

CLUTCH SIZE, TIMING OF LAYING, AND REPRODUCTIVE SUCCESS IN A COLONY OF GREAT BLUE HERONS AND GREAT EGRETS

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ABSTRACT.—During a 13-yr period mean Great Blue Heron (*Ardea herodias*) clutch size at a central California colony ranged between 2.72 and 3.35 eggs, with an overall mean of 3.16. Mean Great Egret (*Casmerodius albus*) clutch size ranged from 2.70 to 3.07 eggs, with an overall mean of 2.87. Annual differences in clutch size were weakly significant in both species, and clutch size in both species declined slightly with relative as well as absolute time of breeding. The overall mean number of fledglings produced from heron nests was 1.45, with annual means ranging from 0.89 to 2.38. Year, clutch size, and relative time of breeding had significant effects on heron fledging success. The mean number of fledged egrets/nest was 0.90, ranging from 0.03 to 2.04 annually; only annual differences accounted for a significant proportion of the variance in fledging success. In both species, the most frequent clutch size was 3 but the most productive size was 4. Overall, 46.8% of the heron eggs and 33.0% of the egret eggs fledged young. The herons nested in smaller numbers and earlier than the egrets. Annual variability in colony mean clutch-initiation dates was less for herons than for the egrets. Egret clutch and brood sizes were smaller before the 1972 ban on DDT and related chemicals than after. Laying dates before and after the ban did not differ significantly. A similar comparison for the herons showed no significant differences associated with the ban on DDT. The herons lost more young to starvation than to predation, and the egrets displayed the opposite trend. Mortality of the young was greatest for the herons in the second week of life and greatest for the egrets in the third; survival for both species was high after 5 weeks. Except for a drop in the number of breeding pairs of egrets after a year of heavy predation, fluctuations in population levels were not correlated with reproductive biology. Received 9 December 1983, accepted 7 July 1984.

CONSIDERABLE attention has been focused on the reproductive success of the Ardeidae in the wake of the discovery that certain species are vulnerable to pesticide-induced eggshell thinning and egg loss during incubation (Vermeer and Reynolds 1970; Faber et al. 1972; Pratt 1972a; Ohlendorf et al. 1978, 1979; Blus et al. 1980; Findholt 1981; Mitchell 1981; Bayer 1982; LaPorte 1982; Custer et al. 1983a, b). However, the relative importance of ecological factors fundamental to productivity and abundance is poorly understood. Long-term studies are particularly valuable in this regard. Most recent studies of these species are of 1–3 years' dura-

tion and thus are limited in their potential for evaluating environmental determinants. Because short-term effects may vary from year to year, long-term trends would become apparent only after long periods of time, and rare but important events may be missed (Wiens 1984).

In this paper we analyze the relationships among clutch size, time of laying, and fledging success, and we evaluate the relative importance of starvation and predation on fledging success in a Great Blue Heron (*Ardea herodias*) and Great Egret (*Casmerodius albus*) colony in central California for the 13-yr period from 1967 through 1979. This paper differs from other heron and egret studies in two respects. It is the first long-term study of the Ardeidae that includes details on the breeding biologies of the species. It is also apparently the only study of the group that has been able to follow the

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breeding biologies of the birds in such detail without observer disturbance. The picture of breeding biology so obtained probably is closer to the natural situation than those obtained at colonies subject to observer disturbance. Nesting success at this colony for 1967–1973 has been reported previously (Pratt 1970, 1972a, b, 1974).

Heron and egret clutch size has been shown to vary with laying date (Jenni 1969, Wolford and Boag 1971, Siegfried 1972, Rodgers 1980a, Custer et al. 1983a). It may differ between years (Wolford and Boag 1971, Custer et al. 1983a) or it may remain constant (Rodgers 1980a, Tremblay and Ellison 1980, Custer et al. 1983a), and mean clutch size sometimes shows intercolony differences in similar habitats (Custer and Osborn 1977). Larger clutches usually produce more young (Tomlinson 1975; Rodgers 1980a, b; Tremblay and Ellison 1980) although St. Clair Raye and Burger (1979) found no significant differences in survival by clutch size for Snowy Egrets (*Egretta thula*) in New York, and results of studies by Millstein et al. (1970) and Morrison and Shanley (1978) are inconclusive.

STUDY AREA AND METHODS

Our data were gathered at the Audubon Canyon Ranch heronry on the central California coast (37°56'N, 122°41'W), where Great Blue Herons and Great Egrets nest in the same colony. The birds nest in or near the tops of 24–30 m tall coast redwoods (*Sequoia sempervirens*) that grow from the bottom and north-facing slope of a narrow canyon. The colony is roughly linear with no well-defined center (Fig. 1). It is known to have been active since 1941 and probably was established well before that time. It is 21 km from the nearest Great Blue Heron colony and 19 km from the nearest Great Egret colony.

Observers watched nests from an overlook approximately 11 × 5 m on the south-facing slope of the canyon above the level of many nests and about 90–180 m from them. This overlook has been heavily used by visiting school groups during the week and by the general public during weekends since 1962, when local Audubon societies purchased the ranch. We believe our results are not biased by investigator disturbance because the birds show no sign of alarm when humans are at the overlook, in part perhaps because of the distance to the nests and in part because the trail up the side of the canyon is concealed by trees and shrubs. The potential for disturbance is limited to the area of the overlook, where observers are quiet and movement is restricted.

Clutch and brood size were determined by looking

into openly visible nests. Where nest placement or intervening foliage prevented accurate egg and chick counts, laying and hatching dates could be established to within 3 days by egg color, chick movement, and behavior of adults. Nest construction for both species is conspicuous, and several days elapse from the beginning of nest-building to clutch initiation. All nests were discovered in the building stage except for 5 or fewer egret nests/year that were built at hidden sites where activity of the adults or, if successful, large young revealed the location. In such cases the timing of nest events could only be inferred.

All nests were plotted and numbered on a diagram of the heronry as they were established, and their progress was followed until the last young left the colony. Observers checked nests using 7× binoculars and 20× spotting scopes at 3- or 4-day intervals, except in 1971 when checks were at 2- or 3-day intervals. On the night of 20 June 1975, when the colony was being devastated by nocturnal predation, observers kept watch from 2030 to 0020 to identify the predator.

The number of breeding pairs was defined as the maximum number of simultaneously occupied nests. Maximum heron nest occupancy occurred before any nests failed, and the number of nest starts after that date was always fewer than the number of early failures. Some egret nests failed before the time of maximum occupancy, especially during the years when thinned-shelled eggs were breaking in the nests, but nest initiations after maximum occupancy did not exceed early failures. We assume that nests built after maximum occupancy were initiated by pairs that failed earlier at Audubon Canyon Ranch, but because none of the birds was marked, we cannot exclude the possibility that birds that failed at other colonies came to Audubon Canyon Ranch to renest.

We considered young successfully fledged when they were old enough to fly across open space to trees away from the nests. This was 7 weeks of age for the egrets (Tomlinson 1976, Pratt MS) and 8 weeks for the herons (Vermeer 1969, Pratt 1970). Because observers did not disturb the young and because young hurried back to the nests when adults arrived to feed, it was possible to associate chicks with single nests until they were able to fly.

Young that died in nests with healthy siblings and young that disappeared sequentially in broods of 2–4 were considered to have died of starvation. Young categorized as lost to predators included losses in nests where there were bloody remains, losses where chicks were found on the ground with evidence of predator attack, and simultaneous losses where the whole brood vanished with no trace.

In our analyses of the effect of the timing on breeding biology, we used two measures of timing: 1) the absolute date of breeding, which corresponds to the calendar date of laying of the first egg, and 2) the



Fig. 1. Nest chart at Audubon Canyon Ranch for a representative year (1973). Triangles = heron nests, circles = egret nests, O = overlook.

"percent-ranked date of egg-laying," which is an index of the relative time of breeding within seasons with differing annual means of laying dates. The latter measure was computed by ranking the dates of nest initiations within each nesting season, dividing by the total number of nests in that season, and multiplying by 100. Thus, a percent-ranked date of breeding of 25 would apply to the third bird to lay in a group of 12, the 40th bird in a group of 160, and the 65th bird in a group of 260.

Statistical analyses were conducted with the Statistical Analysis System (SAS) operating on the University of California at Berkeley's IBM 4341 computer. We used SAS to run *t*-tests using the TTEST procedure, analyses of covariance (ANCOVA's) using the General Linear Models (GLM) procedure, and linear regressions using the SYSREG procedure. The ANCOVA is a statistical analysis similar to the analysis of variance. In the ANCOVA, however, the contribution of each of the various independent variables to the overall variance in the dependent variable is first factored out, if necessary, with linear regression. If, for example, one were to analyze differences in clutch size between years, but clutch size was known to decrease linearly with the time of laying, the most powerful statistical test for the effect of differences in years would be to first adjust for the fact that clutch size differs with time of laying. The ANCOVA's performed by SAS conduct such analyses, and they control for all other variables in the independent variable list when a given independent variable's effect is being tested. A further complication arises when the type of dependence (e.g. positive steep, negative shallow) of the dependent variable on the independent variable depends on the value of another independent variable. Such complications are termed "interaction effects," and in our analyses we tested for all such effects as well as the main effect of each independent variable taken alone. In interpreting ANCOVA's, we relied entirely on the Type IV sums of squares and associated *F*-ratios and probabilities that GLM produces. These probabilities

TABLE 1. Estimated numbers of breeding pairs of Great Blue Herons and Great Egrets at Audubon Canyon Ranch.

Year	Herons	Egrets
1967	50	70
1968	62	74
1969	55	86
1970	50	85
1971	44	85
1972	46	96
1973	58	99
1974	48	96
1975	45	85
1976	40	65
1977	41	84
1978	43	88
1979	35	98
Mean	47	85

tend to be more conservative than traditional Type I or II approaches, and they alone incorporate the distribution of data among effect cells into the design of the model to be tested. For all regressions, the slopes (*m*) and *y*-intercepts (*b*) are presented from the general linear equation for a dependent variable (*y*) on an independent variable (*x*): $y = mx + b$. A slope of zero indicates no relation between the independent and dependent variables, and the probabilities that the slope equals zero [$P(m=0)$] also are reported.

For many analyses R^2 , the proportion of the total variance in the dependent variable that is explained by the specified independent variables, provides a convenient indication of the strength of a relationship. Especially in large samples of data, an independent variable can have a highly significant effect (low *P*) without explaining a very large proportion of the total variance in the dependent variable (low R^2). The calculation of 95% confidence intervals for graphic presentation of some of the data followed the methods of Sokal and Rohlf (1981) with probabilities from Rohlf and Sokal (1981). Means are presented in the text ± 1 SE.

Unless indicated otherwise, the analyses are based on a sample of 729 egret nests and 297 heron nests of known clutch and brood size.

RESULTS

Number of breeding pairs.—The estimated number of breeding pairs of herons during the years of the study ranged between 35 and 62 ($\bar{x} = 47$; Table 1); the estimated number of breeding pairs of egrets ranged from 65 to 98 ($\bar{x} = 85$).

Clutch size.—The overall mean Great Blue Heron clutch size was 3.16 ± 0.04 , with a range

TABLE 2. Great Blue Heron clutch size and fledgling production.

Year	Mean clutch	Clutch size																
		1			2			3			4			5				
		n	Fledged/ nest	Fledged/ nest	n	Fledged/ nest	Fledged/ nest	n	Fledged/ nest	Fledged/ nest	n	Fledged/ nest	Fledged/ nest	n	Fledged/ nest	n	Fledged/ nest	Total fledged/ nest
1967	Successful nests			1	2.00	6	1.83	4	2.50	1	2.00	12	2.08	25	2.08			
	All nests	3.26	0.67	3	0.73	15	0.73	8	1.25	1	2.00	27	0.93					
1968	Successful nests			1	2.00	10	2.10	7	2.00			18	2.06	37	2.06			
	All nests	3.35	2.00	1	1.91	11	1.91	8	1.75			20	1.85					
1969	Successful nests			2	1.50	10	2.60	10	2.80			22	2.59	57	2.59			
	All nests	3.33	1.50	2	2.17	12	2.17	10	2.80			24	2.38					
1970	Successful nests			2	0.00	8	2.25	7	2.00			15	2.13	32	2.13			
	All nests	3.24	0.00	2	1.50	12	1.50	10	1.40			25	1.28					
1971	Successful nests			3	1.67	6	1.83	3	3.33			12	2.17	26	2.17			
	All nests	2.72	0.71	7	1.00	11	1.00	3	3.33			22	1.18					
1972	Successful nests			1	2.00	7	2.43	6	2.67			14	2.50	35	2.50			
	All nests	3.24	1.00	2	1.00	9	1.89	6	2.67			17	2.06					
1973	Successful nests			1	2.00	14	1.93	3	2.00			18	1.94	35	1.94			
	All nests	3.14	1.00	2	1.00	26	1.04	7	0.86			35	1.00					
1974	Successful nests			2	1.50	12	2.17	5	2.40			19	2.16	41	2.16			
	All nests	3.09	1.00	3	1.00	14	1.86	5	2.40			22	1.86					
1975	Successful nests			2	0.00	3	1.67	7	2.43			10	2.20	22	2.20			
	All nests	3.23	0.00	2	0.31	16	0.31	8	2.13			26	0.85					
1976	Successful nests			5	1.60	6	2.33	5	2.60			16	2.19	35	2.19			
	All nests	3.10	1.60	5	1.60	8	1.75	7	1.86			20	1.75					
1977	Successful nests			2	0.00	9	1.87	2	2.00			11	1.91	21	1.91			
	All nests	3.00	0.00	2	0.00	17	1.00	2	2.00			21	1.00					
1978	Successful nests			2	2.00	8	1.75	5	2.00			15	1.87	28	1.87			
	All nests	3.10	1.35	3	1.35	12	1.17	5	2.00			20	1.40					
1979	Successful nests			11	2.45	3	3.33	3	3.33			14	2.64	37	2.64			
	All nests	3.33	2.07	13	2.07	4	2.50	4	2.50	1	0.00	18	2.06					
Total	Successful nests			18	1.72	110	2.13	67	2.45			196	2.20	431	2.20			
	All nests	3.16	0.91	34	0.91	176	1.33	83	1.98	2	1.00	297	1.45					
Fledged/ egg	Successful nests				0.86		0.71		0.61		0.40							
	All nests		0.00		0.45		0.44		0.49		0.20							

of 1-5 eggs (Table 2). Yearly means ranged from 2.72 in 1971 to 3.35 in 1968. Means were relatively constant from 1967 through 1970. After a marked decline in 1971, they fluctuated irregularly through 1978 and returned to the pre-1970 level in 1979 (Fig. 2). An ANCOVA ($R^2 = 0.11$) revealed a weak but significant effect of both year ($F_{12,283} = 1.77, P = 0.05$) and relative time of breeding ($F_{1,283} = 17.11, P = 0.0001$) on heron clutch size. A regression of clutch size on the percent-ranked date of egg-laying revealed a weak decline in clutch size with relative time of breeding [$R^2 = 0.04, b = 3.58, m = -0.61, P(m=0) = 0.0004$]. A similar regression for clutch size vs. absolute time of breeding revealed a similarly weak decline [$R^2 = 0.05, b = 3.67, m = -0.006, P(m=0) = 0.0001$].

The overall mean Great Egret clutch size was 2.87 ± 0.03 with a range of 1-6 eggs. Annual means ranged from 2.70 in 1970 to 3.07 in 1979 (Table 3). Egret clutch size declined from 1967 through 1970 and increased irregularly in the years following (Fig. 3). An ANCOVA ($R^2 = 0.05$) revealed a weak but significant effect of both year ($F_{12,715} = 2.25, P = 0.009$) and relative time of breeding ($F_{1,715} = 14.61, P = 0.0001$) on egret clutch sizes. A regression of clutch size on the percent-ranked date of egg-laying revealed a weak decline in clutch size with relative time of breeding [$R^2 = 0.02, b = 3.16, m = -0.43, P(m=0) = 0.002$]. A similar regression for clutch size vs. absolute time of breeding revealed a similarly weak decline [$R^2 = 0.02, b = 3.32, m = -0.004, P(m=0) = 0.0001$].

Fledging success.—The mean number of young fledged from all Great Blue Heron nesting attempts was 1.45 ± 0.06 (Table 2). Yearly means ranged from 0.85 in 1975 to 2.38 in 1969 without showing any consistent trend (Fig. 2). An ANCOVA ($R^2 = 0.35$) of fledglings produced per nest vs. clutch size, year, relative time of breeding, and appropriate interaction terms revealed a significant effect of clutch size ($F_{4,252} = 2.88, P = 0.02$), year ($F_{12,252} = 4.26, P = 0.0001$) and relative time of breeding ($F_{1,252} = 4.43, P = 0.04$). A regression of fledglings produced/nest vs. percent-ranked time of breeding revealed a poorly defined decline in fledging success with season [$R^2 = 0.03, b = 2.11, m = -0.89, P(m=0) = 0.0048$].

The mean number of fledglings produced/nest for Great Egrets was 0.90 ± 0.04 (Table 3). Yearly means ranged from 0.03 in 1975 to 2.04 in 1979. An ANCOVA ($R^2 = 0.32$) of fledglings

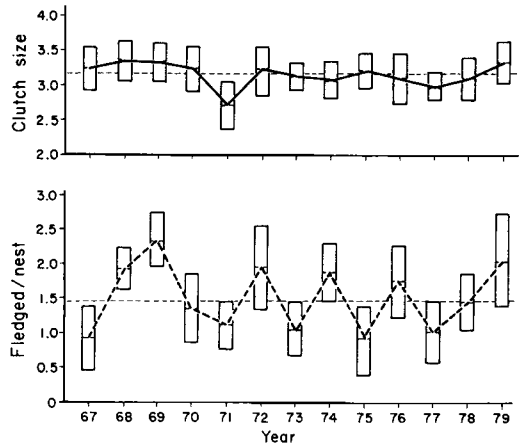


Fig. 2. Annual mean clutch size and fledging success of Great Blue Herons. Rectangles represent 95% confidence intervals. The horizontal line indicates the overall mean. Interyear differences are significant ($P \leq 0.05$) where confidence intervals do not overlap. Yearly means differ significantly from the overall mean where it does not cross the confidence interval.

produced/nest vs. clutch size, year, relative time of breeding, and appropriate interaction terms revealed a significant effect of only year ($F_{12,672} = 3.04, P = 0.0004$). Great Egret fledging success declined from 1967 through 1970, improved somewhat during the following 4 yr, and plunged in 1975 (Fig. 3) due to heavy predation. Success recovered in 1976, and in 1978 and 1979 it exceeded that in all other years.

In successful nests only, the number of young fledged increased with clutch size for both Great Blue Herons (Table 2) and Great Egrets (Table 3). The most productive clutch size for both species was 4.

None of the clutches of 1 was successful for either species. These appeared to be incomplete clutches and, when observed, the birds usually were standing. They seldom settled in incubating position. These eggs often were abandoned with dissolution of the pair bond or were started so late in the season that no more eggs were laid.

None of the 7 egret clutches of 5 or 6 was successful; 1 hatched 1 egg, and the others were incubated well past the normal incubation period without hatching.

Overall, 46.8% of Great Blue Heron eggs ($n = 910$) fledged young. An ANCOVA ($R^2 = 0.31$) analyzing the effect of clutch size, relative time of breeding, year, and appropriate interaction

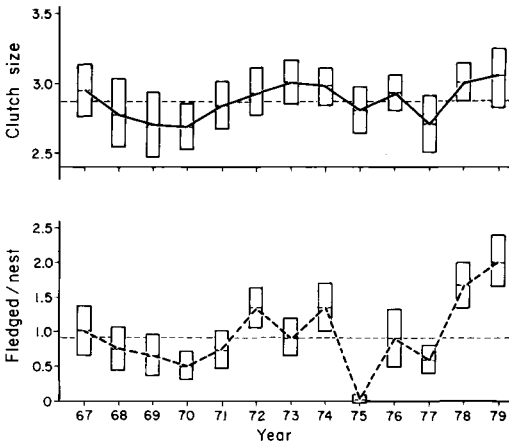


Fig. 3 Annual mean clutch size and fledging success of Great Egrets. Rectangles represent 95% confidence intervals. The horizontal line indicates the overall mean. Interyear differences are significant ($P \leq 0.05$) where confidence intervals do not overlap. Yearly means differ significantly from the overall mean where it does not cross the confidence interval.

terms on the proportion of fledglings produced/egg revealed significant effects of clutch size ($F_{4,243} = 2.56, P = 0.04$), relative time of breeding ($F_{1,243} = 6.38, P = 0.01$), and year ($F_{12,243} = 3.44, P = 0.0001$). A regression of the proportion of fledglings produced/egg vs. the percent-ranked time of breeding revealed a poorly defined decline with season [$R^2 = 0.02, b = 0.61, m = -0.21, P(m=0) = 0.0374$].

Great Egrets fledged young from 33.0% of their eggs ($n = 2,090$). An ANCOVA ($R^2 = 0.29$) analyzing the effect of clutch size, relative time of breeding, year, and appropriate interaction terms on the proportion of fledglings produced/egg revealed a significant effect only of year ($F_{12,671} = 3.12, P = 0.0003$).

Timing of laying.—The earliest heron breeding seasons started with laying of the first egg on 13 February in 1970 and 1971; the latest started with the first egg on 29 February in 1976. Mean clutch initiation dates for the herons varied within a 25-day range from 7 March in 1970 to 31 March in 1971 and 1975 (Fig. 4). The overall mean was 21 March.

Annual variability in clutch initiation was greater for the egrets (Fig. 5) than for the herons. The earliest egret clutch was started on 15 March 1970, and the latest season started on 29 April 1977. The mean egret clutch initiation date was 30 April with a 42-day range across

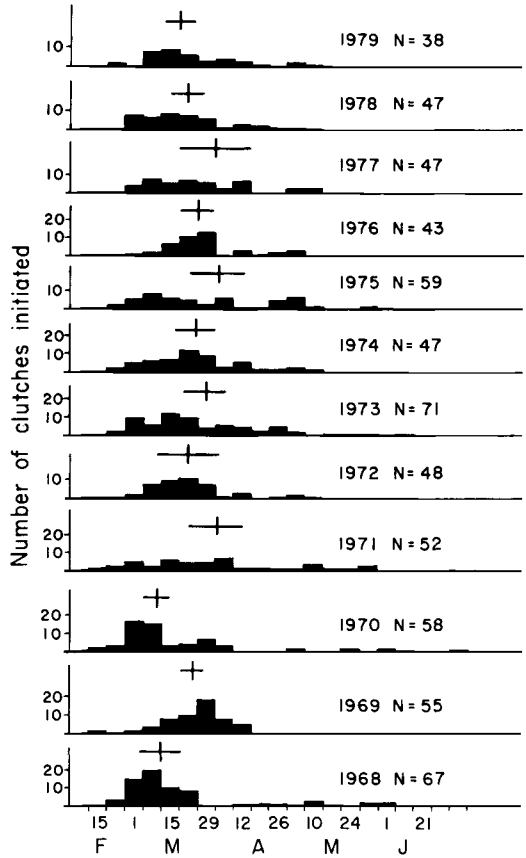


Fig. 4. Frequency distribution for Great Blue Heron clutch initiations. Means (vertical lines) and 95% confidence intervals (horizontal lines) are plotted above each histogram. The year 1967 is not included because observations began in March of that year, after most clutches had been started and too late for accurate dating.

annual means from 14 April 1978 to 25 May 1977.

In general neither species was highly synchronous in laying. Heron clutch initiation in 1971 was unusually asynchronous (Fig. 4). Laying synchrony for the egrets was lowest in 1967 (Fig. 5), probably because many rainy days in April of that year (Pratt 1970) depressed egret nesting activities and resulted in a slow "break-through" effect (Gochfeld 1980). Late arrivals overlapping with renestings contributed to the extended nesting season.

