

PRE-1900 OVERHARVEST OF CALIFORNIA RED-LEGGED FROGS (*RANA AURORA DRAYTONII*): THE INDUCEMENT FOR BULLFROG (*RANA CATESBEIANA*) INTRODUCTION

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ABSTRACT: Pre-1900 frog harvest data from California suggests heavy exploitation of California red-legged frogs (*Rana aurora draytonii*). A comparison with data collected from present-day, non-exploited, healthy populations of *R. a. draytonii* suggest that mostly female frogs may have been harvested. A low reproductive frequency and the probable female frog harvest bias suggest that historical populations could not withstand harvest at pre-1900 levels. The decline in frog harvest observed from 1899–1940 supports this idea. Population depletion and a persisting demand for frogs were probably the inducements to import and introduce bullfrogs (*Rana catesbeiana*). The earliest dates of bullfrog introduction correspond well with these suppositions.

Key words: Anura; Ranidae; *Rana aurora draytonii*; *Rana catesbeiana*; California; Resource exploitation

THE widespread decline of *Rana aurora draytonii* populations in California during the past 50 yr is generally accepted by herpetologists (Anderson, 1983; McKeown, 1974). Moyle (1973) proposed that this decline was largely due to competition and predation from introduced bullfrogs (*Rana catesbeiana*). Our review of the literature between 1850 and 1940 suggests that overharvest of *R. a. draytonii* by the frogging industry is a tenable, but not necessarily exclusive, alternative hypothesis that predates the earliest known introductions of bullfrogs. It is the purpose of this paper to discuss this alternative.

Determination of historical changes in *R. a. draytonii* populations is complicated by nomenclatural confusion in the pre-1900 literature. Therefore, we briefly review the nomenclatural changes crucial to the identification of the populations discussed in the literature.

MATERIALS AND METHODS

Frog harvest data were obtained from the U.S. Bureau of Fisheries and Fish Commissioner's reports for the period of

1888–1922, and from the biennial reports of the California Department of Fish and Game for the period 1914–1935. Additional data were obtained from other U.S. Bureau of Fisheries publications for the period between 1890 and 1910. In addition, most literature that mentions *R. a. draytonii* since its original description in 1852 was examined.

Mean weight of harvested frogs was calculated from U.S. Bureau of Fisheries data for the year 1895 (Table 1) and was compared to regressions of frog weight (WT) on snout-vent length (SVL) (Fig. 1). Regressions were obtained from paired measurements of live *R. a. draytonii* from one population each in San Luis Obispo ($n = 150$) and Santa Barbara ($n = 98$) counties, California, studied by one of us (MPH). Frog measurements were taken with a 15 cm ruler (SVL) and 50 g or 300 g Pesola spring scales (WT). We log-transformed the WT data in order to use a linear regression program and calculate 95% confidence intervals of the estimated mean frog SVL that corresponded to the 1895 mean frog WT estimate. Reproductive frequency and estimates of minimum age at first reproduction come in part from

TABLE 1.—California frog harvest data between 1888 and 1935. Data from Collins (1892), Conner (1937), Taylor (1924), Wilcox (1895, 1898, 1902, 1905) and the State of California Fish and Game Commission Biennial Reports (25th—1916—1918; 26th—1918—1920; 28th—1922—1924; 34th—1934—1936).

Year	Number of frogs taken	kg of frogs taken ^b	Value of harvest (\$)	Value per frog (\$)	Value per kg (\$)
1888	48,000 ^a	—	12,000	0.25	—
1889	54,000 ^a	—	13,500	0.25	—
1890	72,000 ^a	—	21,000	0.29	—
1891	72,000 ^a	—	21,000	0.29	—
1892	96,000 ^a	—	28,000	0.29	—
1895	118,704	22,405.6	12,402	0.105	0.55
1899	—	9383.5	20,638	—	2.20
1904	—	118.4	292	—	2.47
1916	—	47.2	—	—	—
1917	—	2.7	—	—	—
1919	3936 ^{a,c}	595.1	—	—	—
1922	240 ^a	45.4 ^d	—	—	—
		290.3	—	—	—
1934	—	27.2 ^e	—	—	—
1935	—	9.1 ^e	—	—	—

^a Converted from data presented in dozens.
^b Converted from data presented in pounds.
^c San Francisco and San Mateo counties.
^d Alameda and Contra Costa counties.
^e Sacramento and San Joaquin counties.

the study of the above populations and in part from the literature. Distributional data were obtained from collections at museums listed in the acknowledgments.

NOMENCLATURE

The variation within *R. aurora* has been discussed by Hayes and Miyamoto (1984). However, to avoid confusion we restrict our commentary to the large-bodied frogs that occur from Mendocino and Shasta counties, California south into Baja California and are currently classified as *R. a. draytonii*.

Few pre-1900 scientific collections of this frog exist, and these specimens have been classified under several names. Storer's (1925) synonymy of *R. a. draytonii* is fairly complete, but some citations require further discussion. *Rana aurora* was the name synonymized by Storer with *R. a. draytonii* based on Chamberlain (1898). However, this work and statements by

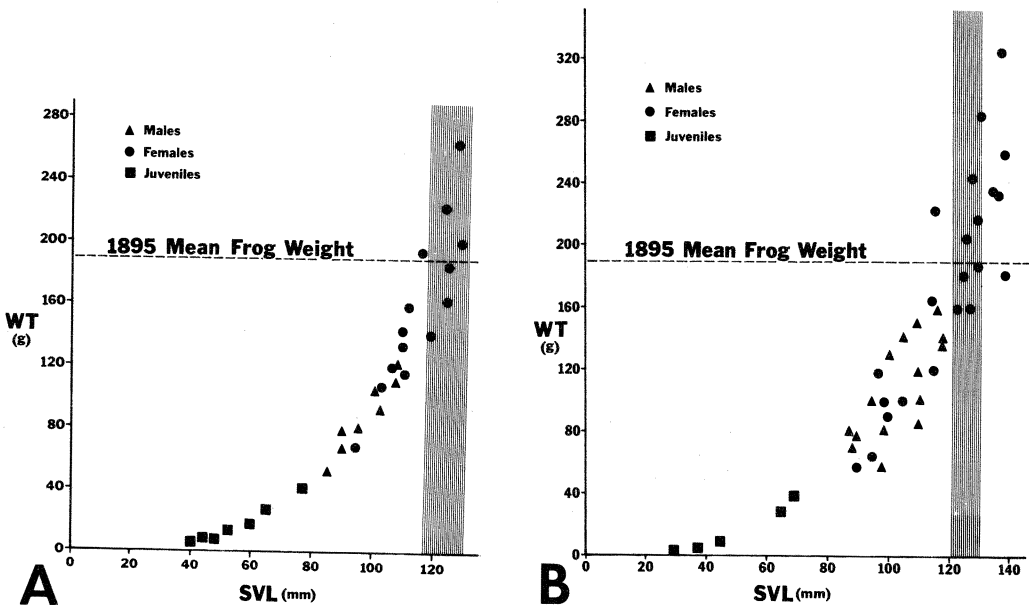


FIG. 1.—Comparison of the 1895 mean frog weight (= 189 g) with extant *R. a. draytonii* size data. Plots represent Santa Barbara (A) and San Luis Obispo (B) populations. For clarity, not all points used to calculate the respective regressions and confidence limits for each population are shown, but the extremes of sex-specific size variation are included. The shaded region is the 95% confidence interval of the 1895 mean SVL based on the 1895 mean WT estimate.

Wright (1920) show this synonymization to be incorrect. