dull brown
15. Upper breast		gray-brown	dark brown	scruffy, flecked, dull brown
16. Jugulum		yellow	yellow	very faded
17. Eye ring		gray-pink	pink	gray
18. Iris		light sky blue	light sky blue	brown
19. Legs and feet		dark gray	black	black

* Colors were matched as closely as possible with those described by Smithe (1975).

** The lower mandible has an area in the medial section usually without the brighter proximal and distal colors, or with a patchy or discontinuous appearance of color. This lower mandible pattern develops into a distinctive, light patch along the lower third of the gape (starting about 3–4 cm distal of the commissural angle) which is at its maximum intensity when young are being fed; it may serve as a signalling function to young.

*** "Salt and pepper" is white with variable flecks of dark feathers.

the nestling period to the end of breeding. Wear of the feathers becomes extensive and obvious toward the last third of the nestling period (which lasts 12–14 weeks; Schreiber, 1976) and after the young fledge. When adults leave the vicinity of the colony (usually July–September), feathers are extremely worn, the birds appear "scruffy," and they begin, or are well into, a major molt (Fig. 1E) that replaces all feathers by late November–December.

INDIVIDUAL, AGE, AND SEX VARIATION

Crest Feathers

The feathers at the back of the head are 60–90 mm long, forming a crest considerably longer than the surrounding head and neck feathers, but they shorten and grade into the feathers at the junction of the head and neck. The color of the crest is highly variable and it may be composed of 0–50 dark feathers (Fig. 4A–D). A dark black-brown crest may appear in August–October and is primarily visible when the surrounding head and neck are yellow and white, but it merges with the dark neck which appears in spring. We suspect that as the bird ages, there are more white and fewer brown feathers in the crest each year.

Breast Patch Vee

A patch of white-yellow feathers on the breast and dorsal portion of the neck appear in the fall. Elongate yellow feathers on the breast are isolated into a vee- or diamond-shaped patch (Figs. 4E, see arrow; 5A–C, E). Although they wear and fade somewhat, these feathers remain through the summer and fall (Fig. 6A, B, D, F), when they are replaced.

White feathers are also isolated dorsally on the neck for a short time when the neck molts to brown during 2–3 weeks in late winter–early spring, resulting in the white yoke shape at the base of the neck on the dorsal side (Figs. 4E, 5B). The yoke does not appear in all birds. It is prominent in a 72-month-old specimen (Fig. 5B) but may not be present in younger birds (Fig. 5D). The yoke may be present in males

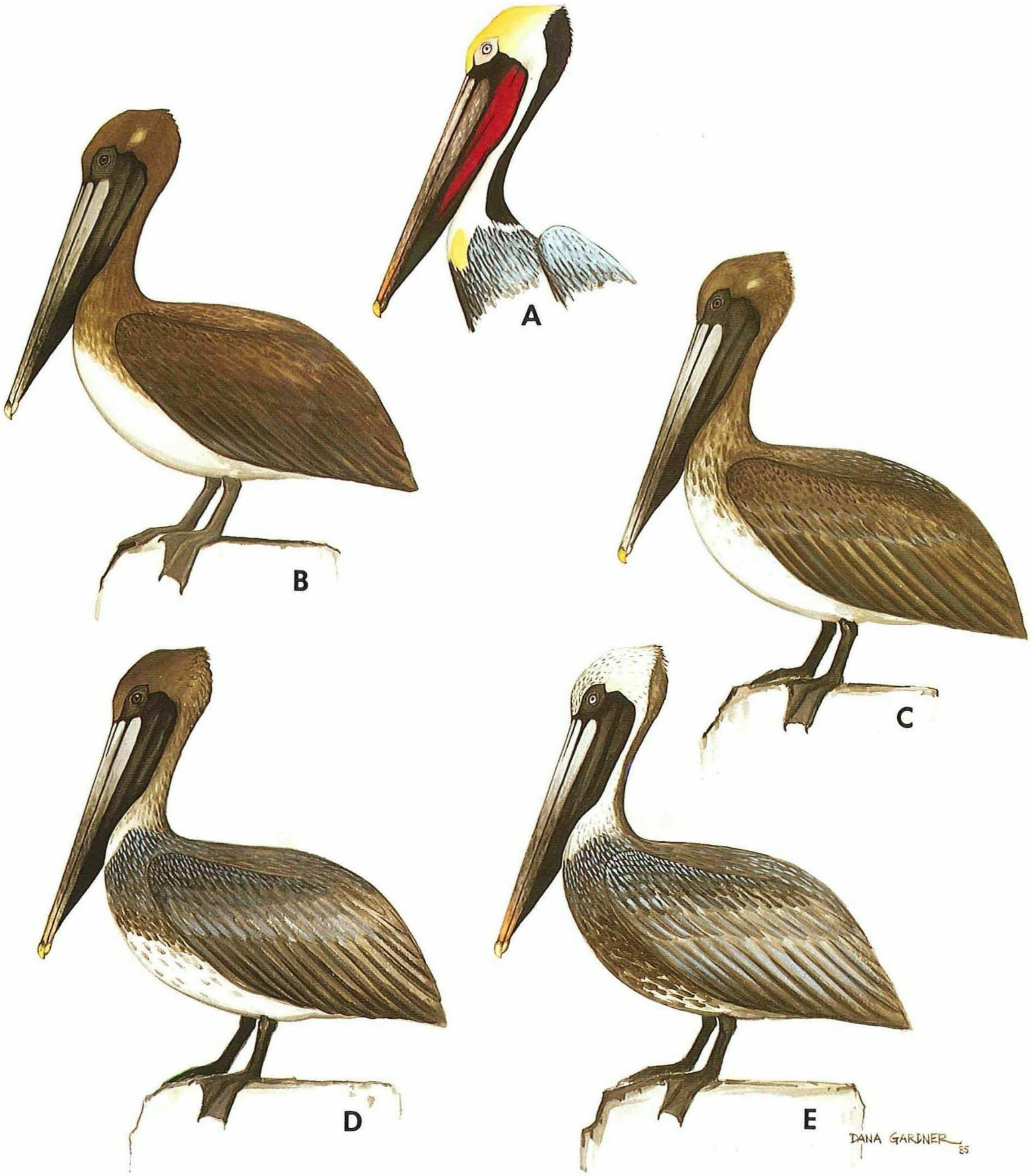

Figure 2. The appearance of juvenal Brown Pelicans as they mature and a California adult showing its bright gular pouch colors. These illustrations were drawn from the following material: **A,** photograph of a Baja California adult in January; **B,** LACM 86153, male fledgling, 4 months old; **C,** LACM 86192, male, 14 months old; **D,** LACM 86211, male, 21 months old; **E,** LACM 86158, male, 36 months old. B, C, and D were all banded and recovered in Tampa Bay, Florida west coast region, and E was recovered in Louisiana.

or females, and its occurrence does not appear to be related to the light breast diamond. We interpret both these light areas as individual differences, which probably help individual birds recognize their mates and perhaps allow nestlings to identify their parents.

Neck Color

The back of the neck in freshly molted birds varies from almost black, to dark brown, to cinnamon brown, or even pale tan. We cannot find a relationship between the intensity

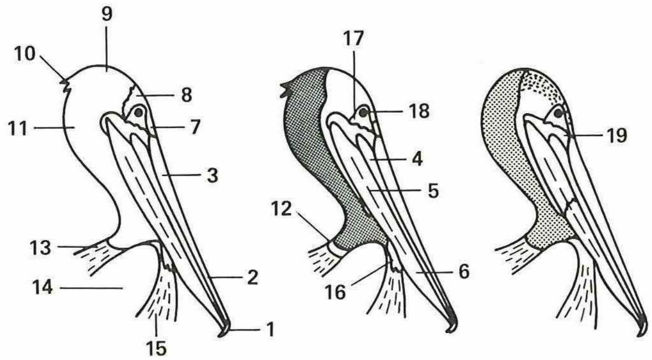

Figure 3. Diagram showing body part regions of Brown Pelicans that undergo the complex seasonal changes in appearance described in Table 2.

of the color and either age or sex, and we believe neck color is an example of individual variation.

Number of Secondaries

In our sample the number of secondaries varies from 27 to 33: 27 = 1, 28 = 6, 29 = 9, 30 = 8, 31 = 5, 32 = 0, 33 = 5; n = 34.

Number and Position of Rectrices

The number of rectrices in our sample of Florida Brown Pelicans varies from 19 to 24 (Table 3), with 22 being the most common (45%) and 19 and 24 uncommon (1% each). We found no differences between adults and juvenals, but males generally have more tail feathers than females ($P < 0.001$).

Most birds have either an equal number of rectrices on each side of the pygostyle or more feathers on their right side; a few birds have more feathers on their left side (Table 4).

Age Adult Plumage is Acquired

Brown Pelicans appear sexually monomorphic in plumage and colors and we find it impossible to age an individual once adult plumage has been acquired. Within our sample, most 32–36-month-old birds are in adult plumage (Figs. 4A, D; 5A) and nearly all birds over 40 months old are adults (Figs. 4C; 5B, D; 6E). A few specimens (Figs. 4C, D; 5A) indicate that females acquire adult plumage earlier than males. We have found one female only 20 months old (Fig. 4B) in adult plumage.

Head Color

Dark speckling may appear on the head in the post-breeding season (July–October) to varying degrees (Fig. 5A, F vs Fig. 6C, D, F). This speckling does not appear to be sex-related but may be age-related since younger birds have more dark feathers in the head than do older ones. Some birds have pure white heads and we suspect that these are older adults. The oldest known-age bird (66 months, Fig. 6E) has many dark feathers.

White on the Lateral Portions of the Proximal Neck

The extent of the white which remains on the sides of the neck is highly variable (see arrows, Fig. 5D and F as extremes). We measured the length of the white (between points indicated by the two arrows in Fig. 5F) along the anterior edge of the neck and from the base of the gular pouch to the change in feather texture on the breast in specimens of known sex from the Natural History Museum of Los Angeles County, Field Museum of Natural History, and United States National Museum of Natural History collections of *Pelecanus occidentalis carolinensis.* The white is significantly longer in males (n = 30, mean = 46 mm) than in females (n = 43, mean = 33 mm, $P > 0.001$). Some females entirely lack the white but it is always present in males.

Contour Feather Color

Birds 32–36 months old generally have the adult dark brown belly, but one 34-month-old female (Fig. 7C) has a white belly with heavy dark speckling. The back of this individual is essentially that of a full adult but with considerable dark edging to the scapulars. Individuals vary widely in the shape and color of the back feathers, which is probably more related to age than sex (Fig. 7B–D). Older adults have silver-gray scapulars (Fig. 9A, B) and younger birds have more dark brown-black on the edges of the feathers (Figs. 7A, C; 8B). By the time feathers are 12 months old they are very worn (Fig. 10D). In some instances, there may be even older feathers on portions of the body which, for some reason, did not molt the previous year.

SEASONAL AND GEOGRAPHIC VARIATION

Seasonality

Our best data on seasonal variability come from Tampa Bay on the middle west coast of Florida, where we made weekly counts of plumage types from January 1969 through April 1976 (Schreiber, 1979, 1980; Schreiber and Schreiber, 1983). Dark necks began appearing in the local breeding population in early January 1972; in the second week of January 1973; in the third week of January 1975 and 1976; in the first week of February 1969, 1970, and 1971; and in the second week of February 1974 (Fig. 11). All adults had dark necks by the first week of June in all years, and usually over 90% of the adults were dark-necked by early May. White necks began to appear in the last week of September or first week of October and all birds had white necks in either late November or early December. The cycle appears to be closely tied to the onset of nesting, which in this population is proximately controlled by winter temperatures (Schreiber, 1980).

Data for other areas of west coast Florida indicate a similar cycle to that in Tampa Bay, with dark-necked birds appearing 2–3 weeks earlier in the warmer, more southern region and in the Pelican Island population on the east coast of Florida. Yellow heads are also acquired earlier in the fall (Schreiber and Schreiber, unpubl. data). Observations from Puerto Rico (Schreiber et al., 1981) and St. Thomas and St. Croix, U.S. Virgin Islands (Schreiber and Schreiber, unpubl. data) in-

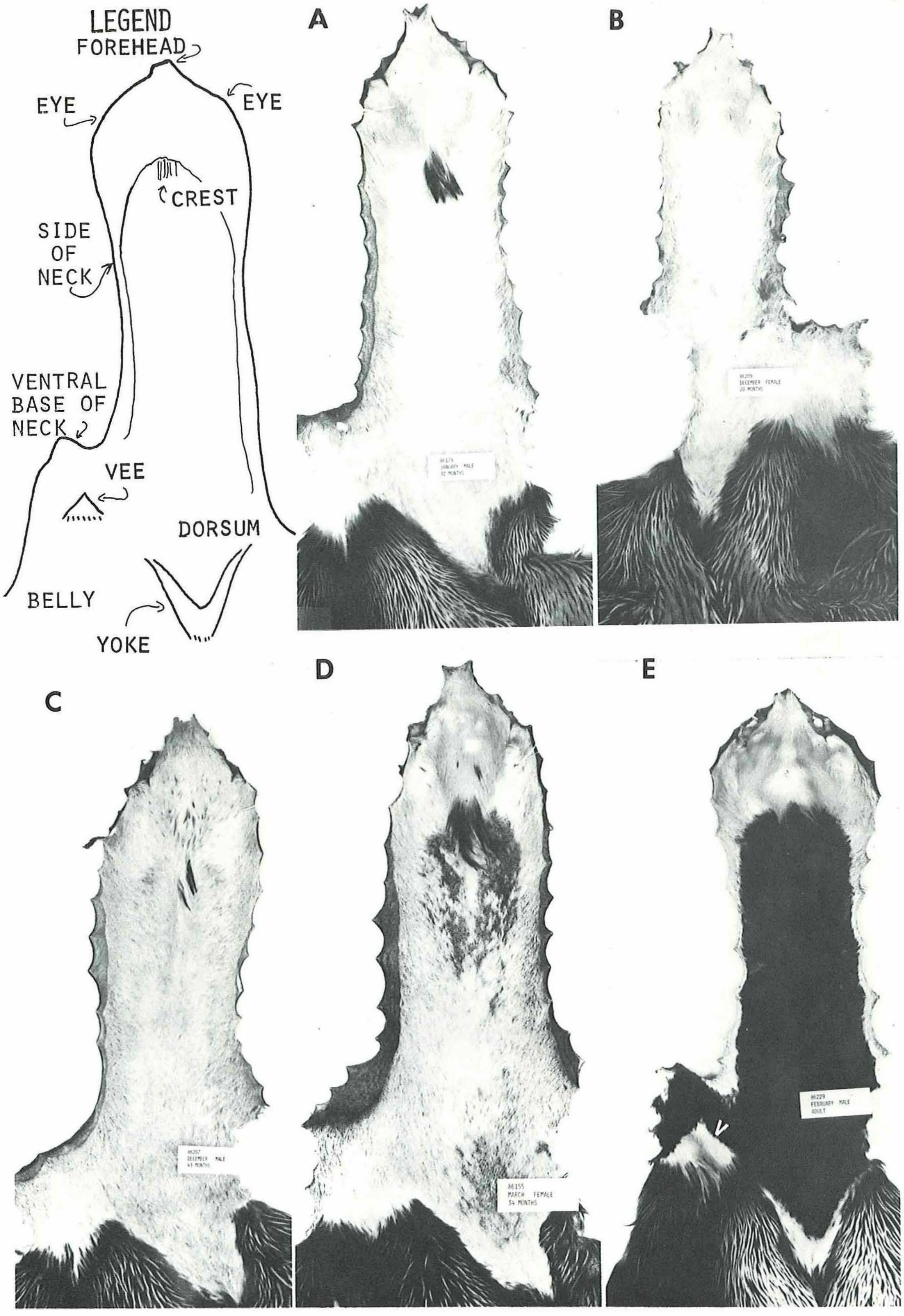

Figure 4. Adult Brown Pelican head and neck feathers: **A,** LACM 86179, January, male, 32 months old; **B,** LACM 86209, December, female, 20 months old; **C,** LACM 86207, December, male, 43 months old; **D,** LACM 86155, March, female, 34 months old; **E,** LACM 86229, February, male, adult.

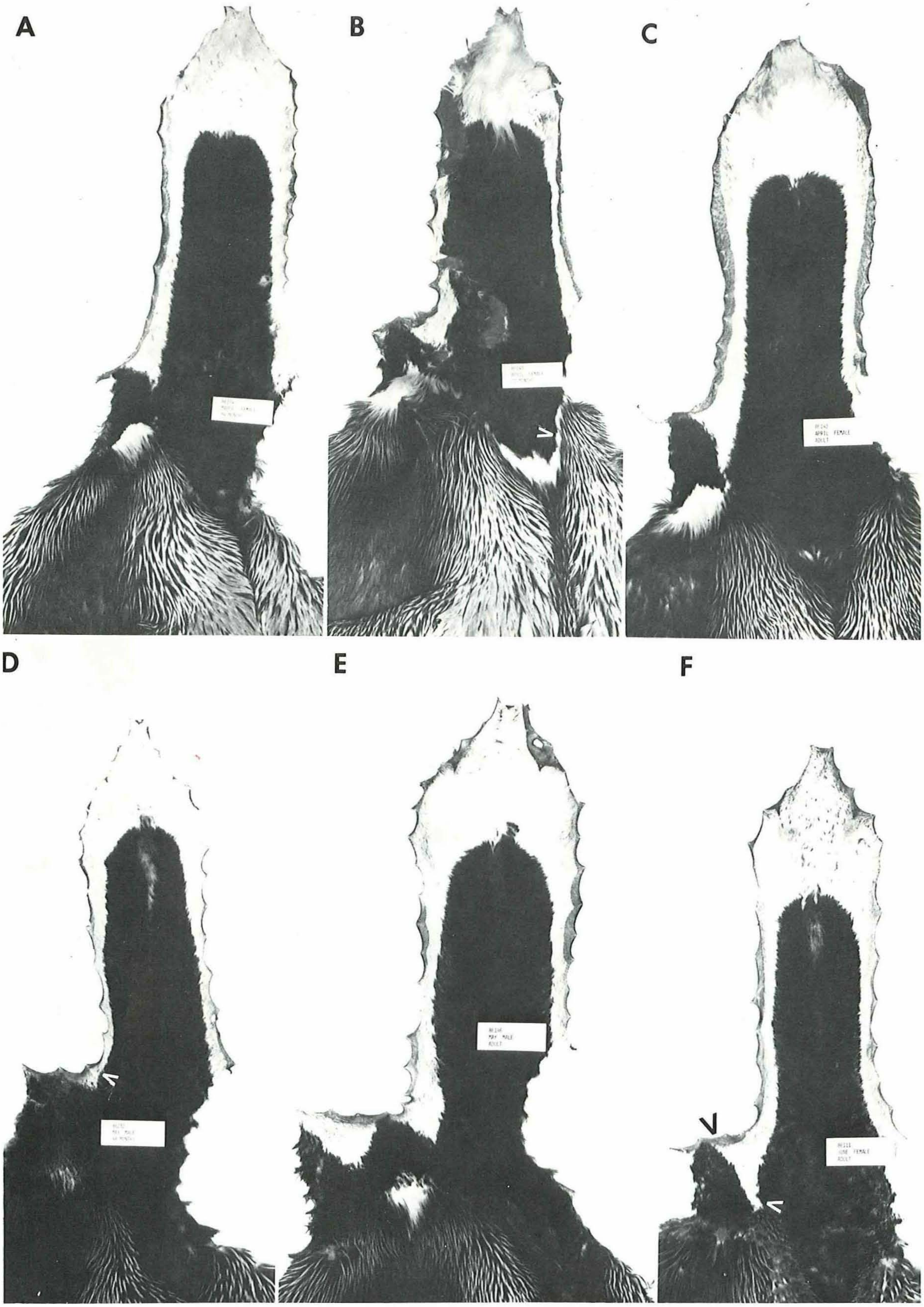

Figure 5. Adult Brown Pelican head and neck feathers: **A,** LACM 86154, March, female, 34 months old; **B,** LACM 86149, April, female, 72 months old; **C,** LACM 86142, April, female; **D,** LACM 86232, May, male, 48 months old; **E,** LACM 86146, May, male; **F,** LACM 86111, June, female.

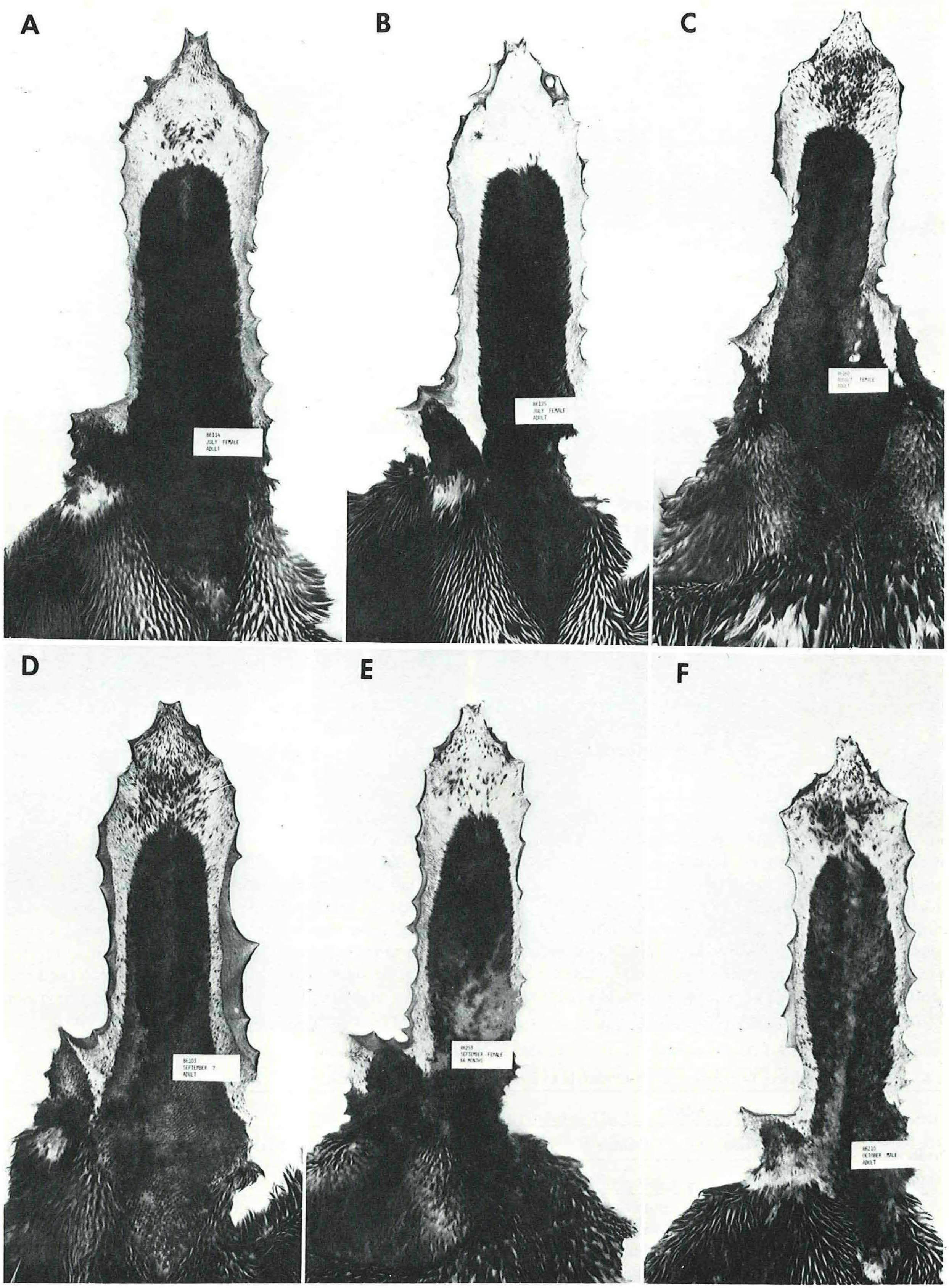

Figure 6. Adult Brown Pelican head and neck feathers: **A,** LACM 86114, July, female; **B,** LACM 86125, July, female; **C,** LACM 86160, August, female; **D,** LACM 86103, September, ? sex; **E,** LACM 86253, September, female, 66 months; **F,** LACM 86210, October, male.

Table 3. Number of rectrices in Brown Pelicans from Florida.

Number of rectrices	Adults				Juvenals				Total				Sum	
	Male		Female		Male		Female		Male		Female			
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
19	0	—	1	4	0	—	0	—	0	—	1	2	1	1
20	1	3	10	37	3	8	2	8	4	6	12	23	16	13
21	9	30	6	22	10	27	10	37	19	28	16	30	35	29
22	15	50	10	37	16	43	13	50	31	46	23	43	54	45
23	4	13	0	—	8	22	1	4	12	18	1	2	13	11
24	1	3	0	—	0	—	0	—	1	2	0	—	1	2
	30		27		37		26		67		53		120	

The mean number of feathers of males is significantly greater than for females: $t = 3.687$, $P < 0.001$.

dicate less rigorous scheduling of head and neck molt in adult pelicans in those regions. Interpopulational variation in timing of molt may be quite considerable depending on both climatic control on breeding and variation in the food supply during breeding and molt.

Our data for the east coast of the United States indicate that while breeding populations are separate, wintering populations are mixed (Schreiber, 1980; Schreiber and Mock, 1988), thus confusing any interpretation of timing of molt from field observation only. This is probably also true for west coast U.S. birds seen away from their nesting areas.

Geographic Variation

The major external characteristic used to discriminate *Pelecanus occidentalis californicus* (Fig. 2A) from the eastern *P. o. carolinensis* and *P. o. occidentalis,* in addition to their smaller size (Palmer, 1962; Wetmore, 1945), is the color of the gular pouch. *Pelecanus o. californicus* have bright red on the proximal end of the pouch in December, the first sign of oncoming breeding condition. With the molt of the neck feathers in January–February, as birds move to the nesting colonies, the pouch stays red at the proximal third and the distal half changes from dark gray to dark green-gray.

Nearly all breeding birds in California and Baja California colonies have red pouches. The vast majority of breeding birds in Florida have blue-black-green pouches and we have seen only three individuals with red pouches. About 1% show some orange or yellow coloration.

JUVENAL PLUMAGES

First Year

The development of feathers during the nestling stage was described by Schreiber (1976). When young leave the nest site and colony they are a uniform brown-tan color with a white belly (Figs. 2; 13A; 14A, C; 17A). The marginal coverts have tannish (cinnamon) brown edges that wear off in 1–2 months. The white belly grades gradually without a distinct demarcation to brown on the sides. Most coverts and contour feathers are oblong and rounded, and their tips are light tan.

During the first year of independence little fundamental change occurs in the appearance of Brown Pelicans; however, molt does occur. The gray head and neck feathers of nestlings (acquired at 2 months of age) molt after fledging, and by 5–8 months of age they are darker brown. This molt progresses generally from posterior to anterior, spreading laterally on the head. On the neck new feathers grow up from the dorsum (Fig. 4C). Also at this time the white belly becomes more clearly demarcated from the dark sides (Fig. 12B, C). Light-shafted feathers begin to appear on the back, and gray scapulars appear (Fig. 14A–D).

The coverts of the underwing (the lining) are largely white at fledging, and during the first year this gives the young birds in flight the appearance of having white "wing-stripes." At 9–10 months post-fledging, the wings begin to molt, which is a good aging characteristic. Gaps appear in the secondary greater and middle coverts (Fig. 16B), and this absence of feathers is a clear indication of a 1-year-old bird.

Table 4. Position of rectrices in relation to the pygostyle in Brown Pelicans from Florida.

Position of rectrices	Adults				Juvenals				Total				Sum	
	Male		Female		Male		Female		Male		Female			
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
More on right side	12	40	9	33	16	52	12	46	28	46	21	40	49	43
Both sides equal	13	43	15	56	11	35	12	46	24	39	27	51	51	45
More on left side	5	17	3	11	4	13	2	8	9	15	5	9	14	12
	30		27		31		26		61		53		114	

Both males and females have significantly more feathers on the right side: paired comparisons, $t = 7.60$ (males), 5.63 (females); $P < 0.001$.

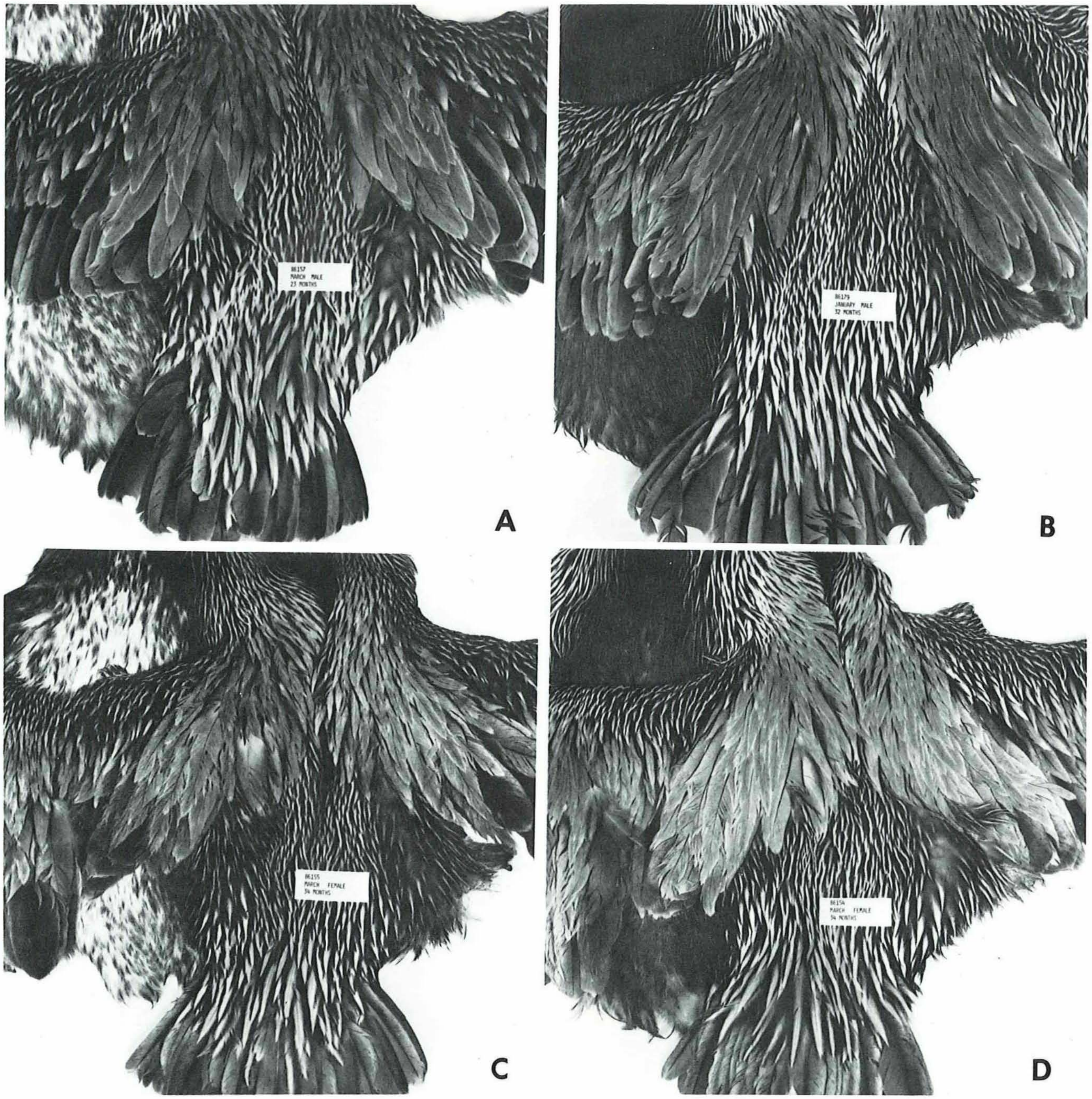

Figure 7. Adult Brown Pelican back and wing feathers: **A,** LACM 86157, March, male, 23 months old; **B,** LACM 86179, January, male, 32 months old; **C,** LACM 86155, March, female, 34 months old; **D,** LACM 86154, March, female, 34 months old.

Second and Third Years

During the second 12 months of independence, fundamental color changes gradually occur as juvenal Brown Pelicans begin to take on the patterns of adults. Much of the individual variation arising during this period may be sex-related, with females usually maturing more rapidly than males. Between 12 and 16 months of age, and sometimes for several more months, Brown Pelicans look ragged and scruffy with many gaps in the flight feathers and coverts. Contour feathers are very worn. The first full molt begins now and we suspect this is a time of stress for the birds since there is high juvenal mortality.

White feathers begin growing first on the sides of the head at 12–15 months and then on the neck (Fig. 12E–H); dark feathers grow on the sides of the body and begin to encroach onto the previously all white belly (Figs. 12D, E, G; 14B; 16A–D). The adult head pattern becomes more distinctive during the third year and at 32–36 months is fully developed. A white but increasingly speckled belly remains on most birds

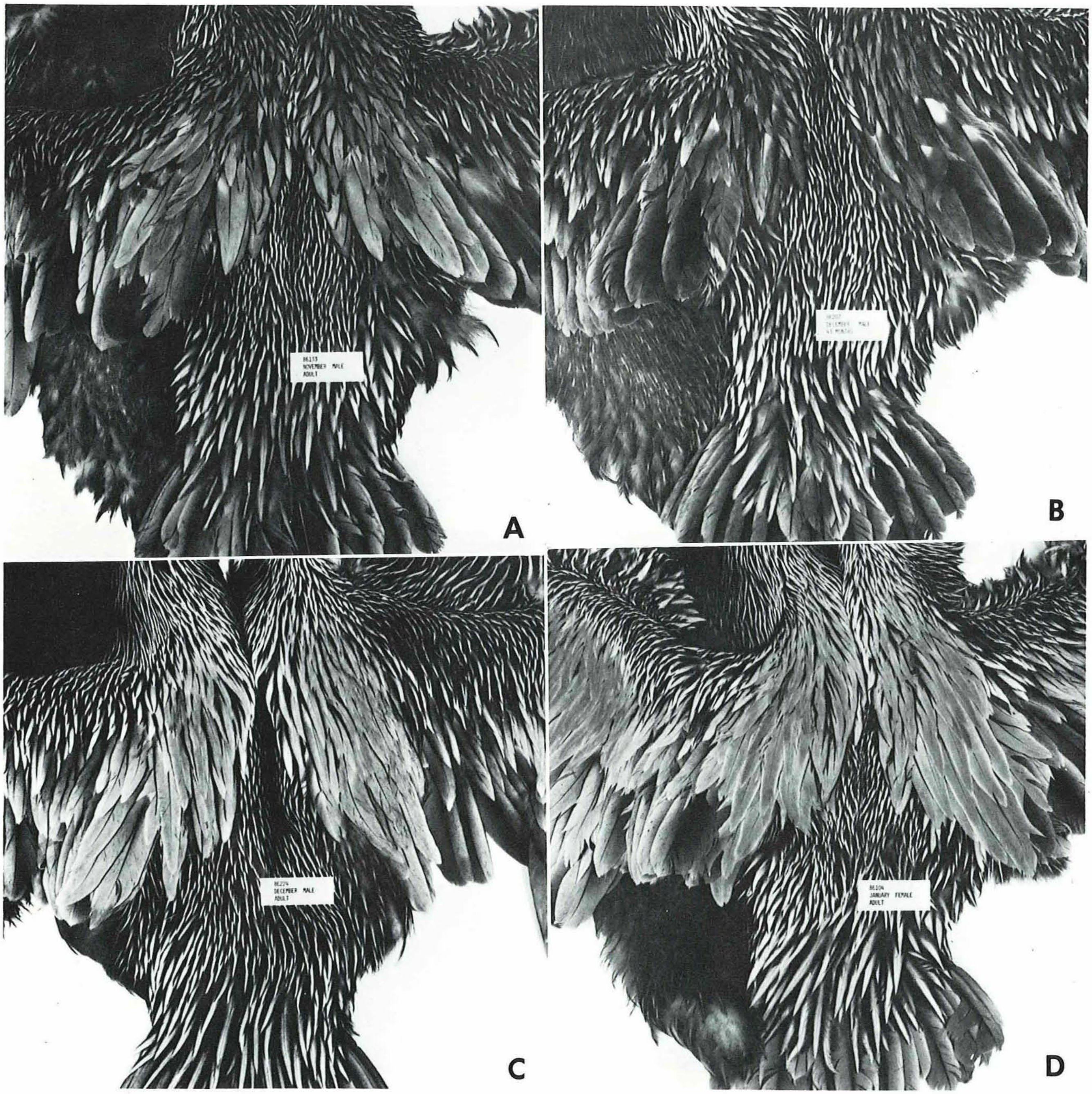

Figure 8. Adult Brown Pelican back and wing feathers: **A,** LACM 86133, November, male; **B,** LACM 86207, December, male, 43 months old; **C,** LACM 86224, December, male; **D,** LACM 86104, January, female.

during their third year. The 20-month-old female (Fig. 15B) with an all dark brown belly is unusual; the full dark belly is acquired at 32–36 months in most birds. White-shafted, dark-edged feathers fully cover the back at 20–24 months (Fig. 15C, D) but the amount of silver-gray is not as extensive, and the feathers are shorter and more rounded than in older adults. The scapulars, especially in the central area, still show dark feather edges and the wing coverts are less sharply demarcated than in adults.

Molt of coverts proceeds during the second year and much white appears in the wings because the white underlying feather bases are exposed (Fig. 16C). It is completed by 15–17 months. A 2-year-old bird (Fig. 16D) presents a combination of adult gray and juvenal brown feathers, with a preponderance of feathers similar to a 3-year-old or full adult (Fig. 16E) in which all coverts are gray and elongate and the marginals are white-shafted with dark brown-black edges. Wear occurs during February–July and by May (Fig. 16F)

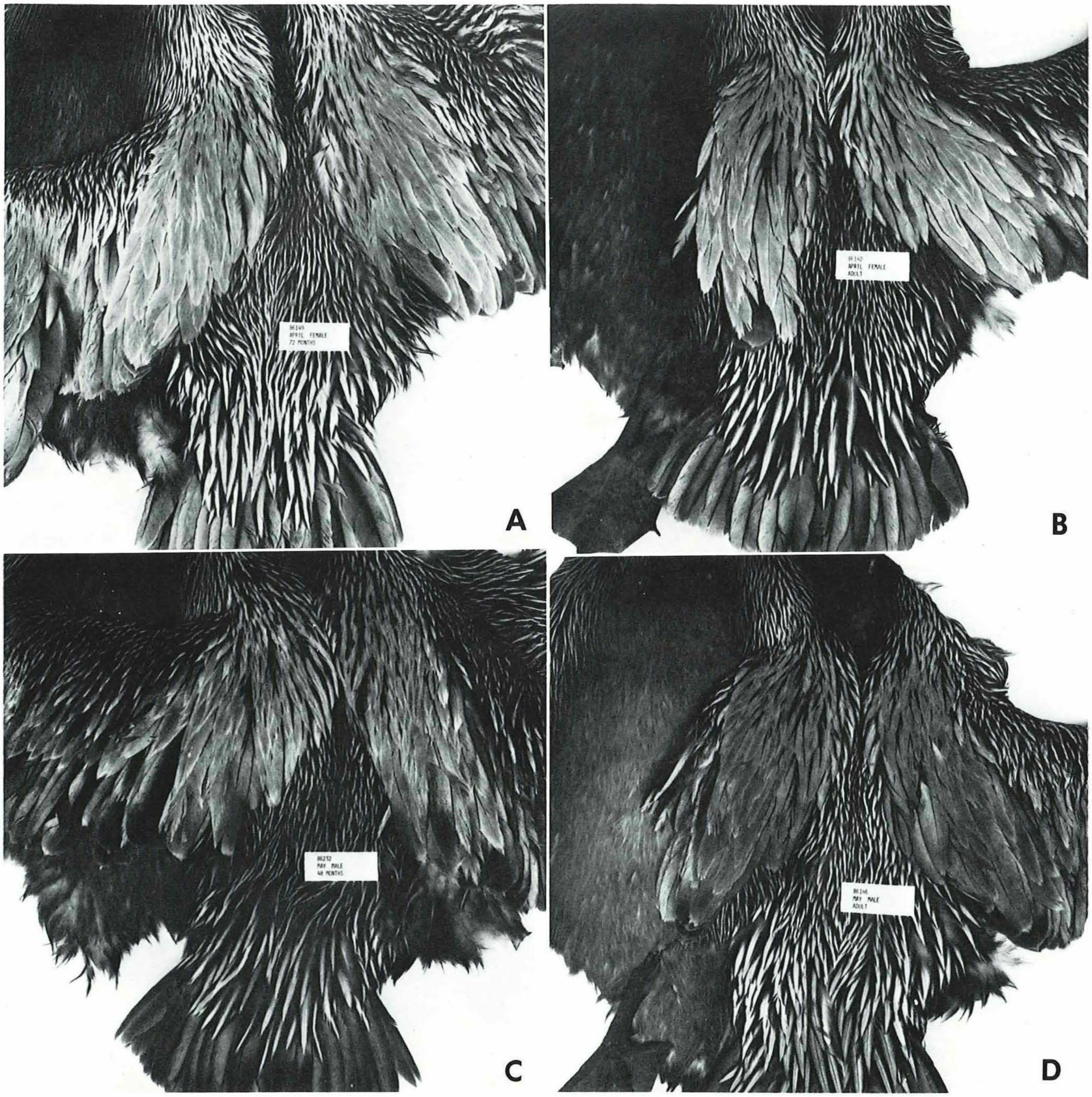

Figure 9. Adult Brown Pelican back and wing feathers: **A,** LACM 86149, April, female, 72 months old; **B,** LACM 86142, April, female; **C,** LACM 86232, May, male, 48 months old; **D,** LACM 86146, May, male.

the wings look tan and worn, rather than being fresh silver-gray. The underwing coverts gradually are replaced by silver-brown feathers, and the underwing-stripe of young birds disappears. This happens at about the same rate and time as the color change of the belly; however, a few adult-plumaged pelicans on both coasts still retain the wing-stripe. We suspect these are young adults, and with further research this character may prove useful as an additional field mark for age determination.

Captives

We made the following observations on two captive birds that provide details not available from specimens or field observations. At 12–14 months of age, as the first molt occurs, the new marginal coverts are very dark, in sharp contrast to their very worn and tan appearance until this age. Some pale yellow appears at the tip and on the sides of the all brown-gray juvenal bill. Between 16 and 19 months the bill

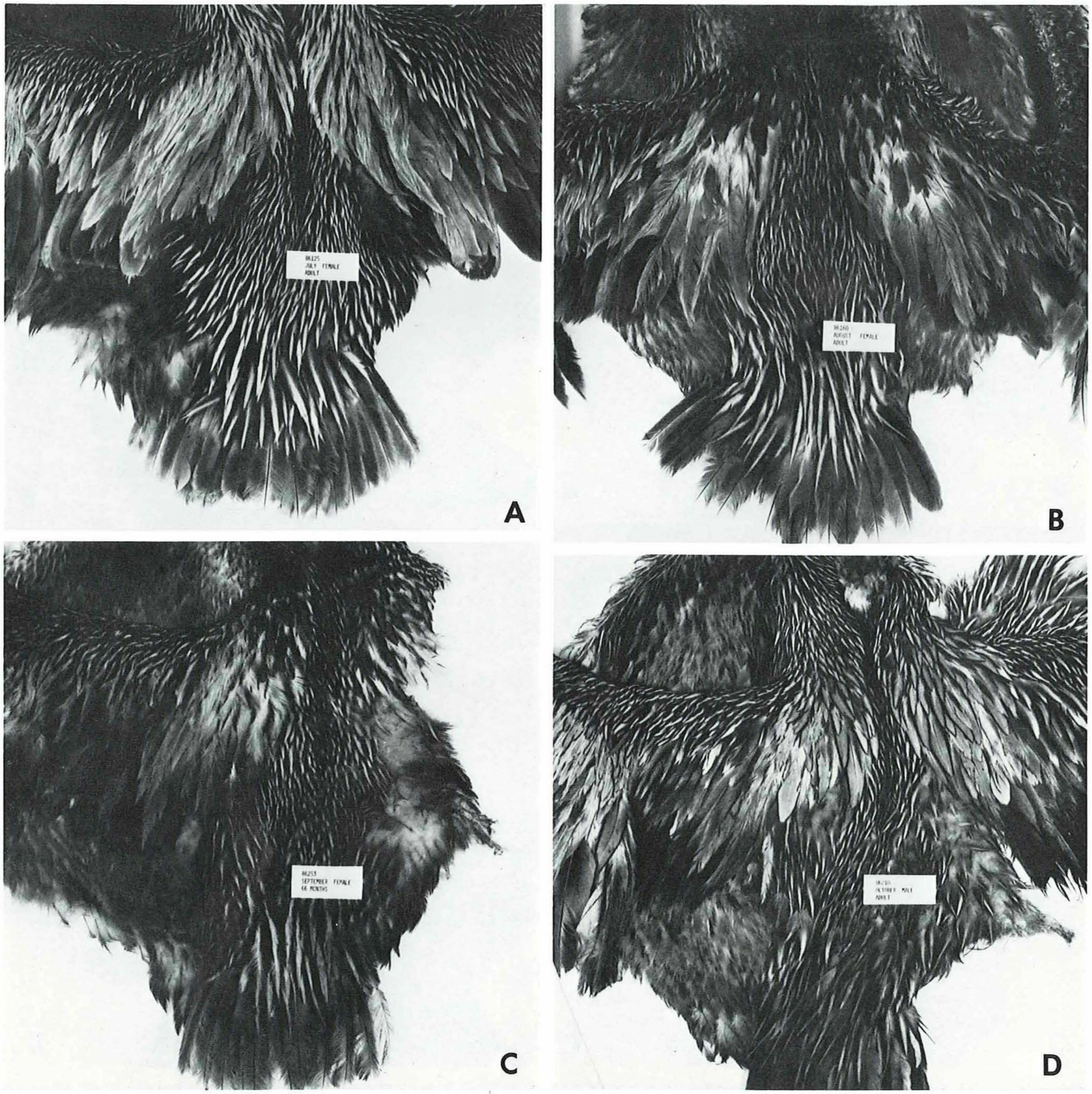

Figure 10. Adult Brown Pelican back and wing feathers: **A,** LACM 86125, July, female; **B,** LACM 86160, August, female; **C,** LACM 86253, September, female, 66 months old; **D,** LACM 86210, October, male.

becomes gray-green-yellow with some orange. The eye ring becomes lightish pale blue rather than black. A 2-year-old bird retains the same color and pattern as a juvenal but has undergone a complete molt of the secondaries and all body feathers; it will have some white in the head and may have a pinkish eye ring. By 29 months of age the wing coverts have molted into all gray feathers; white-edged, elongate feathers are common on the back and white feathers are quite distinct on the head. At 29–37 months, orange becomes more distinct on the bill, the flanks are distinctly striped, the white vee or diamond on the chest becomes distinct, and the head acquires the adult pattern (taking about 6 weeks to molt all head feathers). A 31–33-month-old bird has a pale yellow head, tan neck, orange bill, white belly, and still-dark eye.

During the following 2 months speckles appear in the belly, the bill continues to brighten, and the pouch may become reddish (in California birds only).

At 34–35 months the head is yellow, the neck dark, the bill orange, the belly speckled, the back and wings brown-gray, the eye light, and the eye ring pink. The colors in the bill fade over 1 month, and by 38 months of age all soft part and head colors have faded and the eye is again dark. The back of a 39–41-month-old bird is much darker brown than the silver-gray or worn gray of full adults. Additionally, the belly contour feathers maintain white centers and many speckles remain in the head. The final molt to full adult plumage of dark brown belly, yellow head, white neck, gray back, orange bill, and pink eye ring requires 1 month in captive birds. This timing is similar to what we noted in the field for the general population.

SOME COMPARISONS BETWEEN ADULT AND JUVENAL CHARACTERISTICS

Skin and Feather Weight

We compared the weight of birds with the dried weight of their skin and feathers (Table 5). Males are heavier (and larger) than females and their skin and feathers are also heavier. Both sexes of adults are heavier than similar-sexed juvenals. However the skin and feathers of adult males comprise a lower percentage of body weight (8.3%) than those of juvenal males (9.4%): the same is true for adult females (8.5%) versus juvenal females (8.9%). Some of that weight is of course the skin, but we believe it is minimal compared to the feather weight. Feather weights are known to comprise approximately 10% of body weight in birds (Lucas and Stettenheim, 1972).

Color and Shape of Contour Feathers

The contour feathers of Brown Pelicans not only undergo changes in color and shape during the annual cycle of the adult but also change in color and shape as the birds mature (summarized in Table 6). In Brown Pelicans all feather tracts are connected and if apteria exist they are not obvious. For ease of discussion we name the locations of the tracts from which we used feathers.

Juvenal feathers are oblong-elongate with rounded tips. Adult feathers are narrow and pointed and tend to be smaller than those of younger birds. In all areas of the body the plumaceous portion of the vane is more highly developed in juvenals than in adults (terminology of Lucas and Stettenheim, 1972, see fig. 158). There are shape changes which occur in feathers of adults as they wear.

In Figures 17–21 we illustrate shape and color of feathers taken from the same location within a feather tract of four individuals: LACM 86117, August, female, 6 months old; LACM 86192, June, male, 14 months old; LACM 86154, March, female adult, 36 months old; and LACM 96160, August, unknown-age female adult. The differences illustrated and discussed are not related to sex but rather are influenced by age and time of year.

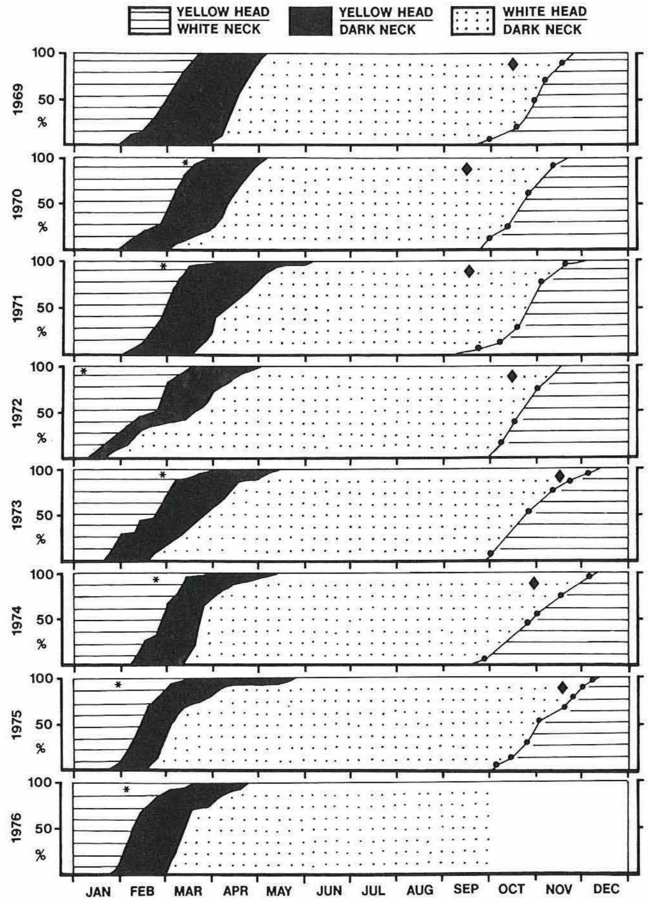

Figure 11. The annual cycle of head and neck coloration of the Brown Pelican population on Tarpon Key, Tampa Bay, Florida west coast in 1969–1976. The diamond in September–November indicates the date the colony was abandoned, and the * in January–March indicates the date nests were first observed (see Schreiber 1980 for details on nesting chronology).

The feathers from the crest in the capital tract on the back of the head (Fig. 17) are wider in shape in juvenals (Fig. 17A) than in adults (Fig. 17B–D). Both white (Fig. 17B) and dark (Fig. 17C) feathers found in the same individual adult in March are essentially the same shape. The rachis and portions of the vane wear drastically through the year in adult feathers (Fig. 17D) but wear to a lesser extent in younger birds (not illustrated).

Feathers from the right side of the interscapular tract at the posterior end of the scapulae (Fig. 18, upper) show the distinctly more rounded shape of younger birds (Fig. 18A, B vs C, D). Feathers less than 1 year old (Fig. 18A) are brown in the distal portion with large areas of white basally. The amount of white decreases during the second year (Fig. 18B) and is essentially gone in adults (Fig. 18C, D). These feathers are gray-brown distally and have dark margins. Fresh adult feathers are gray without distal dark margins. The distal portion of the vane wears drastically and by the time a feather is 8–10 months old, it appears white or tan rather than silver-

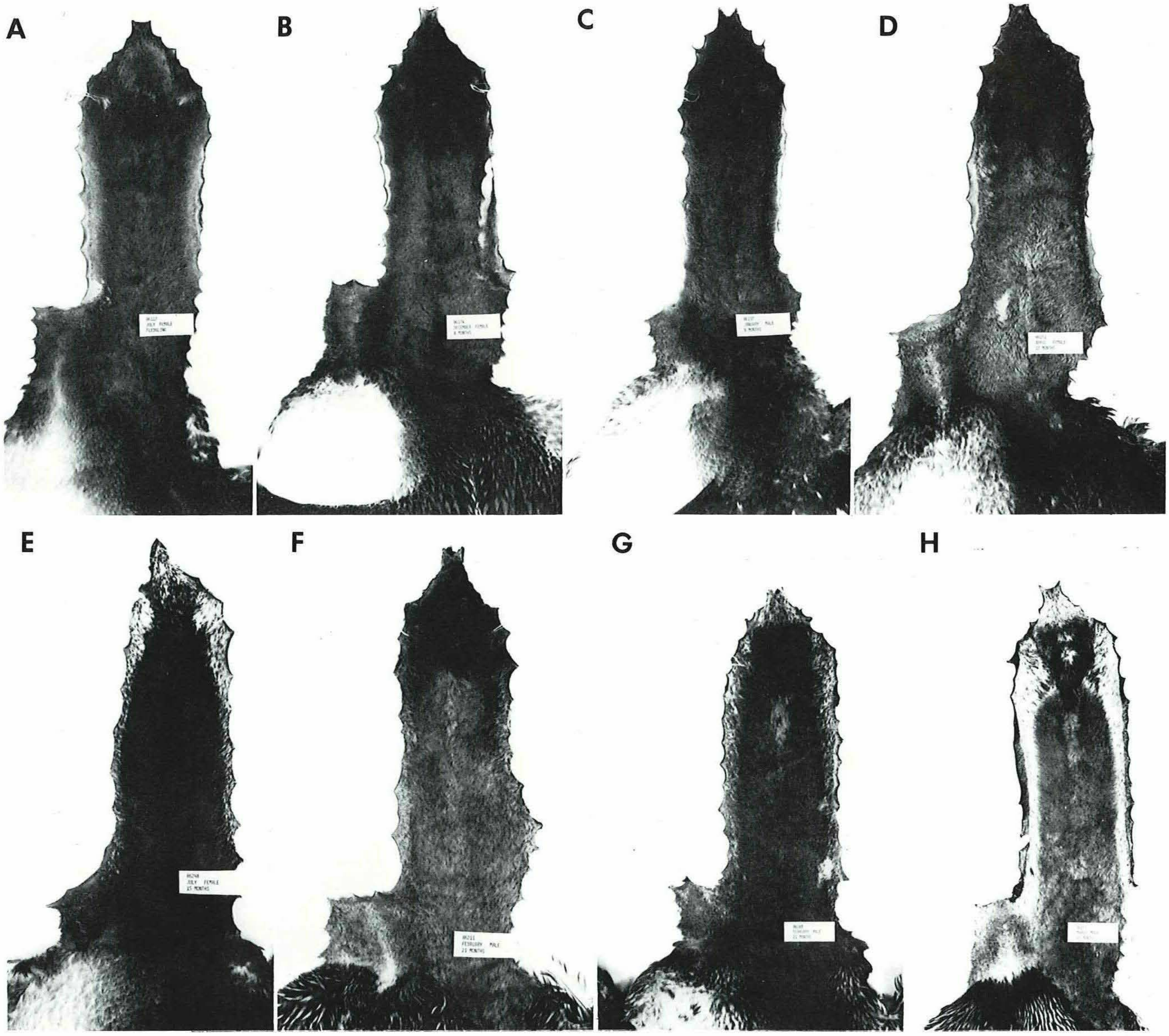

Figure 12. Juvenal Brown Pelican head and neck feathers: **A,** LACM 86117, July, female, "fledgling"; **B,** LACM 86174, December, female, 8 months old; **C,** LACM 86137, January, male, 9 months old; **D,** LACM 86151, April, female, 12 months old; **E,** LACM 86248, July, female, 15 months old; **F,** LACM 86211, February, male, 21 months old; **G,** LACM 86183, February, male, 21 months old; **H,** LACM 86157, March, male, 25 months old.

gray. The "downy" bases of the adult feathers do not appear to wear, probably because they are protected from abrasion.

The mid-back feathers of juvenals (Fig. 18E) frequently retain vestiges of natal down (prepennae) on the rachis tip and show wear distally even when only a few months old. The proximal "downy" portions of the vane are large and the feathers of this tract in the first pennaceous plumage are larger than when birds are older. They also are brownish gray, the same color as the 14-month-old bird (Fig. 18F), whose feathers are quite short. The mid-back feathers of adults are strikingly silver distally along the rachis but have dark brown-black margins (Fig. 18G). Within 5 to 8 months these feathers become shorter, colors fade, the surface is abraided, and the rachis and barb tips wear off (Fig. 18H).

The greater secondary coverts in juvenals (Fig. 19A) are somewhat more pointed at the tips than those in adults and are brown where fresh adults' vanes are gray (Fig. 19C). Adult feathers when 8–10 months old are worn at the tip and the gray is gone from the vanes, giving the feathers a more blunt shape (Fig. 19D). Lesser secondary coverts (Fig. 19E–H) are distinctly different between juvenals and adults. During the birds' first year, feathers are larger than after the first molt but the amount of white basically remains the same (Fig. 19E, F). Second-generation feathers (Fig. 19F) are shorter

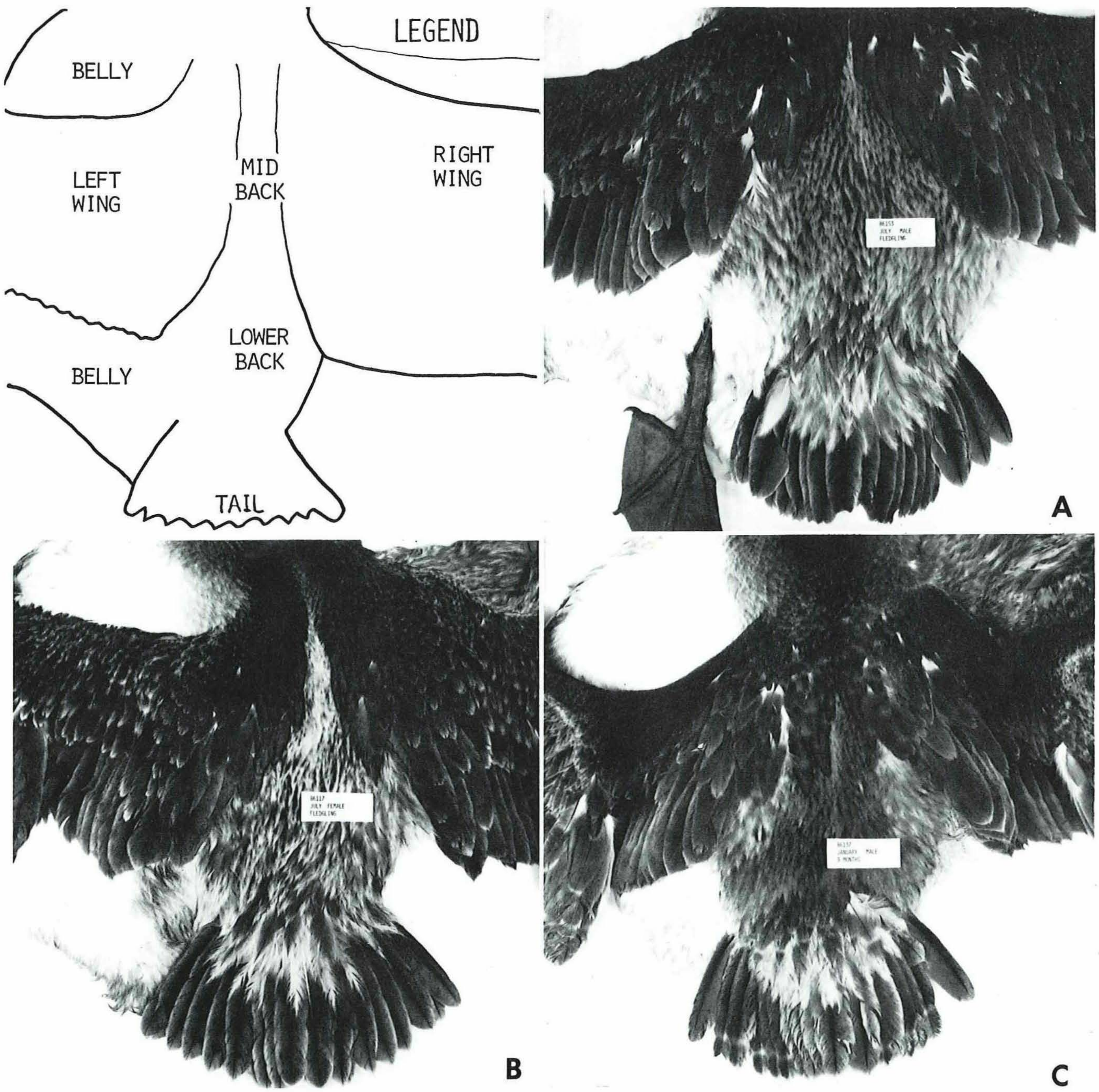

Figure 13. Juvenal Brown Pelican back and wing feathers: **A,** LACM 86153, July, male, "fledgling"; **B,** LACM 86117, July, female, "fledgling"; **C,** LACM 86137, January, male, 9 months old.

than those of adults, which are narrower and lack any white in the bases (Fig. 19G, H).

Marginal coverts from the proximal manus (Fig. 20, upper) of juvenals have white bases and are more rounded than the silver-centered, black-margined adult feathers (Fig. 20B). Marginal coverts from the distal manus (Fig. 20, upper trio on right) illustrate a gradual change from first year (Fig. 21C) to adult (Fig. 20E), becoming shorter, more pointed, and more distinctly colored as the bird matures.

Contour feathers from the mid-line of the belly (Fig. 20, lower) have considerable development of the plumulaceous portion of the vane. Juvenal feathers (Fig. 20F, G) are shorter than those of adults (Fig. 20H, I); first-year feathers are all white, second-year feathers are grayish brown, and fresh adult feathers are dark brown-silver. These wear uniformly to brown, with tips and distal portions wearing the most.

Feathers from the left femoral tract just anterior to the head of the femur (Fig. 21, upper) show a pattern similar to

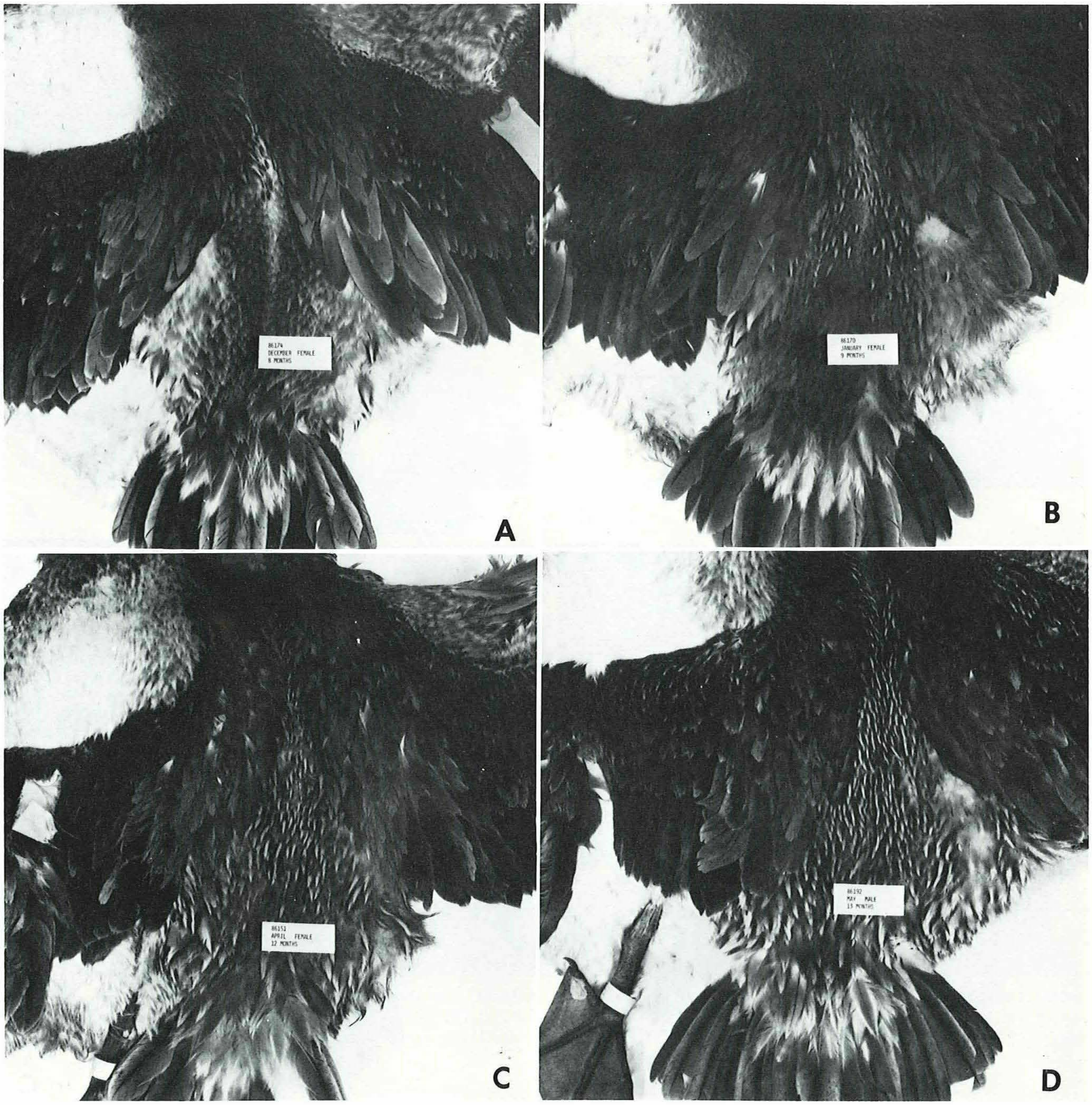

Figure 14. Juvenal Brown Pelican back and wing feathers: **A,** LACM 86174, December, female, 8 months old; **B,** LACM 86170, January, female, 9 months old; **C,** LACM 86151, April, female, 12 months old; **D,** LACM 86192, May, male, 13 months old.

that of feathers from the back. Juvenal feathers (Fig. 21A) are oblong-ovate while adults are elongate-pointed (Fig. 21B, C). Adult feathers wear during the year, particularly the dark margins and gray distal half. Underwing coverts [illustrated by a feather from the second row, Secondary (S) 10, Fig. 21D] of juvenals are white with a pale brown wash on the vanes. They are longer and wider than the white-centered, dark-margined adult feathers (Fig. 21E). Underwing coverts from the center of the humerus (Fig. 21F, G) show similar differences between juvenals and adults. These underwing coverts do not wear dramatically in adults.

In summary, the body and contour feathers of adults and juvenals are distinctly different in both color and shape (Table 6). As birds mature, brown or white feathers are replaced by silver-gray or black ones which are frequently two-toned in color.

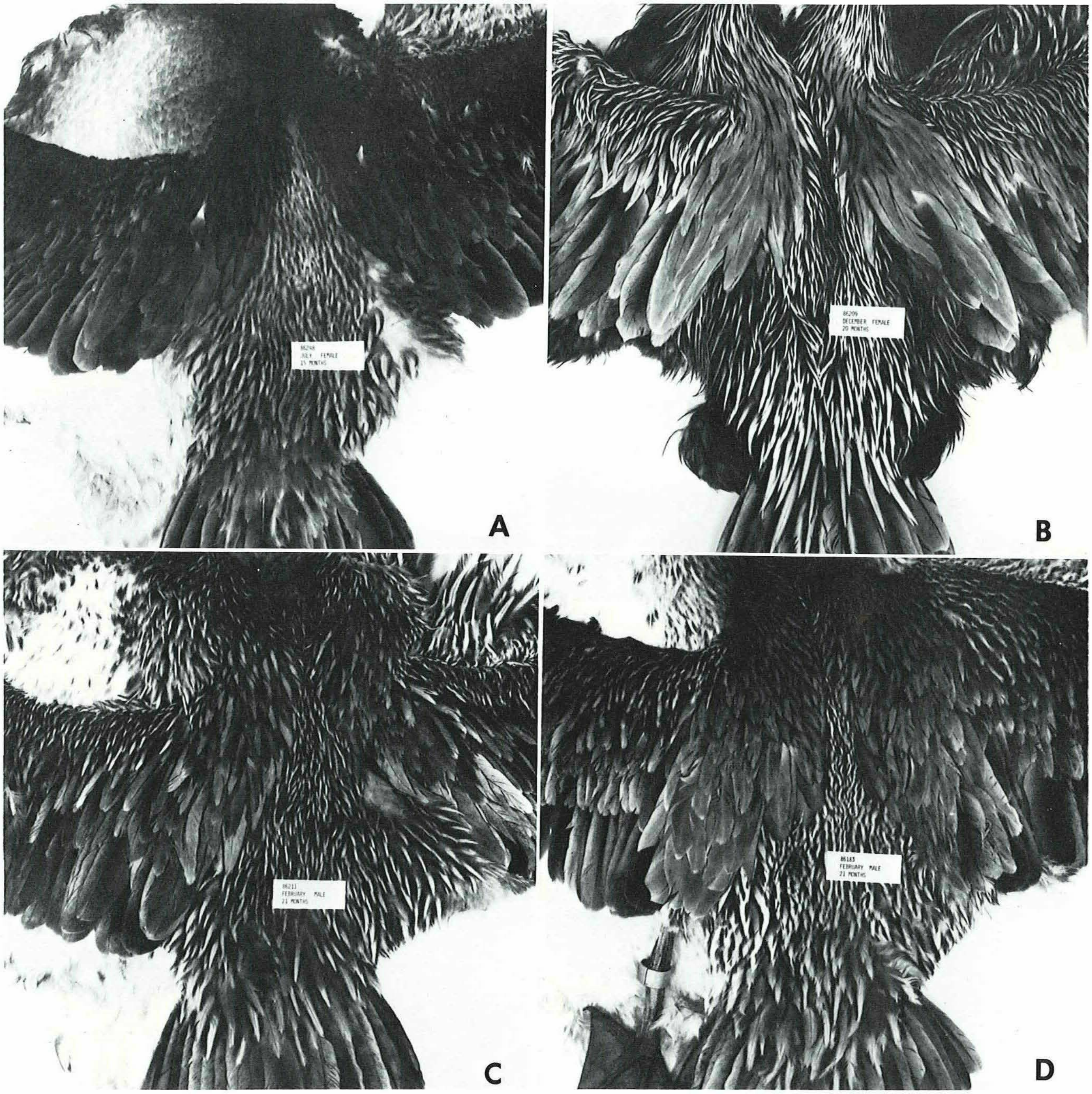

Figure 15. Brown Pelican back and wing feathers: **A,** LACM 86248, July, female, 15 months old; **B,** LACM 86209, December, female, 20 months old; **C,** LACM 86211, February, male, 21 months old; **D,** LACM 86183, February, male, 21 months old.

TIMING OF MOLT

In this section we present data on symmetry and presence/absence of molt, molt in individual feathers, and molt in individual birds.

An analysis of molt in primaries, secondaries, and rectrices of 524 specimens available from North and South Carolina (10), Florida (490), and Texas–Louisiana (24) shows the annual pattern of molt and differences between juvenals, subadults, and adults (Figs. 22–24).

Symmetry of Molt

Of 101 Florida adults, 92 (91%) showed no differences between the right and left wings in primary molt; of 130 juvenals (up to 2 years old), 129 (99%) showed no differences. Differences that did occur were of the following nature:

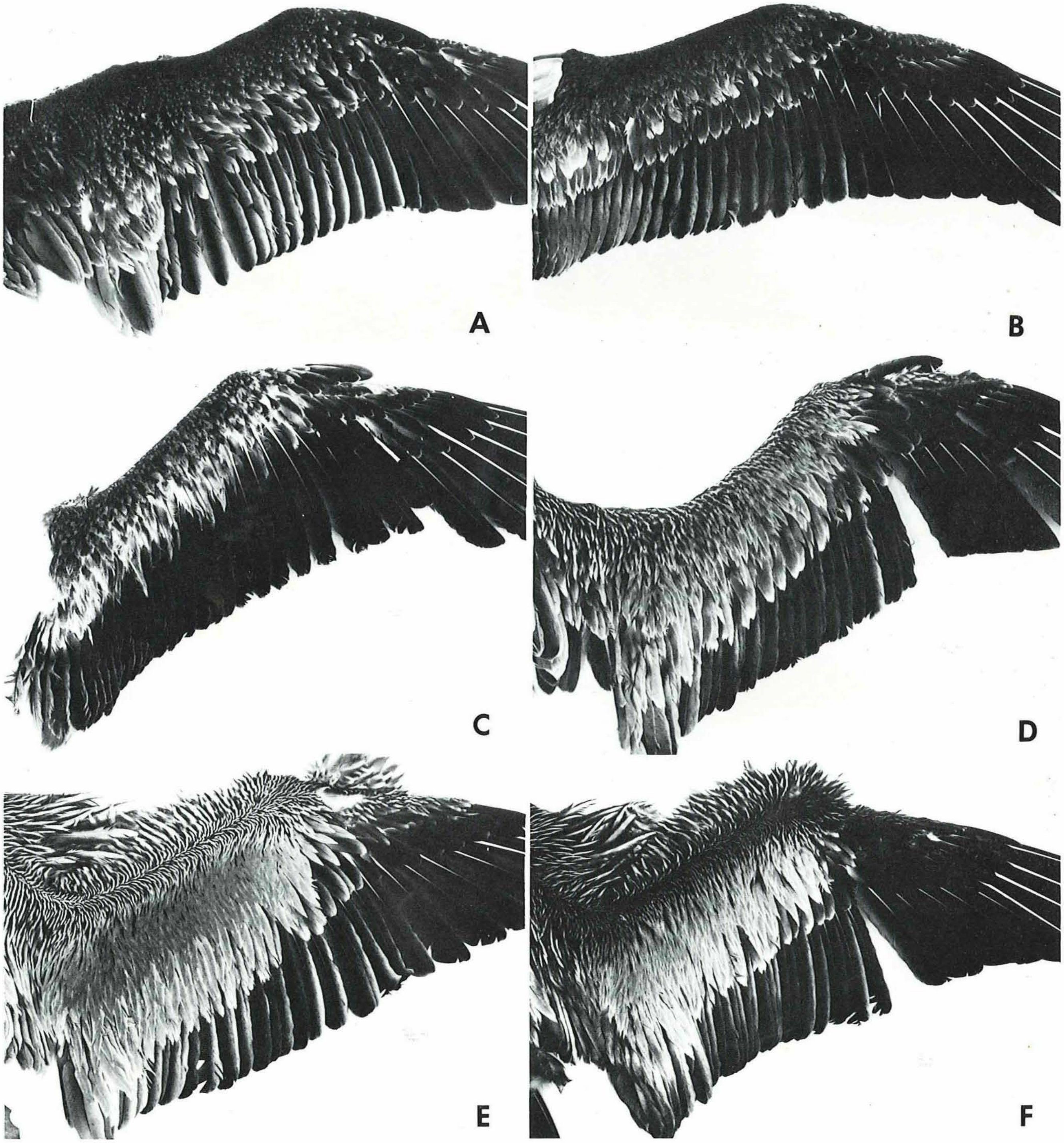

Figure 16. Brown Pelican wings: **A,** LACM 86137, January, male, 9 months old; **B,** LACM 91278, February, male, 10 months old; **C,** LACM 91240, May, male, 13 months old; **D,** LACM 86152, March, male, 23 months old; **E,** LACM 86179, January, male, 32 months old; **F,** LACM 86232, May, male, 48 months old.

A. Right primary: 1–5 new, 6 old, 7–10 new.
   Left primary: 1–5 new, 6 growing 1/8, 7–10 new.

B. Right primary: 1–4 old, 5 growing 1/2, 6–10 old.
   Left primary: 1–10 old.

C. Right primary: 1–5 new, 6 growing 1/2, 7–10 old worn.
   Left primary: 1 growing 1/2, 2–6 new, 7 socket, 8–10 old worn.

Secondary molt was the same in both wings of 53 (87%)

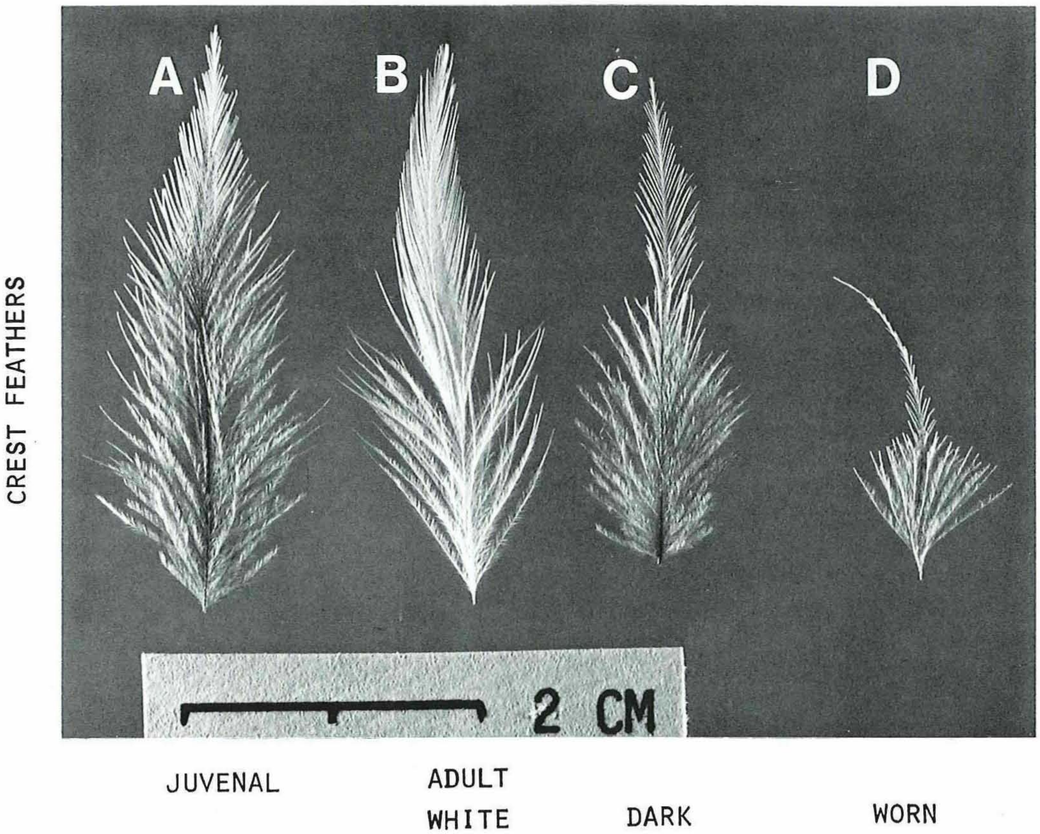

Figure 17. Brown Pelican crest feathers from the back of the head: a juvenal 6 months old (LACM 86153) and an adult (LACM 86179) fresh, white and dark in January, and worn in August. **A,** LACM 86153, juvenal, 6 months old; **B–D,** LACM 86179, adult, fresh in January (B, C), and worn in August (D).

adults and in 56 (89%) juvenals. When differences did occur between wings, they were generally in S 18–30. As in primary molt, the pattern remained the same, but the timing was shifted slightly.

These data indicate that primary and secondary molt of Brown Pelicans are essentially similar for both wings on a bird. In the following discussion, right wing data are used wherever possible, both for live birds and museum study skins.

Molt Patterns

In order to examine patterns of molt, and to provide data on the maturation process, we present illustrations of molt in two ways. First, in a sample of birds from the Florida west coast we recorded each feather as either fully grown (old or new), missing, or in some stage of growth (Figs. 25–27). We subjectively categorized each fully grown feather as new or old, based on color and condition (an index of wear) or obvious wear. Second, we drew molt maps of wings and tails illustrating the stage of molt of each feather of known-age, banded birds (Figs. 28A–C; 29; 30A–C), with age, sex, and date of examination noted. Individuals shown in Figure 29 are from the Florida west coast; these birds were born in Florida, transported to and released as fledglings in Louisiana, and later collected by the Florida Fish and Game Commission for pesticide analyses. Birds in Figure 30 are from Baja California and California. Essentially all specimens are in the Natural History Museum of Los Angeles County, prepared as flat skins, and the LACM specimen number or U.S. Fish and Wildlife Service band number is given. In Figures 28–30 each feather is shown as new or growing (shaded black) or as old or intermediate (unshaded). A new feather retains its new look for approximately 3–4 months. The amount of shading shows the feather length (drawn by eye), from an empty socket (shown as a line across the base of the feather; see Fig. 28A, third from bottom, S 26) to fully grown. Age estimates were determined by assuming a 1 April hatch date for both the Florida and California specimens. Since the number of rectrices and secondaries varies (Tables 3, 4), each wing or tail in the figures accurately represents the number present in that individual. We include all the illustrations of known-age birds over 12 months of age and a selection of younger specimens illustrating the variety. Those maps show the transition from juvenal to adult patterns and the adult cycle.

Adults. A few adults molt primaries in March–May (Fig. 22). The number of molting birds increases in June–July and most birds are molting in August–November. Primary molt is basically completed by December, 1–2 months prior to onset of nesting in most years (Schreiber, 1980). A few birds molt secondaries in March–June but most begin in July–

Table 5. Wet weights of Brown Pelicans from Florida and the dry mass of their skin and feathers.

	Adults			Immatures		
	Males	Females	Total	Males	Females	Total
Sample:	13	13	26	12	16	28
Wet weight						
Mean (g)	3,290	2,824	3,023	2,628	2,316	2,528
SD	509	677	644	962	661	676
Range	2,380–4,040	1,830–3,990		1,950–4,240	1,400–3,800	
Dry weight (skin and feathers)						
Mean (g)	274	241	258	247	207	224
SD	16.2	21.9	25.0	24.9	16.9	28.6
Range	240–310	220–270		220–300	180–235	

Adult male wet mass heavier than immature male wet mass: $t = 2.13$, $P < 0.05$; adult male dry skin heavier than immature male dry skin: $t = 3.18$, $P < 0.01$; adult female wet mass heavier than immature female wet mass: $t = 2.03$, $P < 0.05$; adult female dry skin heavier than immature female dry skin: $t = 4.59$, $P < 0.001$; adult wet mass heavier than immature wet mass: $t = 2.75$, $P < 0.01$; adult dry skin heavier than immature dry skin: $t = 4.66$, $P < 0.001$; adult male wet mass only marginally heavier than adult female wet mass: $t = 1.90$, $P < 0.1$; adult male dry skin heavier than adult female dry skin: $t = 4.157$, $P < 0.001$.

Correlation coefficients: adult wet mass versus dry skin: $r = 0.556$; adult male wet mass versus dry skin: $r = 0.498$; adult female wet mass versus dry skin: $r = 0.495$; immature wet mass versus dry skin: $r = 0.744$; immature male wet mass versus dry skin: $r = 0.694$; immature female wet mass versus dry skin: $r = 0.703$.

August, slightly later than primary molt. By September–November all birds are undergoing secondary molt. Frequency decreases in December–January and is completed by February, just as nesting begins.

Rectrix molt, which begins in May–June, while the adults may still be feeding large nestlings, takes longer than secondary molt and is not completed until February. The fewest birds are molting rectrices during February through May. Some adults with molt in their rectrices are found in all months of the year but probably few actually molt during nesting. The annual cycle of rectrix molt is not as distinct as that found in the primaries and secondaries.

Two simultaneous waves of molt involving Primary (P) 1 to P 4 or 5 and P 5 or 6 to P 10 are apparent, beginning with the inner feathers (P 1 and P 5 or 6). Secondaries and rectrices have no simultaneous waves of molt but rather clumps or foci of molting feathers occur.

In Figure 31 we graphically illustrate the generalized pattern of molt of the flight feathers and the color variations found in the remainder of the body in adult Brown Pelicans. We have represented the most commonly found condition in pelicans at each stage. These changes also represent, in a general way, subspecies from both coasts of the United States. The annual cycle and complicated nature of contour feather molt and coloration is visible here.

Juvenals. Head and neck feathers are replaced immediately upon independence, at the same season of year when these feather tracts are molting in adults. It may be that these feather tracts are worn in juvenals due to feeding inside the pouches of adults, but the immediate synchrony with adults in their molt may have no functional or adaptive significance.

Molt of the primaries and secondaries starts when juvenals are 12–14 months old (April–June) although some individuals may not molt any primaries or secondaries during their first year. Molt begins with feather 1 in the primaries and proceeds distally to P 10 in one wave through July–August,

Table 6. Summary of color and shape differences between juvenal and adult feathers.

Region	Juvenal Color	Juvenal Shape	Adult Color	Adult Shape
Head crest	brown	rounded, ovate	white or black	long ovate
Scapulars	brown	rounded, wide	gray-silver	narrow elongate
Mid-back	brown	rounded, wide	black edges, silver middle and tip	elongate
Greater secondary coverts	brown	wide round	gray-silver	wide rounded
Marginal coverts (mid-manus)	brown	wide pointed round	gray-silver	long pointed
Marginal coverts (proximal manus)	brown	wide pointed round	dark edges, gray middle	pointed
Belly	white	rounded, wide	black	long, oblong
Flanks	brown	rounded, ovate	black edges proximal, gray middle	narrow pointed
Underwing coverts	white	rounded	black edges proximal, gray middle	narrow pointed

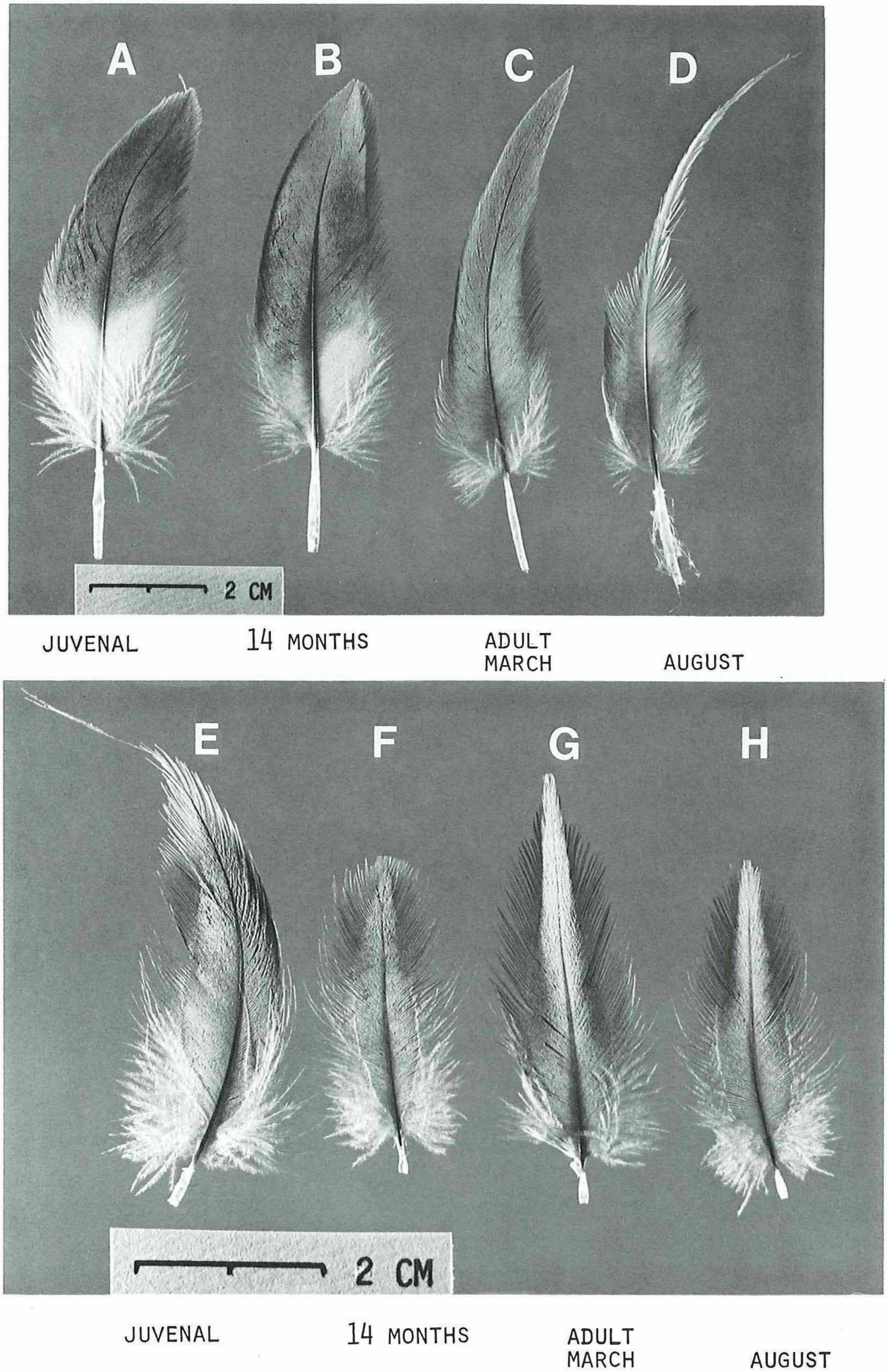

Figure 18. Brown Pelican mid-scapular feathers (upper) and mid-back feathers (lower): a juvenal 6 months old, a bird 14 months old, and an adult in March and August.

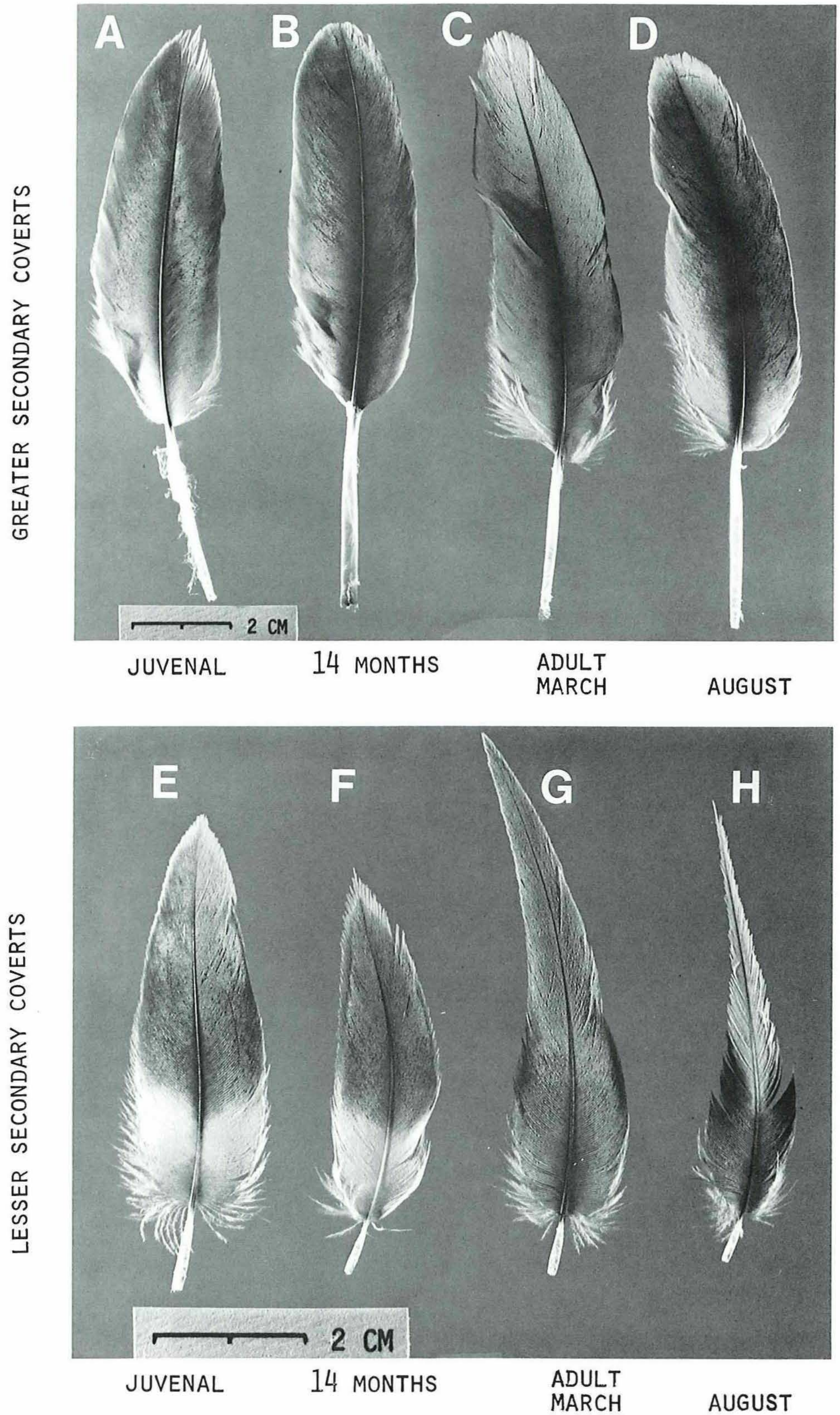

Figure 19. Brown Pelican greater secondary coverts; S 3, right wing (upper), and lesser secondary coverts from mid-humeral tract, right wing (lower). A juvenal 6 months old, a bird 14 months old, and an adult in March and August.

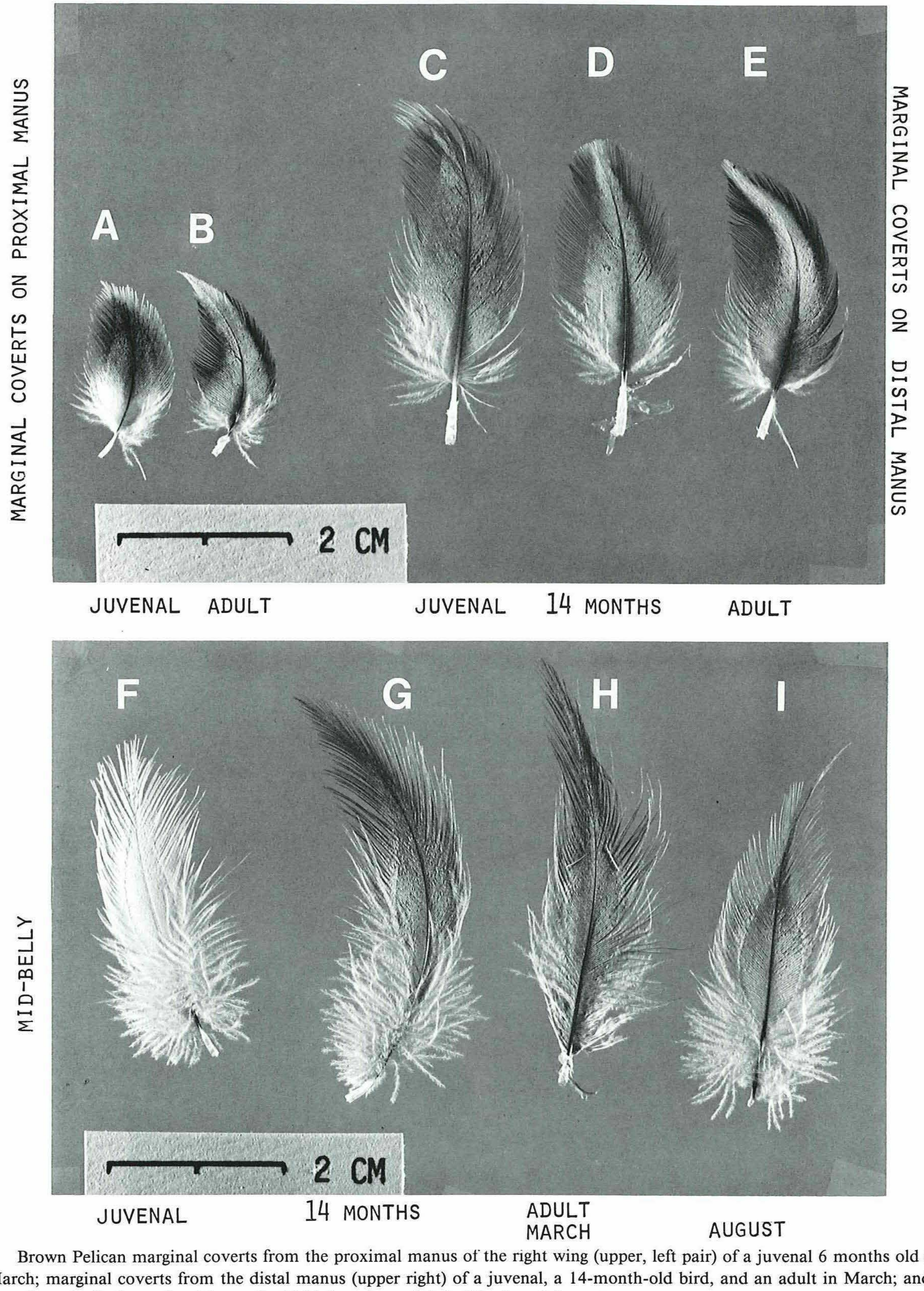

Figure 20. Brown Pelican marginal coverts from the proximal manus of the right wing (upper, left pair) of a juvenal 6 months old and an adult in March; marginal coverts from the distal manus (upper right) of a juvenal, a 14-month-old bird, and an adult in March; and mid-belly feathers (lower) of a juvenal, a 14 month old bird, and an adult in March and August.

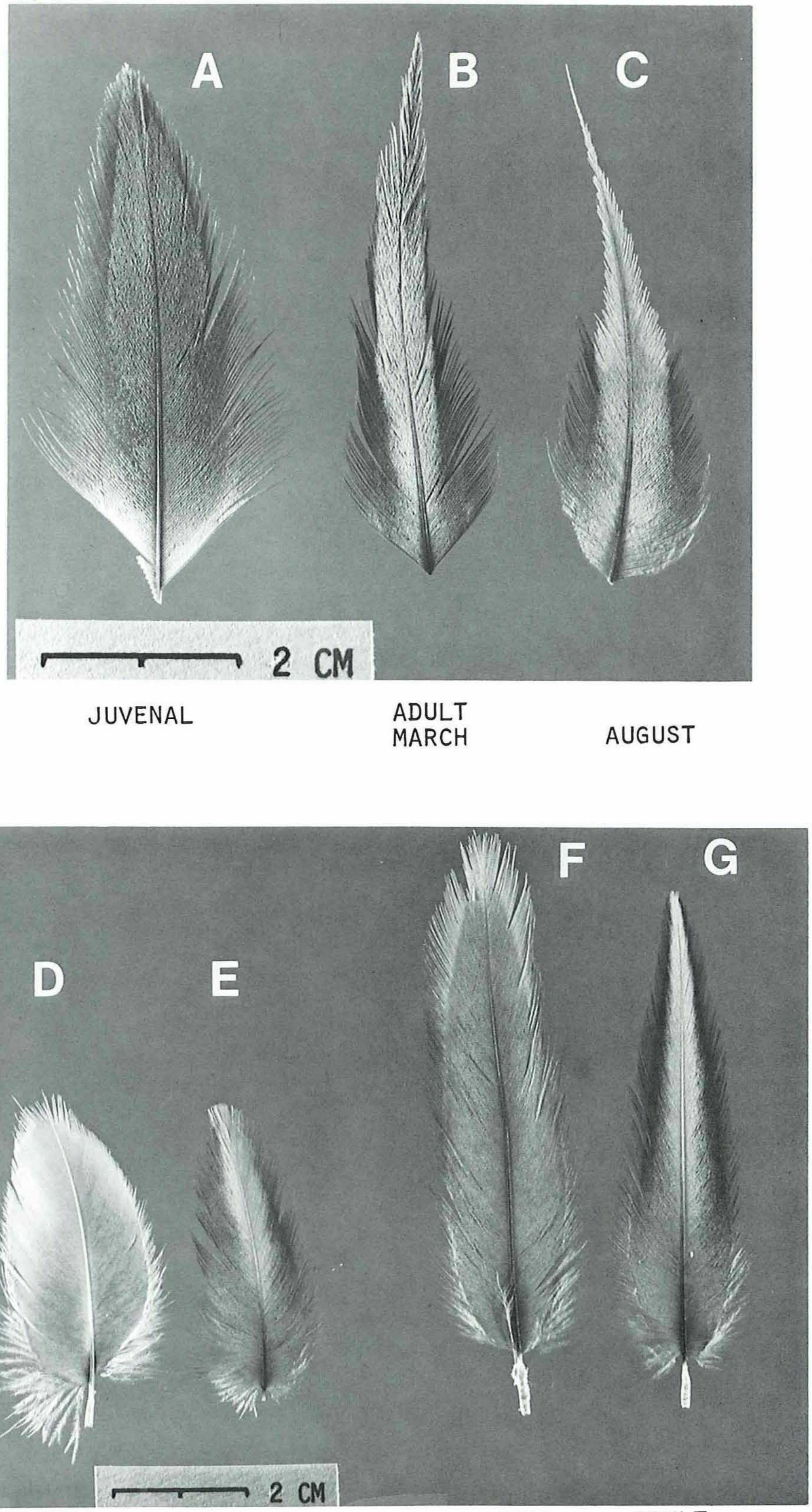

Figure 21. Brown Pelican left mid-flank feathers (upper) of a juvenal and an adult in March and August; and underwing coverts (lower) of a juvenal and a 14-month-old bird, from the second row of the distalmost secondary feather (left pair) and of a juvenal and an adult in March, from the inner humeral tract.

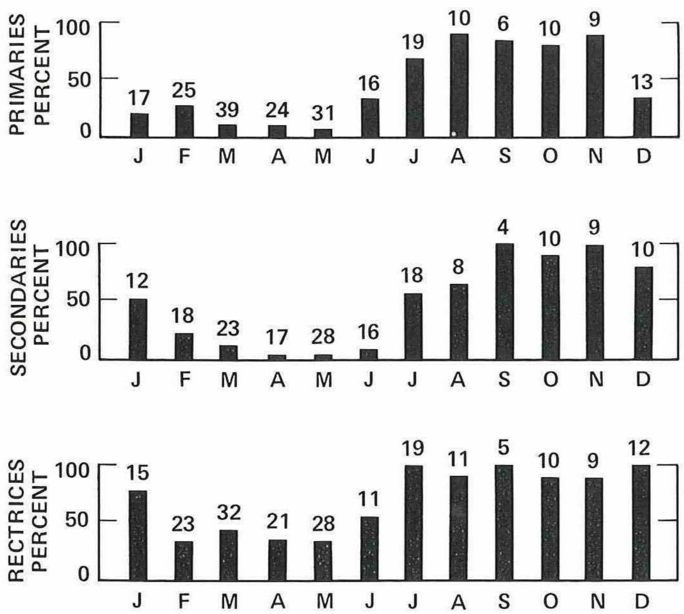

Figure 22. Incidence of one or more growing or missing flight feathers in adult Brown Pelicans from Florida, the Carolinas, Texas, and Louisiana. Sample sizes above each month.

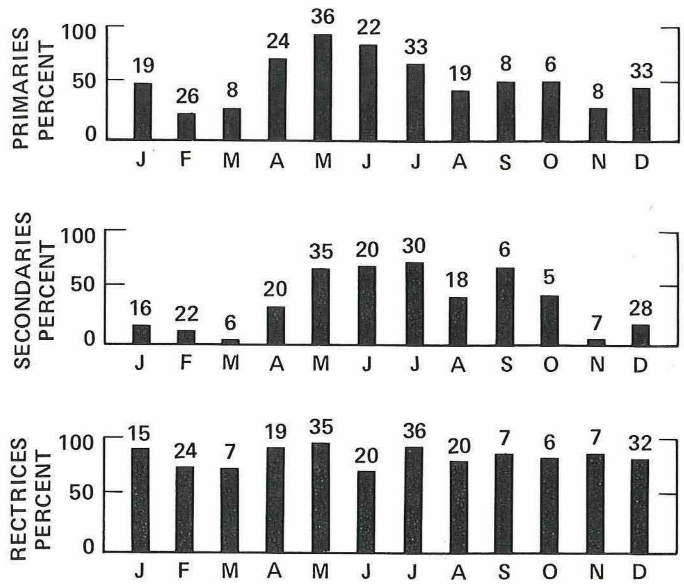

Figure 23. Incidence of one or more growing or missing flight feathers in Brown Pelicans 3–18 months old from Florida, the Carolinas, Texas, and Louisiana. Sample sizes above each month.

when the birds are 12–15 months out of their nests (Fig. 28). Molt of the secondaries occurs during a shorter period some time between April and October, beginning with S 27–32, but skips around rather than proceeding in a wave (Fig. 28B). Rectrices undergo almost continuous molt (generally bilaterally symmetrical) during the birds' first 10–12 months out of the nest (Fig. 28A). As in adults the foci of molt are obvious in secondaries and rectrices. At 18 months of age most primaries are new and the rectrices are probably being replaced a second time.

Subadults. Subadult birds show an intermediate pattern between juvenals and adults (Fig. 24). Our sample is small but molting birds are found in every month, with somewhat fewer birds in November–March.

The two-wave molt pattern of adults begins to be apparent in the primaries at 2 years of age (Fig. 27): P 1 and 6, 2 and 7, 3 and 8, etc., are replaced simultaneously (Fig. 28B). This pattern is established in the fall and is maintained through all adult plumages (Fig. 28C). Secondary and rectrix molt show the foci patterns of both juvenals and adults. The molt is slightly more extended in subadults than in adults, although on basically the same time schedule. Rectrix molt is found throughout the year but is lowest in January–May.

The samples available from California indicate a general pattern similar to those from Florida (Fig. 30A–C). Nestlings hatched in Florida, transported to Louisiana, and released show the same subadult molt patterns (Fig. 29). These data do not allow us to determine the rates of feather growth, a subject in need of further study.

DISCUSSION

Molt sequences and plumages follow distinct seasonal and age-related patterns, which we discuss in the following sections. In this exposition of the schemes, we describe an idealized system.

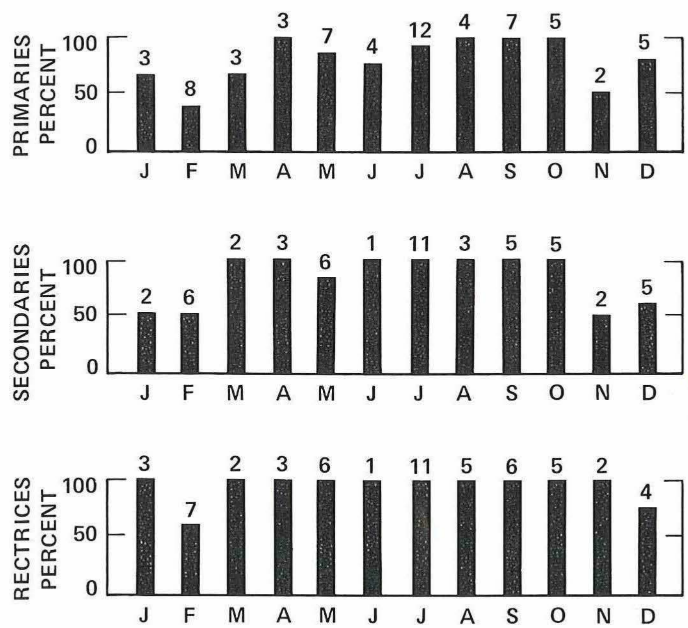

Figure 24. Incidence of one or more growing or missing flight feathers in Brown Pelicans 19–38 months old from Florida, the Carolinas, Texas, and Louisiana. Sample sizes above each month.

MOLT TERMINOLOGY

Palmer (1962) provided a fine review of the coloration of Brown Pelicans, both adult and juvenal, and followed the nomenclatural scheme proposed by Humphrey and Parkes

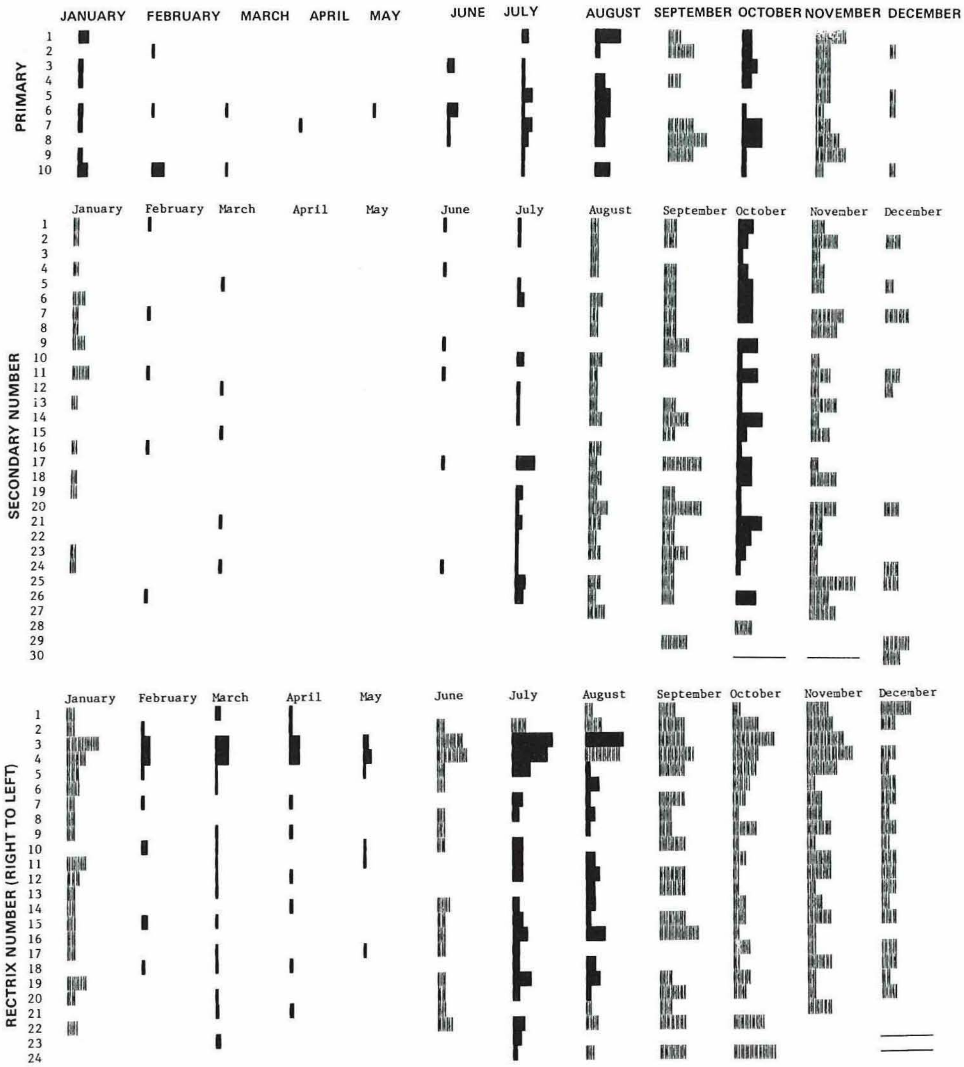

Figure 25. Molt of individual flight feathers of adult Brown Pelicans from the Florida west coast. Primary and secondary feathers are numbered in the usual manner. Rectrices are numbered from outer right to outer left. This system is used because of the variable number of rectrices and the difficulty in standardizing for computer analysis this variance causes. Length of the bar indicates the percent molting from 1% to 100%. Solid bars indicate samples of at least 10 birds and hatched bars occur for samples of fewer than 10 birds. A thin horizontal line indicates no data for that feather.

(1959). We have made no specific references to Palmer's descriptions, which are essentially correct despite their reliance on unknown-age museum specimens; rather, we provide details from our more extensive study and provide a more precise description of changes between what Palmer called the basic and alternate I, basic and alternate II, and basic III plumages (Table 7).

Amadon (1966) provided an alternative to the Humphrey/Parkes scheme (Humphrey and Parkes, 1959, 1963), and the gist of the difference between the two lies in whether molt should be discussed in relation to the life cycle (courtship, nesting, development: Amadon) or independent of the life cycle (so that one can compare homology of plumages among species: Humphrey/Parkes). Amadon uses the term "plumage" as the collective term for a bird's feathers while Humphrey and Parkes use "plumage" to mean a single generation of feathers. In Table 7 we summarize the Humphrey/Parkes (Humphrey and Parkes, 1959, 1963) and Amadon (1966) nomenclatural schemes as they apply to Brown Pelicans.

Brown Pelicans do not adhere strictly to either scheme; some individuals breed in either of the two adult feather coats, not always in the one termed "nuptial plumage." Further, juvenals and subadults molt almost continuously for 2–3 years, and birds in the later stages of subadult plumage do occasionally breed (Blus and Keahey, 1978). Due to the extremely complex and highly variable pattern of molts, seasonally and geographically, and due to age variation, we presently cannot accurately homologize plumages of young

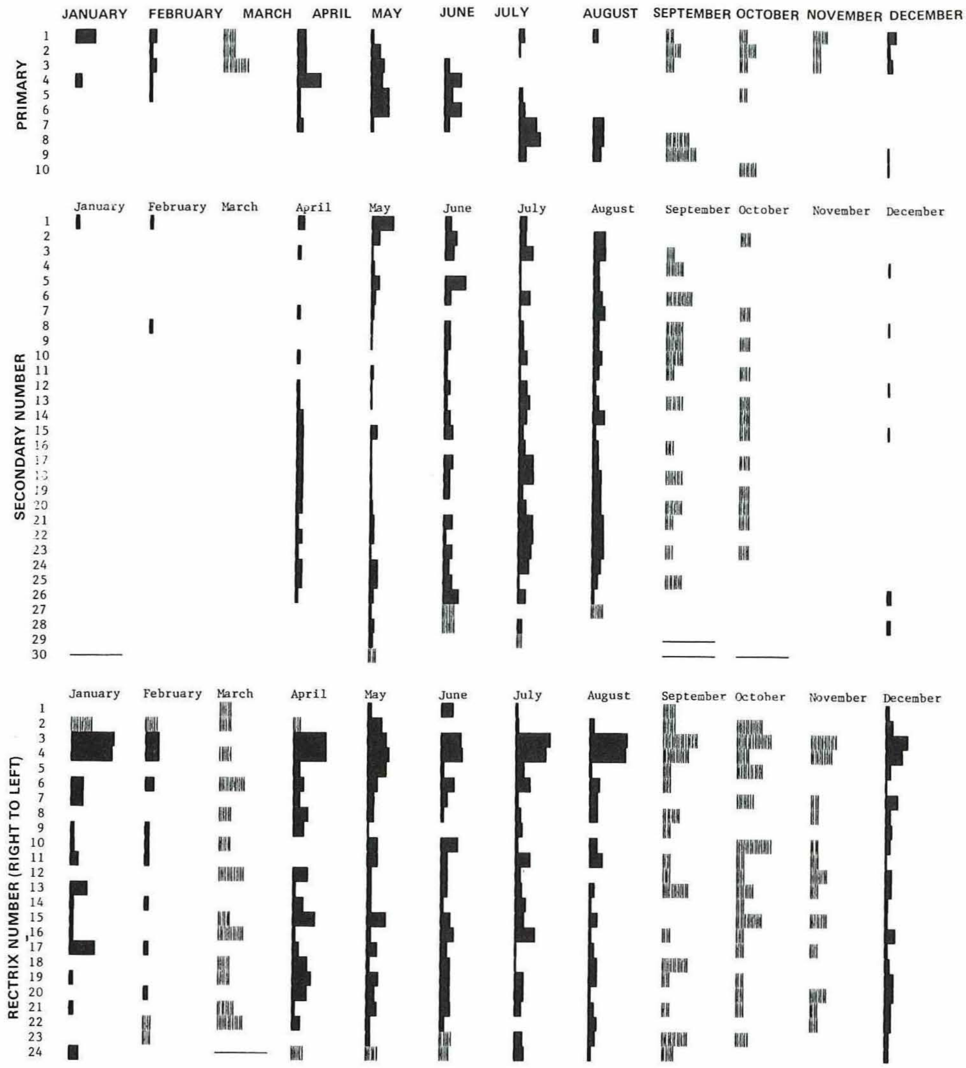

Figure 26. Molt of individual flight feathers of juvenal Brown Pelicans 3–18 months old from the Florida west coast. Data tabulated as described in Figure 26.

birds and are reluctant to define feather generations in adults. Perhaps with further study such homologizing and naming can be accomplished.

Adult Plumages (Amadon Scheme)

Amadon uses "adult" to describe the coloration of the breeding plumage; and while some birds may not actually breed for some time after achieving that adult plumage, his scheme allows for precision in describing specific behavioral/ecological activities of individual birds (and thus populations). He notes that exceptional species will need to be handled on an individual basis. We believe Brown Pelicans are one of these exceptions.

Amadon (pers. comm.) describes adult annual cycle phases as activities carried out while birds are in a specific plumage. Amadon has not described or named plumages, but rather "aspects" (sensu Humphrey and Parkes) that include soft part colors and the degree of wear in feathers. Amadon describes what a bird looks like while it goes about various annual cycle activities. His scheme is not directly related to plumage replacement but rather to plumage as a secondary part of the annual cycle. The following four phases of adult appearance (with our addition of a nestling stage) are our classification under the Amadon scheme:

1) Courtship—Brightest soft part colors: iris light, eye ring pink, bill bright orange-red, pouch colorful (bright red in *Pelecanus occidentalis californicus,* metallic green in *P. o. carolinensis*); dark brown neck, yellow head, fresh body feathers, clean appearance, white yoke on back of neck, bright silver back, and dark black-brown belly.

2) Nesting—Fading soft part colors; all brown neck, white head or yellow feathers of head being replaced by white; beginning to show wear of all feathers.

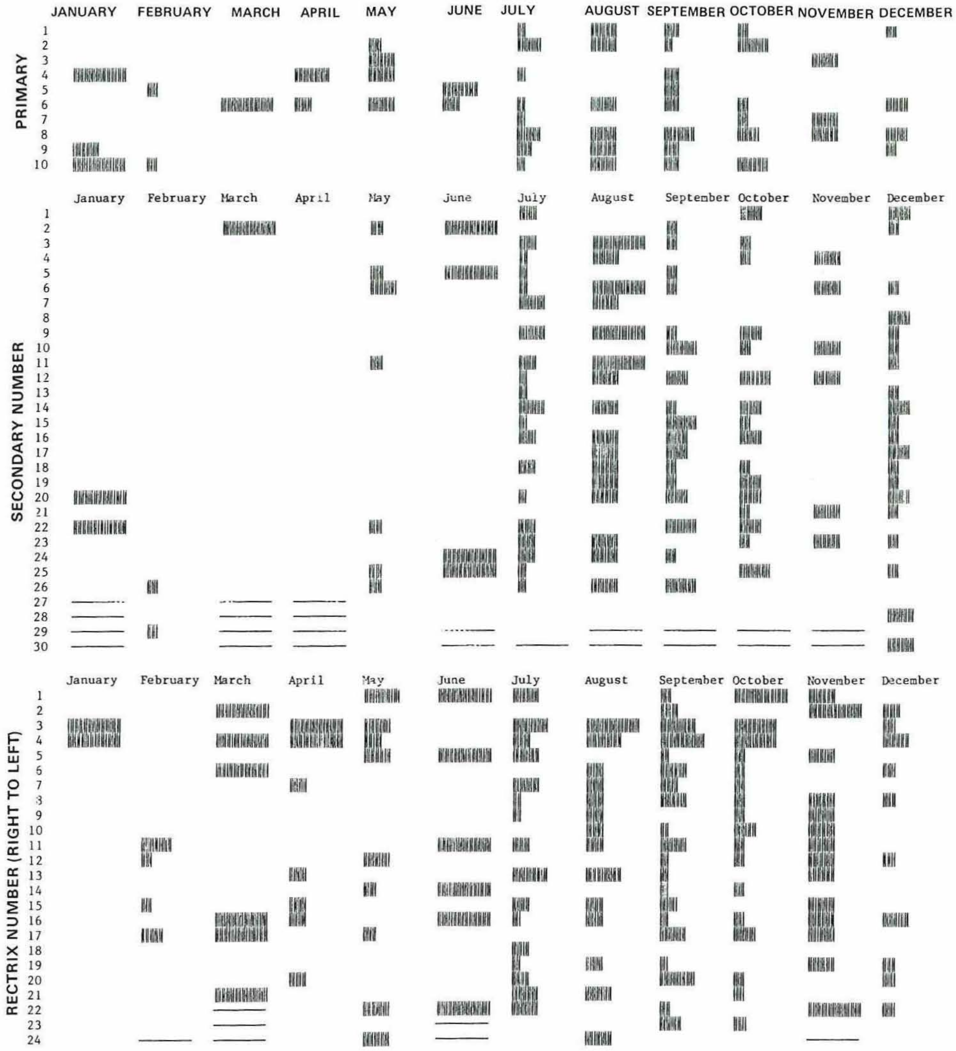

Figure 27. Molt of individual flight feathers of subadult Brown Pelicans 19–38 months old from the Florida west coast. Data tabulated as described in Figure 26.

3) Nestling Stage—Faded soft part colors: eye dark, no pink eye ring, yellowing or gray pouch, bill mottled slate with yellowish spot on lower proximal mandible; rhamphotheca shedding; neck fading to lighter brown, head white or with heavy speckling; body fading and worn looking; beginning flight feather molt as nestlings fledge.

4) Non-Breeding—Faded soft part colors which heighten in brightness at end of this phase; all white neck, pale yellow head; complete molt of all flight and body feathers, which look extremely worn early in phase and fresh at end.

Definitive Plumages (Humphrey/Parkes Scheme)

Because of the lack of information on homologies, and because we cannot determine exactly which is the definitive basic or definitive alternate plumage, we cannot fully adapt the Humphrey/Parkes scheme to Brown Pelicans. Based on when the major molt occurs, the definitive basic plumage in Brown Pelicans under the Humphrey/Parkes scheme should be predicted to be the one *normally* seen in "winter."

We cannot determine if this definitive basic plumage should be the white neck or dark brown neck, or the yellow head or white head. Since the pre-basic molt of the flight feathers is completed at the same time that the white neck feathers and yellow head feathers are new, those might be considered parts of the definitive basic plumage. The dark neck feathers acquired just prior to onset of breeding and the white head feathers acquired just after egg-laying should be considered as an alternate plumage acquired by a pre-alternate partial molt. The loss of all body feathers after breeding then leads to the definitive basic plumage. The few brown feathers that appear on the heads of most adults may be an additional molt called the pre-supplemental molt.

The pre-basic molt involves all or most of the body, wings, tail, head, and neck. The pre-alternate molt involves only the head and neck. A pre-supplemental molt (if it exists) primarily involves the head.

The definitive (adult) plumage is achieved in the third or fourth year (36+ months old), apparently seldom sooner,

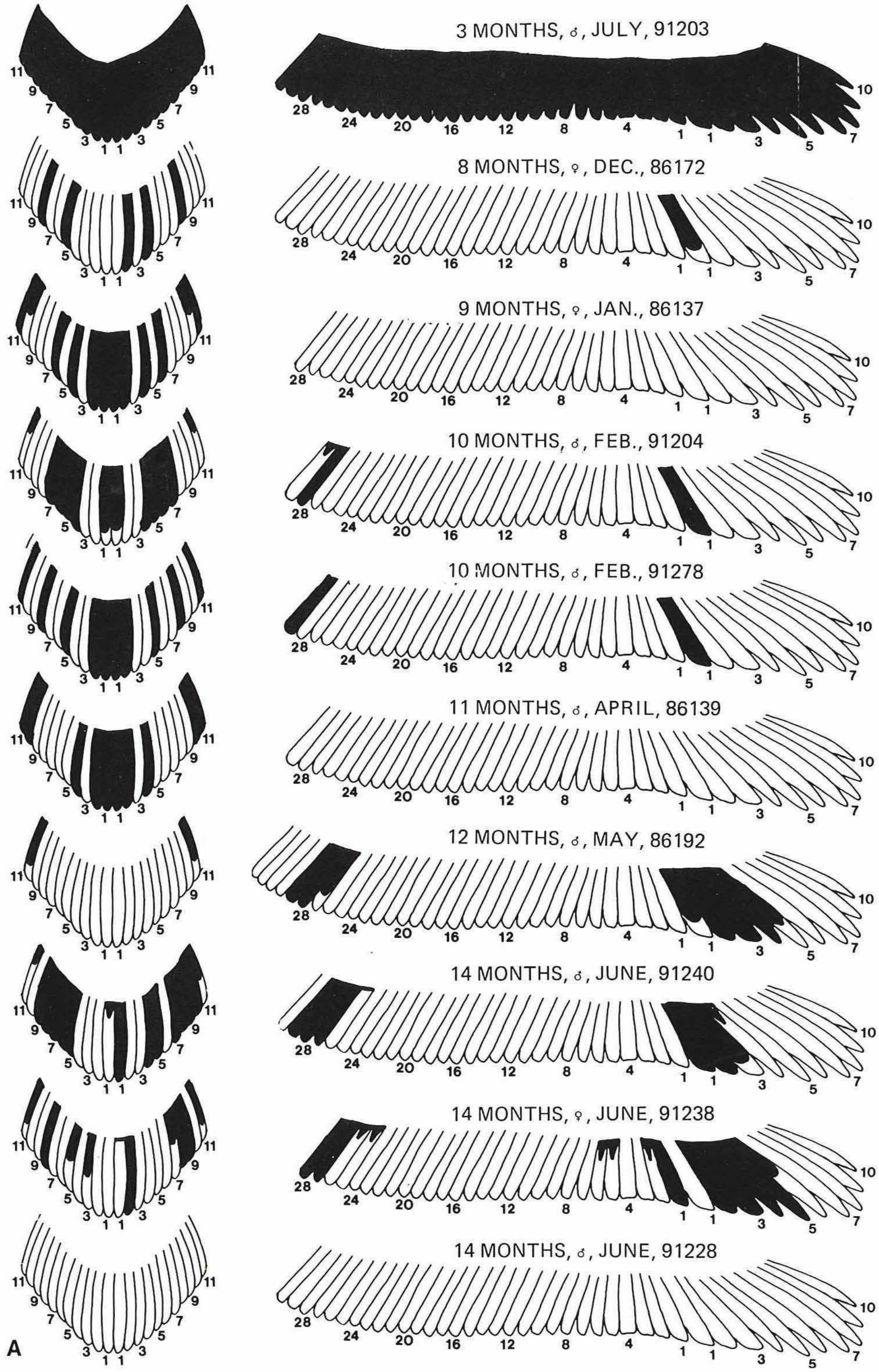

Figure 28. **A–C,** Individual known-age Brown Pelicans from the Florida west coast showing presence of old, new (dark), and growing feathers. (Parts B and C of this figure appear on following pages.)

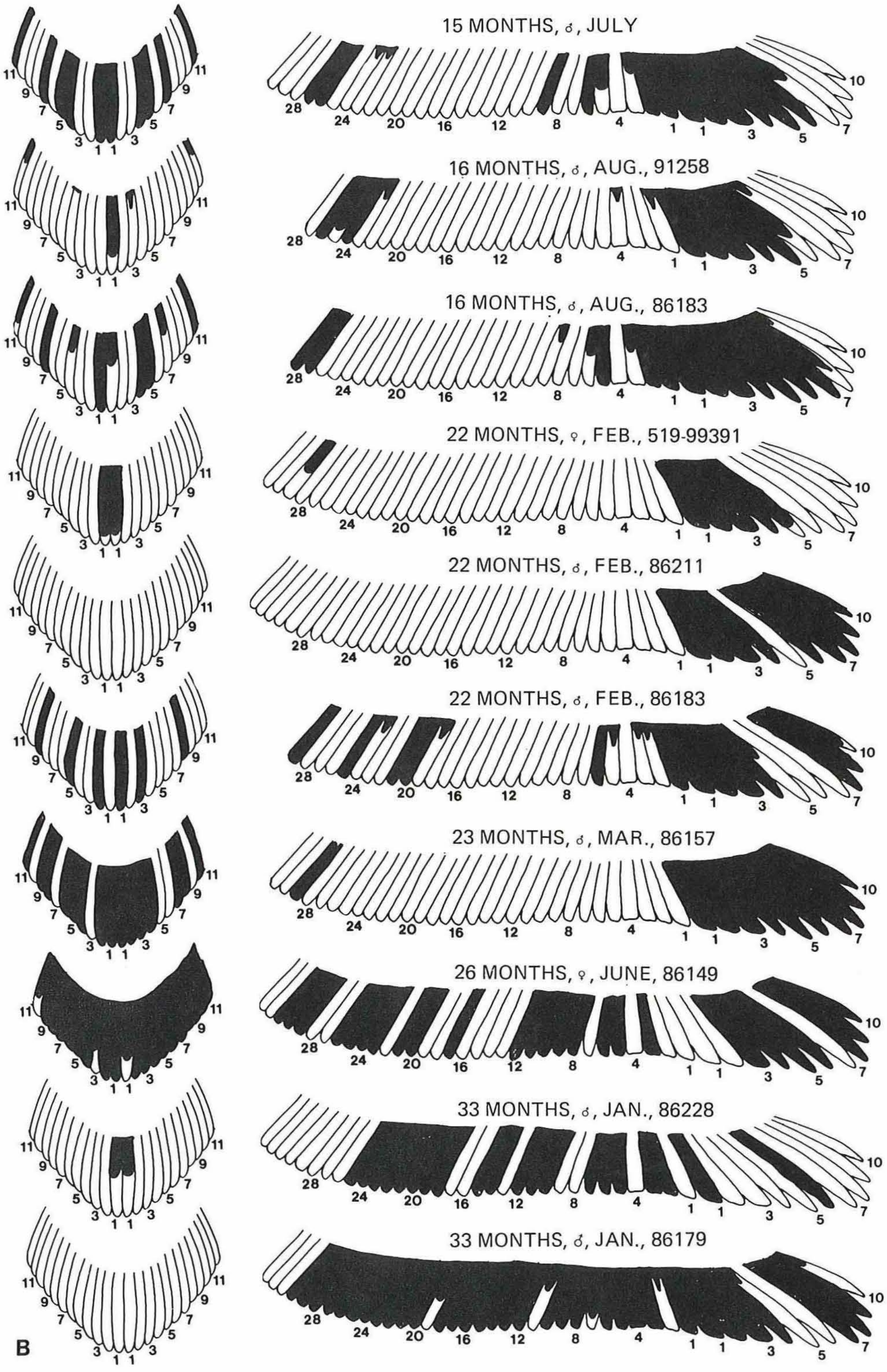

Figure 28. Continued.

but occasionally later. Brown Pelicans have three easily defined aspects (appearances) per annual cycle: 1) dark brown neck with yellow head obtained by one pre-alternate molt of the neck feathers just before breeding; 2) worn-looking dark brown neck with white or speckled head; and 3) white neck with pale yellow head appearing just after breeding is completed. The belly is always black-brown and the body feathers are either fresh gray or worn gray-brown. Wear of the feath-

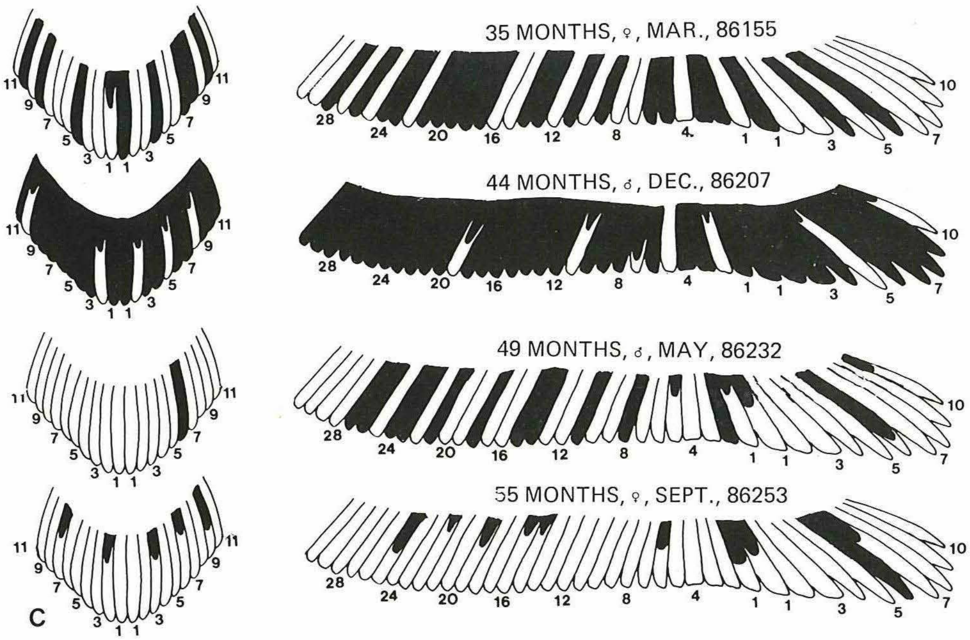

Figure 28. Continued.

ers, especially of the upper body surface, causes considerable change in the appearance of the adults.

Parkes (in litt.) notes that attribution of the scattered brown head feathers to a third molt (properly called pre-supplemental) depends on whether the individual follicles grow three generations of feathers per cycle (yellow, white, and brown). The fact that only a limited number of feathers is involved does not disqualify these from being a third supplemental plumage generation. This occurrence in Brown Pelicans, however, may be a protracted pre-alternate molt, with early feathers white and later feathers brown. Evidence for this latter interpretation would be the presence of old yellow generation (basic) feathers among the newer white (alternate) head feathers at the time that the appearance of new brown feathers begins, suggesting that the basic feathers are replaced gradually, with hormonal changes perhaps stimulating the earlier ones to be non-pigmented. We believe the former situation describes what happens in Brown Pelicans. This is a major unanswered question, however, and study of captive birds of known age will be required for a solution.

TIMING OF MOLT AND MOLT–BREEDING OVERLAP

Molt in birds is influenced by both environmental conditions and internal physiological state (Payne, 1972). Breeding seasons and molt vary with temperature, day length, and food availability, and we are unable at present to separate the influence of these factors or to distinguish how they interact as ultimate and proximate cues for breeding. We suspect that temperature, which has a major effect on food supply, is the overriding factor (Schreiber, 1980), at least in the Florida west coast population.

Most adults have completed the annual molt of their flight feathers by December in all years and locations. However, breeding usually does not commence until late February in Florida. The years when breeding occurs earlier lack freezing temperatures in November–January (Schreiber, 1980). The molt of the head and especially of the neck feathers appears to be more conservative and regular than the molt of the flight feathers (see Figs. 11 and 31). In unusually warm years (e.g. 1971 and 1974) Brown Pelicans sometimes breed without bright colors of the face, head, and neck fully developed (Fig. 10). We interpret this as a good indication of some independence between hormonal/breeding and hormonal/plumage cycles.

Breeding requires approximately 5 months (Schreiber, 1979), with 3–4 months needed to complete a molt. The birds are then apparently ready to breed again in less than a year but are inhibited from breeding, possibly by the cold or a limited food supply, entraining breeding and molt into an annual cycle (Schreiber, 1980).

Molt–breeding overlap has received some attention in recent years (Foster, 1974, 1975; Thompson and Slack, 1983). Without physiological data, we can say little about the specific mechanisms controlling molt and the possible constraints molt might have on Brown Pelican breeding biology, but there does exist some molt and breeding overlap: neck and head feathers are molted again during courtship and incubation; molt of the flight and body feathers begins at the end of the breeding season, when many adults are still feeding large nestlings; and a few rectrices may molt throughout the year. Energetic constraints apparently do not make molt and breeding mutually exclusive. Additional physiological studies of these factors need to be done (Wolf et al., 1985).

Bright pouch color may serve primarily to indicate to other

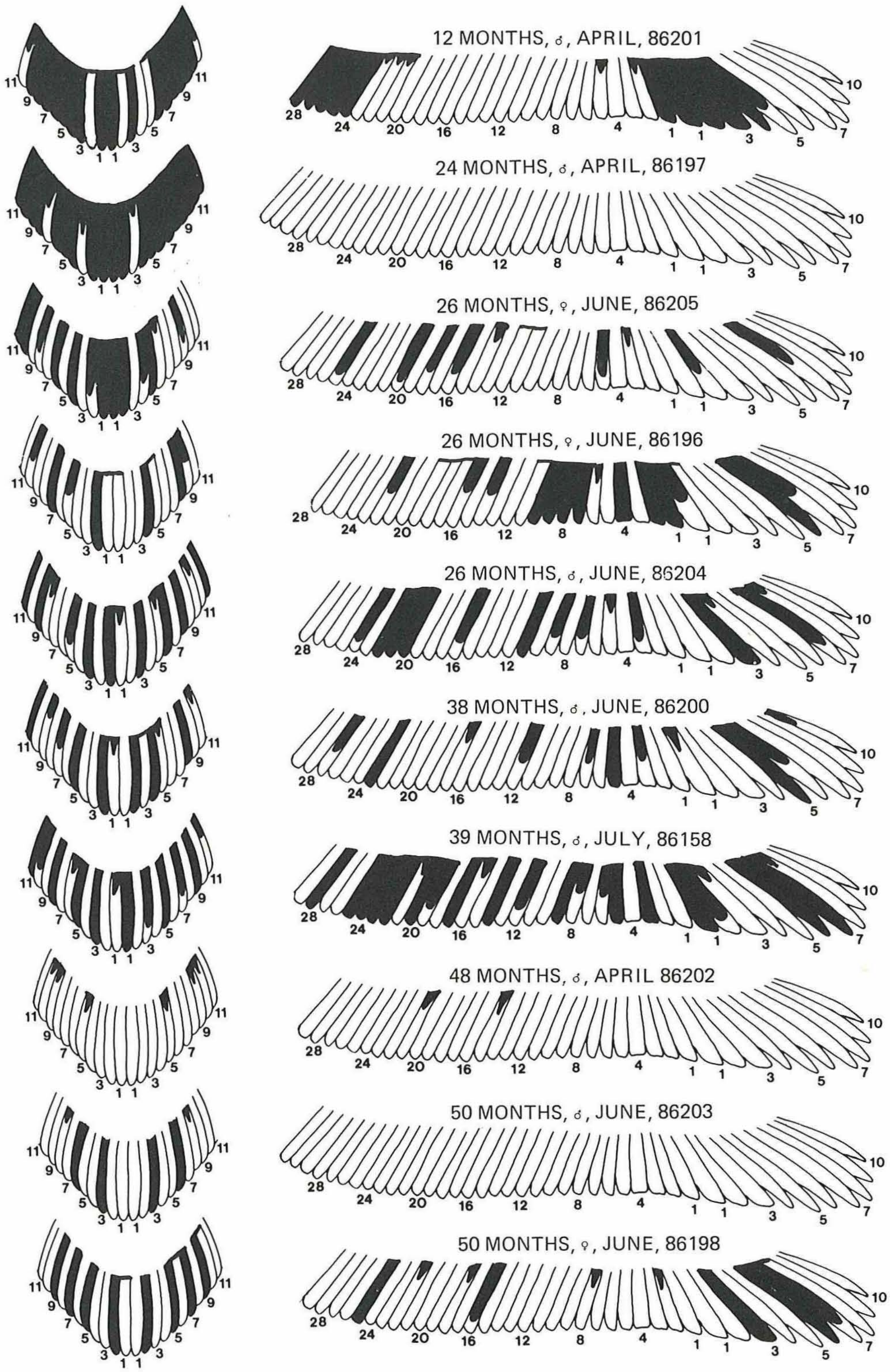

Figure 29. Individual known-age Brown Pelicans hatched in Florida, transported to and released in Louisiana as fledglings, and then recaptured there, showing presence of old, new (dark), and growing feathers.

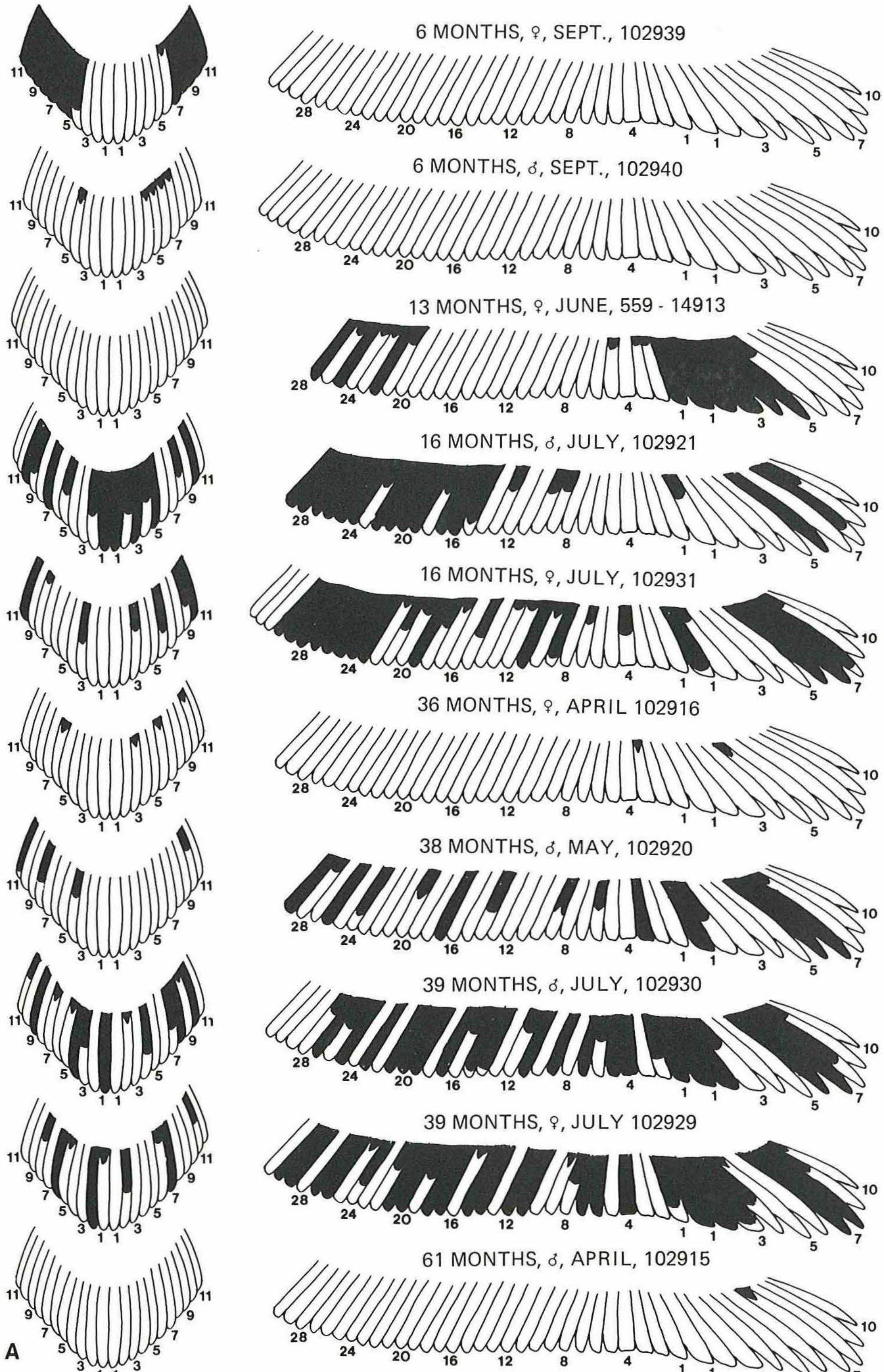

Figure 30. **A–C,** Individual known-age Brown Pelicans from Baja California, Mexico, showing presence of old, new (dark), and growing feathers. (Parts B and C of this figure appear on following pages.)

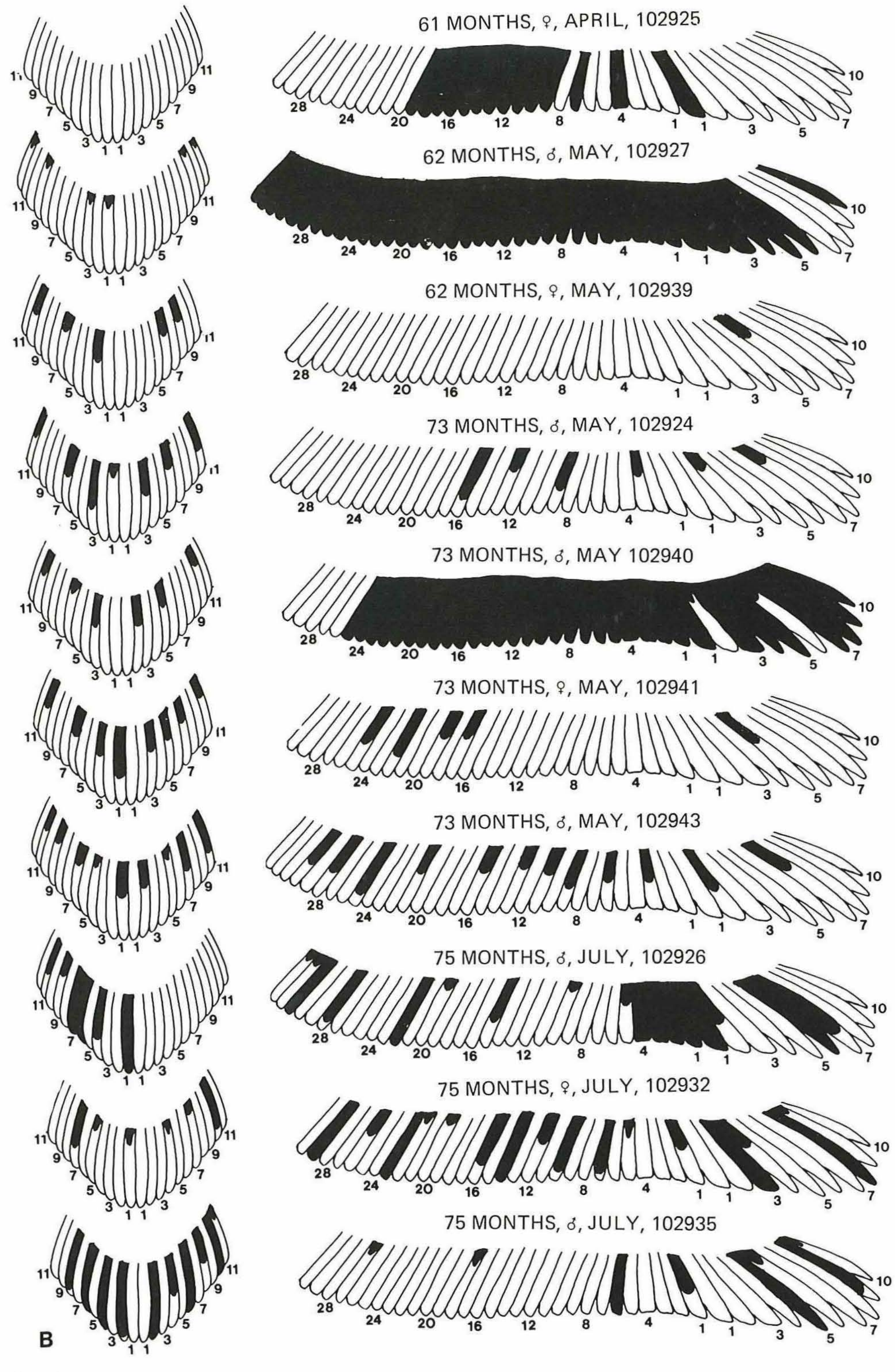

Figure 30. Continued.

adults the displaying bird's condition of sexual readiness. The bill color, since it changes more slowly, may serve as a longer-term individual recognition signal to members of a pair or to surrounding territory owners (Schreiber, 1977). The other soft part colors similarly show sexual readiness but could also serve in individual recognition.

Birds in the eastern part of the range are not known to skip a breeding season; however, the Gulf of California may

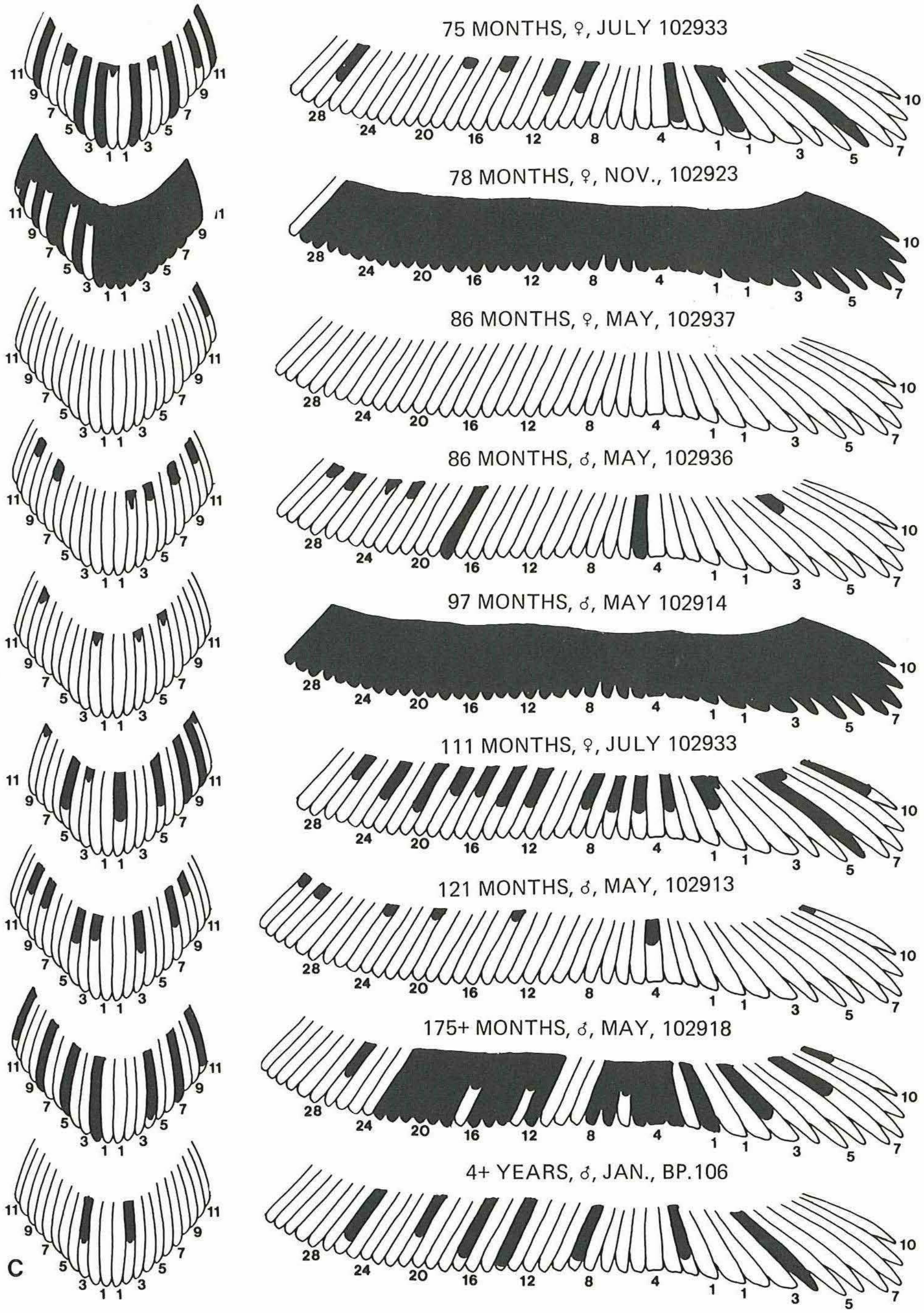

Figure 30. Continued.

provide an interesting contrast. There, breeding is strongly influenced by El Niño–Southern Oscillation events (ENSO) (Barber and Chavez, 1983). When weather events reduce the food supply, pelicans may fail to breed. During years when breeding does not occur, adult pelicans continue to molt approximately on schedule (Anderson, unpubl. data).