Effects of the pesticide ban.—Before 1972, when DDT was legal to use, the Great Egrets at Audubon Canyon Ranch lost many eggs due to

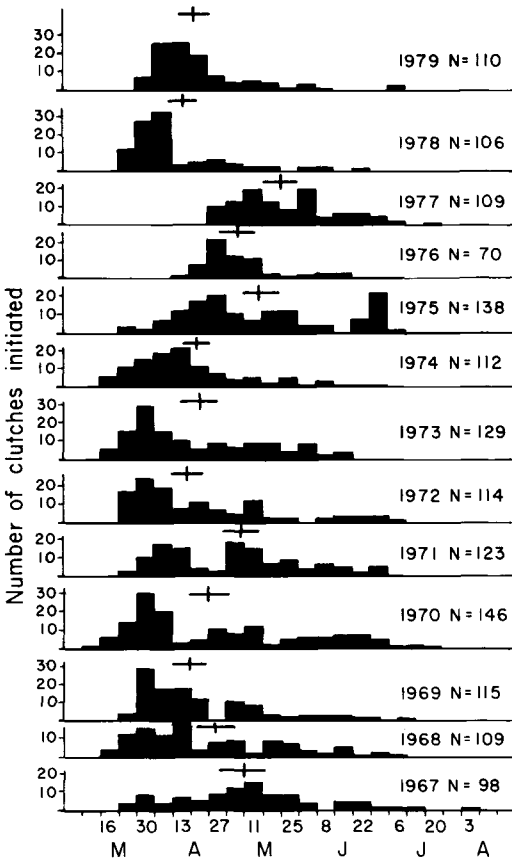


Fig. 5. Frequency distribution for Great Egret clutch initiations. Means (vertical lines) and 95% confidence intervals (horizontal lines) are plotted above each histogram.

pesticide-induced shell thinning (Faber et al. 1972, Pratt 1972a). To test for changes in egg loss and nesting success after the ban on DDT, the years 1967-1972 were pooled and compared with mean clutch size, brood size, and clutch initiation dates for the years 1973-1979. Mean egret clutch size for 1967-1972 was 2.81 ± 0.04 ($n = 353$), whereas mean clutch size for 1973-1979 was 2.93 ± 0.03 ($n = 363$; for the comparison: $t = 2.22, P = 0.0270$). Mean brood size for 1967-1972 was 2.35 ± 0.06 ($n = 193$), and from 1973-1979 it was 2.57 ± 0.05 ($n = 258$; $t = 2.70, P = 0.007$). Mean clutch initiation date for 1967-1972 was 29 April ± 1.56 ($n = 353$) and for 1973-1979 it was 2 May ± 1.44 ($n = 363$; $t = 1.21, P = 0.23$). Thus, clutch size and brood size increased significantly after the ban

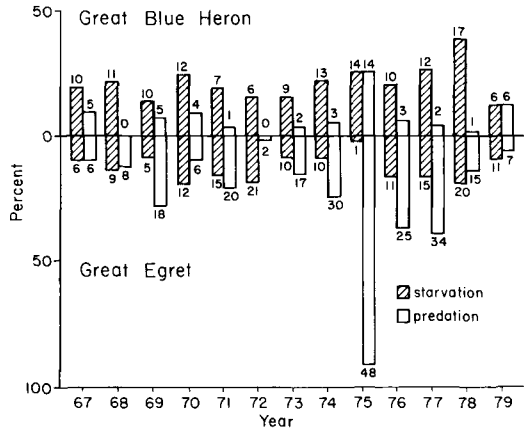


Fig. 6. Percentage of Great Blue Heron and Great Egret young lost to starvation and predation. Numbers above and below bars are sample sizes.

on DDT, but mean laying dates were not affected.

Although Great Blue Herons suffered shell thinning during the DDT era, they lost fewer eggs, and reproductive success apparently was not affected (Faber et al. 1972, Pratt 1972a). Heron clutch size was 3.18 ± 0.06 before 1973 ($n = 130$) and 3.14 ± 0.05 after ($n = 158$; $t = 0.57, P = 0.57$), brood size was 2.79 ± 0.08 before ($n = 107$) and 2.81 ± 0.08 after ($n = 129$; $t = 0.19, P = 0.85$), and mean clutch initiation date was 20 March ± 2.24 before ($n = 130$) and 24 March ± 1.83 after ($n = 158$; $t = 1.43, P = 0.16$). Thus, there was no significant difference in heron clutch size, brood size, or laying dates associated with the ban on DDT.

Effect of predation vs. starvation.—Although predation was nocturnal and attacks rarely witnessed, circumstantial evidence for repeated predation by Great Horned Owls (*Bubo virginianus*) and raccoons (*Procyon lotor*) was strong. J. Kipping (pers. comm.) discovered a Great Horned Owl one morning eating a young heron on the ground beneath a nest. In addition, M. Schwartz (pers. comm.) found an owl feather stuck to a clump of bloody egret feathers from a kill of the previous night. Great Horned Owls have been implicated in predation at other heron colonies as well (Cottrille and Cottrille 1958, Callahan and Carey 1979). In 1975, when it was obvious from bloody bodies of egret chicks in the nests that predation was almost completely destroying egret production,

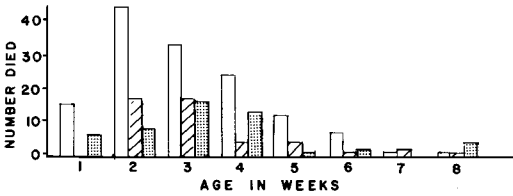


Fig. 7. Mortality of Great Blue Heron chicks per week. Open = starved, hatched = preyed upon, shaded = other.

observers on the night watch of 20 June saw a raccoon invade nests of both herons and egrets. By morning all nests in that section of the colony were destroyed (Pratt MS). Lopinot (1951) also witnessed raccoon predation on Great Blue Herons, and raccoons have been suspected of predation in ardeid colonies by Teal (1965), Taylor and Michael (1971), and Hjertaas (1982).

Loss of young to predation and starvation varied from year to year for both species (Fig. 6). Herons were more likely to lose chicks to starvation than predation. In a sample of 243 heron nests with known clutch and brood size, 65% of the 672 chicks fledged, 20% starved, predators took 7%, and 7% were lost to other causes. In 453 egret nests with known clutch and brood size, 58% of the 1,124 chicks fledged, 13% starved, predators took 21%, and 8% were lost to other causes.

Age of chick death.—The second through fourth weeks of life were the most hazardous for chicks of both species. Of the 233 heron chicks that died, 76% died during this period (Fig. 7), with greatest mortality occurring in the second week. Of the 471 egret chicks that died, 70% died in the second through fourth weeks (Fig. 8), with greatest mortality in the third week.

DISCUSSION

This study revealed significant reversals in trends in timing of breeding, reproductive success, and to a lesser extent, clutch size of Great Blue Herons and Great Egrets that would not be apparent in short-term studies. In addition, it was apparent that ecological factors affecting reproduction varied among years and between the two species.