Occasionally a feather may be retained during the annual molt. This occurs infrequently in tertiaries and inner secondaries (less than one feather per 200 birds examined) and we have never found a primary or rectrix feather in this extreme condition. Many other large birds (Bloesch et al., 1977; and see also Stutterheim, 1980, and Sutter, 1984) do retain feathers longer than 1 year. Storks and vultures, which retain some feathers for 2 years, both migrate longer distances than do pelicans (Cramp et al., 1977 and later). Migration may be energetically costly enough that extensive post-breed-

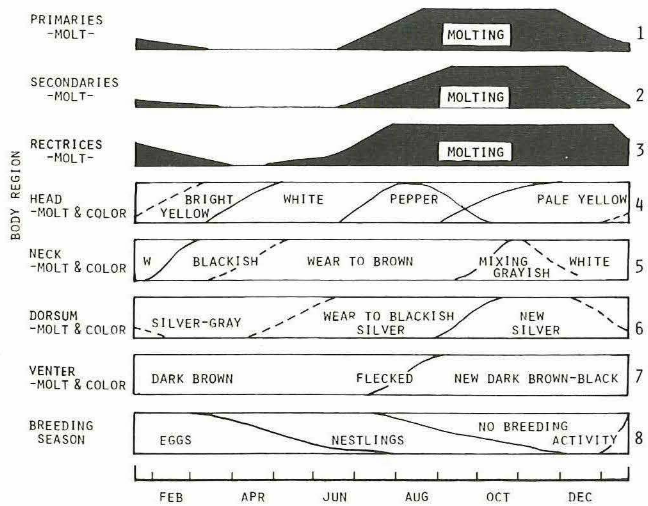

Figure 31. A diagram showing the major molts and associated color changes (soft part color changes are not given here) in a typical adult Brown Pelican. Panels 1–3 represent molt intensity only; the remainder also represent color changes in the feathers, or variations seen due to the mixing of feathers from two generations. Panels 4–7 indicate molt by solid lines. Color changes in a given feather generation are indicated with dashed lines.

ing molt cannot occur at the same time, causing some feathers to be retained each year.

Although molt has been described in some seabird species (i.e. Ainley et al., 1976; de Korte and de Vries, 1978; Schreiber and Ashmole, 1970; Thompson and Slack, 1983, and references therein), little study has been done on pelecaniforms (Palmer, 1972; Cramp et al., 1977 and later; but see de Korte and de Vries, 1978). Further data on species similar to pelicans in size and ecology are needed before comparisons will be fruitful.

PRIMARY MOLT AND THE STAFFELMAUSE

Stresemann and Stresemann (1966) stated that *Pelecanus (occidentalis) thagus* molt the primaries like *Sula*. The *Sula* data came from Dorward's (1962) study of nesting adults on Ascension Island, and the pelican data from an examination of five specimens in the American Museum of Natural History. The pattern described as Staffelmause is explained somewhat differently by various authors (Potts, 1971; Ginn and Melville, 1983; Cooper, 1985). We agree with Parkes (in litt.) that understanding what the Stresemanns meant by Staffelmause is difficult. It appears that they were describing a system where only the inner primaries were molted in the first year after fledging. Thereafter, the outer primaries were a generation behind the inner ones. Molt after the first year proceeded as we have described, in two simultaneous waves. Ginn and Melville (1983), however, have interpreted Staffelmause to be the beginning of a new molt cycle before the previous one has ended, so that there are two concurrent molt centers which have started at different times.

In Table 8 we illustrate the supposed Staffelmause and the actual pattern of molt. With our large sample size of maturing juvenals we were able to determine that primaries are molted in sequence from P 1 to P 10 in the first year after fledging; therefore, if we have translated the Stresemanns' paper correctly, their description of first juvenal molt is incorrect. The difficulty in understanding exactly what the Stresemanns meant and our additional data lead us to suggest that the term Staffelmause not be used (see Prevost, 1983, and Cooper, 1985, for example).

SUBSPECIFIC DIFFERENCES

Our data describe *Pelecanus occidentalis carolinensis* and *P. o. californicus.* Few data are available for *P. o. occidentalis* or *P. o. thagus.* The basic patterns appear to be similar in all subspecies, however, we have noted some differences based on the literature, photographs, and limited field observations. The first difference is the high proportion of birds with adult-like heads and necks but white bellies in both loafing groups and breeding colonies of *P. o. thagus.* Such birds are rare in our study areas. Second, the pouch of *P. o. thagus* is blue and the upperwing coverts form two distinct white patches on each side (one over the primaries and secondaries, the other over the tertiaries) which are separated in mid-back and at the elbow by dark brown, shorter feathers. Many birds seem to have an overall dark appearance on the dorsum, rather than being silver-gray.

Forbes (1914) was accurate in predicting that 3–4 years were required for *Pelecanus* to acquire the full adult plumage. He noted, based on his visit to a nesting colony in November, that incubating birds in Peru had three plumages: birds' necks were either pure white, sooty gray, or jet black. He thought these neck differences were related to age differences rather than what we can now interpret as the seasonal cycle of plumages for adult birds. Forbes gave valuable descriptions of specimens and had excellent color illustrations by H. Gronvold. In plate XIII (between pp. 410 and 411), Forbes indicated the four figured birds are different ages; however, we believe that his figures 1 (specimen in November), 2 (December), and 4 (January) clearly illustrate the plumages worn in those months by the majority of adult pelicans in the region and are comparable to our Figure 1. Forbes' figure 3 may be of a younger bird (November) but we suspect it is merely a further development of plumage and actually is in a stage between 2 and 4 in that plate. The difference in the extent of the brown on the back of the head in the crest region is less in *P. o. thagus* than other forms, as illustrated in Forbes' plate. However, since Gronvold drew the illustrations from study skins, this difference may be an artifact. It has not been noticeable in our brief studies of live Peruvian birds.

Peruvian pelicans often breed in what we would call an "advanced juvenal plumage." We speculate that in the coastal upwelling systems, which experience frequent and severe ENSO events, there has been selection to breed at an early age due to high adult mortality. Duffy (1980) reported higher mortality rates on the Galapagos Islands than we observed in our Florida and California study populations.

Table 7. **Our attempt to combine two frequently-used systems of avian plumage and molt nomenclature with feather changes seen in Brown Pelicans. Some of these changes are more evident when soft part color changes (not indicated here) are included in description.**

Approx. age (months)[1]	Humphrey/Parkes Nomenclature: Overall plumage[2]	Humphrey/Parkes Nomenclature: Molt	Amadon's nomenclature[3]: Overall plumage[2]	Amadon's nomenclature[3]: Molt
0.25–2	natal down		downy	
	↓	pre-juvenal	pennaceous	post-natal
3	juvenal	↓	juvenal	↓
	↓	pre-basic I	↓	post-juvenal
7	basic I	↓	immature	↓
	↓	pre-alternate I	↓	immature
10	alternate I*[4]	↓	immature	↓
	↓	pre-basic II	↓	immature
19	basic II	↓	immature	↓
	↓	pre-alternate II	↓	immature
22	alternate II–III*[4]	↓	immature/subadult	↓
	↓	pre-basic III	↓	immature
31	basic II–III	↓	immature/subadult	↓
	↓	pre-alternate III	↓	immature
22–34	alternate III–IV*[4]	↓	subadult	↓
	↓	pre-basic (complete)	↓	immature/adult
34–44	definitive basic (IV)	↓	adult/subadult	↓
	↓	pre-alternate (partial)	↓	pre-breeding partial
36–46	definitive alternate (IV)	↓	adult-courtship	↓
	↓	neck ↓	↓	breeding partial
	definitive supplemental	head	adult-nesting	↓
	↓	pre-supplemental head (partial)	adult-nesting care	breeding partial
	definitive basic	↓	↓	↓
		pre-basic (complete)	adult-nonbreeding	post-breeding complete

[1] Ages show variability presumed due to sex and nutritional differences. In some birds the intermediate, pre-definitive plumages may even be extended a year more than shown.

[2] "Overall plumage" here is based on the appearance of the bird in its entirety, combining all feather tracts into one image.

[3] Amadon's (1966) nomenclature has been somewhat modified here by us to be as descriptive as possible.

[4] Although "supplemental" conditions (Humphrey and Parkes, 1959) are not readily distinguishable at the points marked "*", we think they are represented nonetheless (at least in the definition given by the Humphrey/Parkes scheme). The supplemental plumage (seen only in changes of the head) becomes more distinguishable toward definitive condition, but may also lessen with age within the older "definitive" individuals. Supplementals are not defined at "*" because they are not readily distinguishable in overall pelican appearance.

BREEDING IN "IMMATURE" PLUMAGE AND SEXUAL DIFFERENCES IN ACQUIRING ADULT PLUMAGE

Brown Pelicans do breed in immature plumage (Blus and Keahey, 1978). We can give approximate ages to the birds illustrated in the South Carolina colony studied by Blus and Keahey (fig. 1, p. 129): B is in its third year (36± months old), C is a younger bird (24± months old), and D is approximately the same age as B but shows less "adult" development of the head region. Based on bill lengths we suggest that A, B, and C are females (shorter bills) and D is a male. These immatures were less successful at nesting than adults in South Carolina, near the northern periphery of the nesting range of the species. Blus and Keahey (1978) also note that immatures were reported breeding in Peru. In California, where the population was greatly reduced in the late 1960s due to pesticides, some white-bellied birds bred and others attempted to breed (about 20%; Anderson and Gress, 1983). This was much less common (5%) in the Gulf of California colonies, where populations remained more stable (Anderson, unpubl. data). As previously stated, no immatures were known to form pair bonds and establish nests in Tarpon Key, Tampa Bay, Florida. We have no explanation as to why females sometimes mature earlier (at 34–36 months) than males (at 36–42 months), but there is extensive individual variation.

NUMBER OF FEATHERS

The number of feathers comprising the primaries, secondaries, and rectrices has been a matter of interest to ornithologists over the years. Coues (1890) noted for the Steganopodes (=Pelecaniformes) that there are "usually 22–24 tail-feathers in the pelicans" (p. 719) and that the remiges "are from 26 to 40 in number, of which 10 are always long,

Table 8. Origin of the molt pattern of primary feathers of Brown Pelicans.

	1	2	3	4	5	6	7	8	9	10
Supposed Staffelmause										
Primary number										
First year of molt	Cycle 1									
Second year of molt	Cycle 2									
Third year of molt	Cycle 3					Cycle 2				
Fourth and following years	Cycle 4					Cycle 3				
What we believe happens										
Primary number	1	2	3	4	5	6	7	8	9	10
First year of molt	Cycle 1									
Second year of molt	Cycle 2					Cycle 2				
Third year of molt	Cycle 3					Cycle 3				
Fourth and following years	Cycle 4					Cycle 4				

strong, pointed primaries." However, Clark (1918) said that *Pelecanus* species have 10 rectrices on each side of the pygostyle. His sample size is not indicated and the specimens he examined are unknown. Palmer (1962) lists 22 tail feathers in *Pelecanus.*

Parkes (1950) used the term "supernumerary rectrices," and Somadikarta (1984) then coined the unfortunate term "polyrectricycly," to mean "the occurrence of more than a normal number of tail feathers." We prefer the older term. Hanmer (1985) used "anisorectricial" to describe "tails with an abnormal number of rectrices, that is the number that is unequal to the normal or with an unequal number on the two sides."

We have no explanation for the varying number of rectrices (19–24; Tables 3, 4). The greater number of feathers on the right side of the pygostyle than the left side may be due to the fact that the bird's body rotates to the left as it hits the water during a dive (Schreiber et al., 1975). Anatomically the trachea and esophagus are fixed in the throat on the right side of the neck (Schreiber and Schreiber, unpubl. data from examination of over 500 specimens) and when the birds rotate, the pressure of hitting the water is on the left side away from the trachea. Having an increased number of feathers in the steering surface of the tail on the right side might facilitate this rotation (Paul McCrady, pers. comm.).

We have never seen anything but 10 primaries in over 2,000 birds examined. The varying number of secondaries may be related to the length of the ulna but this needs to be verified.

ABERRATIONS: ALBINISM

Nesbitt and Barber (1979) and Nesbitt and Fisher (1984) reported on a "non-eumelanic schizochromatic" (J.P. Hailman terminology) Brown Pelican: a pale white bird living on the east coast of Florida which behaved "normally" and probably lived for at least 4 years in the same region. We know of four other Brown Pelicans with white feathers: (1) a nestling in the Tarpon Key colony of Tampa Bay, 1980, with white P 3; (2) an adult female found by P.A.M. Stewart in Bradenton, Florida, in May 1973, with P 10 all white, apparently the result of damage to the wing (LACM specimen 86217); (3) a leucistic adult seen by D.W.A. on a nest on Isla San Lorenzo Norte, Gulf of California, Mexico, 1973; and (4) a leucistic bird reported by M. Harms in San Luis Obispo County, California, 1978 (Harms, unpubl. data). We have looked at over 100,000 other adults and juvenals and noticed no other white feathers or other color aberrations. We conclude that such conditions are very rare in this species.

The presence of an aftershaft has not been previously noted in a pelecaniform. Aftershafts occur in many groups (Van Tyne and Berger, 1976) and, since thought to be non-adaptive and primitive, they are useful to taxonomic decisions. An aftershaft is "never found on the rectrices or larger remiges but commonly occurs on all of the other contour feathers of any bird that has the structure at all" (Van Tyne and Berger, 1976, p. 125). We found one example of an aftershaft on P 4 (Fig. 32) of an adult male Brown Pelican from Santa Barbara County, California (Schreiber field number 496). This aftershaft is almost as long as the main rachis but its vanes are poorly developed. It arises from the upper umbilicus and, most strikingly, the barbs of the proximal vane of the main shaft grow into the aftershaft rachis for about 1 cm of its length. This feather is in very worn condition, especially along the posterior vane where the aftershaft appears to have rubbed. Clearly, this is an unusual embryological anomaly in this individual.

CAPTIVES AND AGING INDIVIDUALS

We have examined a number of both short-term and long-term captive pelicans on an irregular basis. The unusual molt patterns, timing of molt, and different look of captive birds may be related to their having an unlimited food supply, or to the trauma or starvation that resulted in their coming into captivity. A careful study of molt in captives along with details on their energy intake will be very useful in explaining plumages and molts in the wild, though injuries and differences in the availability of food must be taken into account.

COMMENTS ON ILLUSTRATIONS OF BROWN PELICANS

Many artists have illustrated Brown Pelicans. While considerable artistic license is involved in some drawings, we believe it worthwhile to briefly comment on the colors and plumages of some bird guidebook illustrations of Brown Pelicans. We avoid extensive comments on the accuracy of the shapes of the birds. Basically, artists tend to draw composite plumages, selecting their desired plumage colors from the various adult plumages.

The most accurate drawings of pelicans that we have found are those by John James Audubon in the hand-colored en-

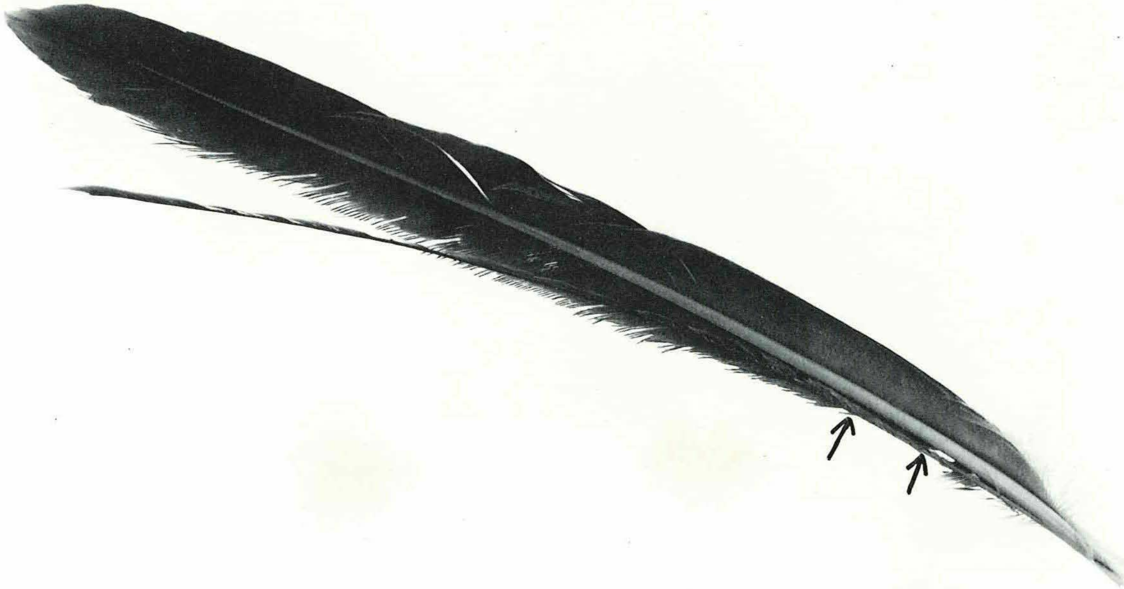

Figure 32. P 4 of an adult Brown Pelican showing the aberrant aftershaft. The barbs from the main rachis in the area of the arrows grow into the aftershaft rachis. (Illustration approximately full size.)

gravings of the *Elephant Folio* of 1827–1838 and later reproduction editions. While the perspective is questionable, the colors of the adult (plate 251) show a bird in the early incubation stage of nesting, and the juvenal (plate 421) is a typical bird less than 1 year old.

Roger T. Peterson portrays the annual cycle of adult Brown Pelicans. In *A Field Guide to the Birds East of the Rockies* (Peterson, 1980) and the somewhat color-shifted reproduction in *National Wildlife Magazine* (August–September 1980, 18:38) seasonal changes in neck color from white to black are shown. However, the head color of all four adults does not vary, nor does the iris, eye ring, or bill; and no mention is made of the wear of the back and shoulder feathers from gray to brown. Thus, these different illustrations are not useful in identifying the various plumages of adult Brown Pelicans. The immature bird is too orange in color, the placement of the eye is too high in the eye ring, and the bill has too much orange for a bird less than 1 year old. Birds in the field never have white necks with pale yellow only on the forehead. The two brown-necked birds are in the same plumage.

The illustration by Arthur Singer in *Birds of North America* (Robbins et al., 1966 and 1983), while showing the neck color changes of adults on the seasonal cycle, fails to show the bill color differences that occur; the placement of the yellow on both heads is incorrect; and the eye and eye ring colors are shown as invarying, although they change seasonally. The immature is in an accurate plumage for a bird less than 1 year old.

The Robert Mengel illustration of two adults in the *Handbook of North American Birds* (Palmer, 1962, p. 92) is basically accurate although the bills do not change color as they should and the yellow breast vee of one bird is missing. The caption to this illustration is incorrect. The bird on the left is a typical bird "At the onset of breeding season" but the bird on the right is not "same bird after molt of at least considerable head feathering during incubation." In fact, both birds have the same yellow head and the bird on the right is in a plumage worn a few weeks *prior* to that of the bird on the left, not after. It is the neck that molts first, usually just prior to onset of breeding. The head feathers usually are molted after incubation begins.

The National Geographic Society's *Field Guide to the Birds of North America* (1983, p. 41) shows an adult listed as "chick-feeding"; this bird has no speckles in the head and the neck should be lighter than the "breeding adult." Neither of these birds shows sufficient orange in the bill (as is illustrated for the "non-breeding" adult), and the "chick-feeding" bird should have the yellow proximal spot on the lower mandible. The eye ring and iris colors are correct in these three birds. The flying individual called "1st year" is most likely a 3-year-old bird, while the juvenal is an individual 14–18 months old. The diving birds show a distinct underwing-stripe that is quite unusual in adult plumages of North American birds (see Schreiber et al., 1975, fig. 1).

Photographs probably best illustrate the plumages and soft parts of Brown Pelicans, and reference should be made to the accurate color reproductions of F.K. Truslow in *Audubon* (September 1969, 71:10–17), C. Singletary in *Audubon* (November 1974, 76:2–17), and W.R. Curtsinger and R.W. Schreiber in *National Geographic Magazine* (January 1975, 147:110–123). *The Audubon Society Field Guide to North American Birds—Eastern Region* (Bull and Farrand, 1977) shows a photograph on page 176 of an adult Brown Pelican in the most highly developed colors—bright pink eye ring, light eye, orange bill, yellow head, and dark neck, worn just as courtship begins—but on page 360 the description says "head whitish in adults, dark brown in young" as the only comment on plumage in the text, not a satisfactory discussion. The western region guide (Udvardy, 1977) shows on page 155 an adult with the white head, light eye, pale pink eye ring, and yellow-based bill of a mid-to-late incubating stage adult. On page 399 the description says "Adults grayish-brown with white heads; immature dark-headed, pale below," and in a later sentence, "Breeding birds have dark chestnut hindneck extending to crested nape." While a somewhat fuller description, this and the eastern guide are clearly incomplete and inadequate in describing the plumages of Brown Pelicans. *The Audubon Society Master Guide to Birding* (Farrand, 1983) presents photographs of an adult with full yellow head whose eye ring has faded during the courtship stage, and a juvenal 10–12 months old. The text on page 90 by Paul W. Sykes, Jr. fails to mention the yellow head but does note the dark neck. We have never seen a gray bill on an adult as noted in the text, and black is not an accurate description of the pouch color. This description should be completely rewritten in the next edition to correspond with the good photographs.

In short then, no presently available field guide can accurately be used to identify the age classes and plumages of the Brown Pelican as they exist.

CONCLUSIONS AND ADDITIONAL QUESTIONS

We believe the value of the descriptions of plumage characteristics given here lies in allowing reasonably accurate age-classing of birds in the field, thus aiding the study of various aspects of behavior (age-related interactions) and population biology (Schreiber and Schreiber, 1983, and others).

Many questions remain: 1) How much energy is required for molt in Brown Pelicans and how does the allocation of energy/nutrients to breeding and molting regulate the annual cycle in the species? 2) What are the effects of day length, temperature, and food supply on the molt cycle? 3) How do molt and timing of molt vary among regions? 4) How much do worn and missing feathers affect flight abilities and temperature regulation? 5) What is the interaction between circulating hormones, blood chemistry, nutrition, and molt patterns? and 6) Why do juvenals show a different primary feather molt pattern than do adults?

We hope these descriptions of the molt cycles and plumage characteristics of the Brown Pelican will stimulate others to undertake more detailed studies. A combination of both field and laboratory investigations involving frequently sampled individual birds is needed to help elucidate the ecological and evolutionary relationships of plumage and molt in the biology of this fascinating species. We believe that it is possible to study many of these changes and variations in captive birds.

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