The greater susceptibility of heron chicks to starvation suggests that the adult herons had

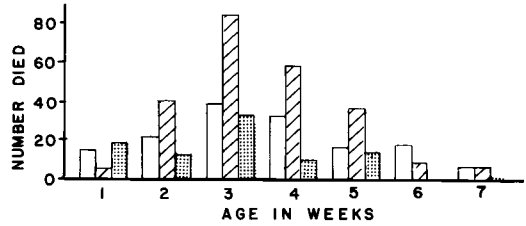


Fig. 8. Mortality of Great Egret chicks per week. Open = starved, hatched = preyed upon, shaded = other.

more difficulty finding sufficient food to raise their young than the egrets. There are no data on prey availability for the herons and egrets at Audubon Canyon Ranch, but judging by the agreement between percents of eggs raising young for this study and most others reporting this measure of success (Table 4), food available to the herons at Audubon Canyon Ranch was not unusually limited. Gill's (1973) egg success of 59% may be an overestimate because he found it necessary to limit observations to minimize disturbance.

The greater susceptibility of egret chicks to predation was unexpected. The only known predators on the Audubon Canyon Ranch colony were Great Horned Owls and raccoons. Both Golden Eagles (*Aquila chrysaetos*) and Bald Eagles (*Haliaeetus leucocephalus*) are known predators on Great Blue Herons (Carnie 1954, Bayer 1979, Kelsall and Simpson 1980), but they are rare winter visitants at Audubon Canyon Ranch and to date have not been observed to prey on either species there. Perhaps the smaller size of egret young compared to the herons increased their attractiveness to owls. Marti (1974) reported a mean prey size for Great Horned Owls in Colorado of 177 g, although the maximum was in excess of 2,500 g. Heron eggs start to hatch in March, a month or more before the egret eggs. By late April, when owls in central California are feeding young (J. Winter pers. comm.), young herons would be more than 4 weeks old and weigh 1,500 g or more (McAloney 1973, Merritt 1981). Egret chicks would reach maximum weights of 600–1,000 g (Tomlinson 1976) in mid-June or later. Egret young also might have been at greater risk because they are white and more conspicuous than herons. However, owls are able to see mice in very low light levels (Marti 1974), and it is

TABLE 4. Clutch size and reproductive success reported for Great Blue Heron colonies.

Location	Latitude (°N)	Years	Clutch size	Successful eggs (%)	Fledged/nest	Fledged/successful nest	Fledged/pair	Source
Southern Alberta	49-55	1967-1968	5.00	—	—	2.2-2.5	—	Vermeer (1969)
British Columbia	49	1977-1979	—	—	—	2.3-2.9	—	Kelsall and Simpson (1980)
Idaho	47	1977-1978	—	—	—	2.20	1.95	Collazo (1981)
Idaho	47	1977-1978	—	—	0.5-2.5	2.6-3.4	—	Warren (1979)
Columbia River	46	1978	4.45-4.49	41-50	1.88-2.29	2.29-2.79	—	Blus et al. (1980)
Western Oregon	42-46	1974	—	—	—	2.18-2.70	—	Werschkul et al. (1977)
Nova Scotia	45	1971	4.17	—	—	3.09	2.84	McAloney (1973)
Central Oregon	45	1975	—	—	2.17-2.71	—	1.96	English (1978)
Western Oregon	44	1970	4.19	—	—	2.61	2.04	Henny and Bethers (1971)
Lake Erie	42	1974-1975	3.39	—	2.27	2.46	—	Edford (1976)
Central California	38	1971	3.36	59	2.14	2.50	—	Gill (1973)
Central California	38	1967-1973	3.0-3.7	—	—	1.8-2.3	1.3-2.0	Pratt (1974)
Central California	38	1967-1979	3.16	46.8	1.45	2.20	—	This study
Texas	28	1979	3.58	45	—	—	1.6	Mitchell (1981)
Florida Bay	28	1981	2.88-3.50	—	1.55-2.04	—	—	Powell (1983)

doubtful that herons would be protected by their dark coloration. Heron chicks probably were less affected than egret chicks in 1975 because the raccoons did not invade the colony until June. By this time some young herons had left, and many of those that remained were old enough to escape by hopping across branches. Egret chicks were younger and were more likely to stay huddled in their nests.

The effect of predation at other Great Blue Heron colonies has not been quantified, but reports suggest that its effect on reproductive success has been minor (Lopinot 1951, Bayer 1979, Kelsall and Simpson 1980). Teal (1965) reported losses of Great Egret young to predators of 11%. Comparable data for other Great Egret colonies is unavailable, but in single-year studies at mixed-species colonies predation has resulted in total or near-total loss of young (Dusi and Dusi 1968, Taylor and Michael 1971).

The Great Blue Heron breeding population showed a decline from 1973 onward (Table 1) that was not matched by a similar decline in reproductive success (Fig. 2). We found no relationship between heron population fluctuations and reproductive biology in the same or preceding years. Egret population levels increased annually, except for a sharp temporary decline in 1976 (Table 1). This decline may have been a reaction to the devastating predation in 1975. Members of the heron family are known

for colony and individual shifts in breeding locations (e.g. Thompson and Littlefield 1979, Kelsall and Simpson 1980), and our results suggest that predation may prompt a move to another breeding site. However, renesting at the same colony is also recorded (Taylor and Michael 1971).

The seasonal decline in mean clutch size for both species would be expected in light of the tendency for clutch size to decrease with season in all birds (e.g. Klomp 1970, Ryder 1980, Winkler and Walters 1983) as well as herons in particular (Jenni 1969, Wolford and Boag 1971, Siegfried 1972, Rodgers 1980a, Custer et al. 1983a). Several aspects of reproductive biology are associated with this trend, including later breeding by younger birds whose clutches tend to be smaller (e.g. Johnsgard 1973, Ryder 1980), smaller replacement clutches by individual females (e.g. Batt and Prince 1979), and possible genetic control of clutch size and laying date interacting with proximate environmental factors (e.g. Batt and Prince 1979). Data relevant to any of these possibilities at Audubon Canyon Ranch are not available.

The mean clutch sizes reported here are somewhat smaller than those in Pratt (1974) because the sample is larger and includes incomplete clutches of 1 and clutches of 2 that formerly were excluded because they were considered incomplete. Henny's (1972) mean

clutch size of 3.66 eggs for Great Blue Herons in central California was based on museum collections, and because egg collectors may have ignored small clutches in favor of larger ones, this measure could be biased toward larger clutches. However, Gill (1973) reported a mean clutch size of 3.63 at a south San Francisco Bay colony in 1971.

Great Blue Heron clutch size was larger during the first 4 yr, declined in 1971 significantly below the overall mean, and returned in 1979 to the level of the first 4 yr (Fig. 2). Great Egret clutch size showed a declining trend from 1967 through 1970, probably in response to pesticide contamination, rose through 1974, and was largest in the final 2 yr (Fig. 3).

Heron clutch size varies geographically, usually increasing with latitude (Palmer 1962, Henny and Bethers 1971, McAloney 1973, Rodgers 1980a, Custer et al. 1983a; but see Custer and Osborn 1977, Gladstone 1979). There is also a tendency for heron clutches to be smaller in coastal and marine habitats than at inland colonies (Henny 1972, Maxwell and Kale 1977). Black-crowned Night-Heron (*Nycticorax nycticorax*) clutches have been shown to be larger in the prepesticide years (Ohlendorf et al. 1978, Findholt 1981), although Custer et al. (1983a) found no relationship between clutch size and DDE concentrations. Recent Great Blue Heron clutches in Ohio (Edford 1976) and Texas (Mitchell 1981) were smaller than the means derived from egg collections for those regions reported by Henny (1972), but means in Oregon (Henny and Bethers 1971, Blus et al. 1980) were about the same. In Florida, most Great White Heron clutches were smaller in 1981 than in 1923 (Powell 1983), but herons that supplemented their natural food by soliciting from humans laid clutches equal in size to those in 1923. Further study of clutch-size trends over time in these species are needed to assess the significance of possible long-term trends.

Although clutches of 4 produced the greatest mean number of young for both species, the most frequent clutch size in both was 3. In most other studies of herons, clutches larger than the mode have been most productive (Millstein et al. 1970; Tomlinson 1975; Morrison and Shanley 1978; Rodgers 1980a, b; but see St. Clair Raye and Burger 1979). These data contradict a strict interpretation of Lack's (1954, 1968) theory that birds maximize their reproductive potential by raising the largest number of young

that the parents can feed and that the most productive clutch size should be the most frequent. Parents of both species obtain progressively less "return for their investment" in successful nests as clutch size increases (Tables 2, 3), and it is likely that modal clutch size is reduced from its most productive in these species in response to optimal working-capacity considerations (e.g. Royama 1966, Drent and Daan 1980). Many other possibilities, especially food supply for the laying female and such life-history strategies as bet-hedging, must be considered (e.g. Winkler and Walters 1983). Because nest failures were not clutch-size dependent, success/egg was about the same for all clutch sizes (Tables 2, 3) when both successful and unsuccessful nests were included. Egg loss as a result of shell thinning may have reduced apparent egret clutch size in 1967-1972 because eggs could have been laid and lost before they were detected by observers, but this effect is likely to be small.

Reproductive success can be expressed as the number of eggs resulting in fledged young, the number of young raised/nesting attempt, the number raised/successful nest, or the number raised/pair or breeding female. The number of eggs fledging young or the number of young raised for each nesting attempt usually understates success/breeding female or pair because renestings are not taken into account. Estimating success can be complicated further when nesting attempts are started and lost between observer visits and thus not detected at all (Erwin and Custer 1982). At Audubon Canyon Ranch investigator disturbance apparently did not affect the colony. Previous estimates of nesting success for this colony thus were based on an estimate of the number of breeding pairs (Pratt 1970, 1972a, b, 1974), but to facilitate comparison with other studies, reproductive success in this paper is expressed as the mean number of young raised/nesting attempt and as the percent success of eggs. The number of young fledged/nesting attempt for the herons was 62-97% of the number raised/breeding pair for 7 yr of this study, and the same for 3 yr; in 1968, 1969, and 1972 the number fledged/nesting attempt was 14-19% greater than the number raised/breeding pair because nests of unknown clutch or brood size were excluded from the statistical analysis. For the egrets the number fledged/nesting attempt was 50-96% of the number raised/breeding pair for 12 yr and the

same in 1. Overall, the number fledged/nesting attempt was 96% of the number fledged/breeding pair of herons and 81% of the number fledged/breeding pair of egrets.

The proportion of Great Egret eggs producing young (33.0%) is lower than the 44% reported by Teal (1965) and the 67% reported by Maxwell and Kale (1977) and about equal to the 35% reported by Morrison and Shanley (1978). Results from these other studies are not strictly comparable to those from Audubon Canyon Ranch, however. Maxwell and Kale (1977) considered a nest successful when chicks reached 10 days of age, but at Audubon Canyon Ranch much egret mortality occurred later in nestling life (Fig. 3). Neither Teal (1965) nor Morrison and Shanley (1978) were precise about the fledging-age criterion.

The fact that Great Egret fledging success/egg was not significantly related to clutch size, even though larger clutches in successful nests produced more young, may be due to the relatively great importance in this species of egg-shell thinning and predation. The intensity of neither of these factors was related to clutch size. The Great Blue Herons were less seriously affected by shell thinning (Faber et al. 1972) and predation (Fig. 6) and showed a significant relationship between clutch size and fledging success/egg.

The mean number of heron young produced/nest was less than the means reported from most other colonies (Table 4), in part because of smaller clutch size. In addition, more complete coverage at Audubon Canyon Ranch may have enabled detection of more nestling mortality and more unsuccessful nests, thus reducing success/nest. At all locations herons in successful nests raised 2-3 young, with 2 usually the mode.

Over the 13 yr of this study, heron fledging success showed a sawtooth pattern, with significant fluctuations above the mean in 1968, 1969, and 1974, below it in 1973 and 1975, and nearly significant lower success in 1971 and 1977 (Fig. 2).

Estimates of reproductive success necessary to maintain a stable population based on banding returns are available for Great Blue Herons north of 40°N (Henny 1972, Bayer 1981), but band recoveries for more southerly latitudes are too few for reliable estimates. Henny (1972) suggested that because mortality probably decreases with a decrease in latitude, a level of

reproduction at Audubon Canyon Ranch of 1.5-1.7 would be adequate to maintain the population. However, he did not adjust his estimates to account for differential survival by region and banding location (Bayer 1981). Thus, his estimate may not be accurate.

Mean fledging success for the Great Egrets of 0.90 (Table 3) was greater than the 0.81/nesting attempt reported by Morrison and Shanley (1978) in Texas. A smaller clutch size of 2.3 eggs in Texas, compared with 2.87 in this study, may contribute to the difference. The difference may be even greater than appears because their visits ceased early due to observer disturbance, and mortality of older chicks may have been missed. Comparable figures for other egret colonies are not available.

Egret fledging success declined from 1967 to 1970 (Fig. 3), with significantly higher success in 1974, 1978, and 1979 and lower success in 1975 and 1977.

The 1971 heron season was notable for the small mean clutch size (Table 2) and for the slow pace of laying (Fig. 4). The tendency for younger birds to lay smaller clutches and to lay later (e.g. Klomp 1970, Ryder 1980, Winkler and Walters 1983) cannot be evaluated as a possible factor because age data for the birds at this colony are not available. However, it seems unlikely that there was a sufficient shift in the age structure of the breeding population for 1 yr to account for the observed effects. Low synchrony is frequently associated with smaller colonies (e.g. Wolford and Boag 1971, Burger 1979). However, the breeding population of 44 pairs of Great Blue Herons in 1971 (Table 1) was near the average of 47 pairs for the 13-yr period. It seems more probable that unknown environmental determinants were responsible for both effects.

Egret clutch initiation showed bimodal peaks in 1971 and 1977 (Fig. 5). Rodgers (1980a) attributed similar bimodal peaks for Little Blue Herons (*Egretta caerulea*) to temporary saturation of nesting territories, which prevented late arrivals from setting up courtship territories. At Audubon Canyon Ranch unused nest sites were plentiful even at peak occupancy. A chance concurrence of late arrivals and re-nesting may have resulted in the second laying peaks. Heavy nest losses in 1975 resulted in an unusually late peak of re-nesting (Fig. 5).

Chick survival for both species overall was relatively high after the fifth week (Figs. 7, 8).

However, interyear variability in age-dependent mortality can be considerable. In 1-2-yr studies, the week of greatest heron chick mortality spanned a 1-6-week range (Pratt 1970; Gill 1973; Collazo 1979, 1981). Unusual circumstances can produce high mortality even in the 6-7-week period (Warren 1979). There are few comparable data for the egrets. In contrast to this study, Morrison and Shanley (1978) reported greatest egret mortality during the first 10 days after hatching and none after 20 days.

Despite the isolation provided by nesting up to 30 m above the ground, predation is an important source of chick mortality for the egrets. The effect of food supply on the breeding biology of these two species requires considerable more research, but food appears to limit breeding success in the heron and to a lesser extent in the egret and may have an effect on clutch size in both species.

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The Frank M. Chapman Memorial Fund gives grants in aid of ornithological research and also postdoctoral fellowships. While there is no restriction on who may apply, the Committee particularly welcomes and favors applications from graduate students; projects in game management and the medical sciences are seldom funded. Applications are reviewed once a year and should be submitted no later than 15 January. Application forms may be obtained from the Frank M. Chapman Memorial Fund Committee, The American Museum of Natural History, Central Park West at 79th St., New York, New York 10024.

Dr. David R. Wells was appointed Chapman Fellow for the period June 1984 through December 1984. He is working on an atlas of the distribution and speciation of oriental birds. Current Chapman Fellow Robert E. Bleiweiss has been granted an extension of his Fellow status through December 1984. He is studying systematics and speciation in Andean hummingbird genera.

Chapman grants during 1984, totalling \$32,781 with a mean of \$537, were awarded to: John G. T. Anderson, cooperative foraging behavior in the White Pelican; Ana Victoria Ayala, observations on the interaction between one species of hummingbird and the flowers it uses as food source in a sub-Andean forest; George Barrowclough, ornithological survey of avifauna of Cerro de la Neblina; Jonathan J. Becker, birds of the late Miocene Love Bone Bed local fauna; Henry Lawrie Bell, composition and foraging behavior of insectivorous birds in mixed-species flocks in montane forests of New Guinea; Robert I. Bowman, a genetic analysis of evolution in Galapagos finches; Charles R. Brown, costs and benefits of coloniality in Cliff Swallows (*Hirundo pyrrhonota*); Kenneth G. Bunch, bolus recovery by Gray Jays; Peter F. Cannell, systematics of the avian orders Coraciiformes and Piciformes and allies based on syringeal anatomy; William Carmen, evolution of non-cooperative breeding in the California Scrub Jay (*Aphelocoma coerulescens californica*); John H. Carothers, microevolution of morphology in the Hawaiian Honeycreeper (*Vestiaria coccinea*); Ralph V. Cartar, can Red Phalarope chicks share post-hatching parental care?; Russell A. Charif, investigation of the function of song matching in mockingbirds (*Mimus polyglottos*); T. M. Crowe, phylogeny of the order Galliformes; C. R. Dickman, diet and prey selection of the Barn Owl in Malaysian oil palm plantations; Euan K. Dunn, census of Roseate Tern (*Sterna dougallii*) population on the Azores; Margaret Elowson-Haley, factors eliciting predator alarm calls in the Florida Scrub Jay; C. Craig Farquhar, breeding ecology of the White-tailed Hawk (*Buteo albicaudatus hypospodius*) in Texas; Peter Crawford Frederick, mating strategies in White Ibis (*Eudocimus albus*); Judy Gradwohl, population stability and rigid territoriality in some insectivorous birds on Barro Colorado Island; Rolf Karl-Heinz Grantsau, field guide to the birds of Brazil; Frederick Pearce Greene, determinants of guild structure among insectivorous birds in the Chiricahua Mountains, Arizona; John Morton Hagan III, colonial nesting in Ospreys; Thomas M. Haggerty, reproductive ecology of Bachman's Sparrow; Sylvia L. Halkin, use of song repertoires by male and female Northern Cardinals; J. Christopher Haney, selection pressures and the evolution of sociality in the White-throated Jay (*Cyanolyca mirabilis*); Russell A. Haughey, investigation of the role of the Western White-winged Dove (*Zenaida asiatica mearnsii*) in the pollination of the saguaro (*Cereus giganteus*); Paul Hendricks, foraging ecology of alpine Water Pipits; Holly H. Hobart, cytosystematics of some Arizona birds; Sylvia Hope, phylogeny of Corvidae; H. A. Isack, biology of the Greater Honeyguide (*Indicator indicator*) with emphasis on guiding behavior; Jan Kalina, socioecology of Black-and-white Casqued Hornbills and their role as seed disperser for tropical rain forest trees; Alan C.

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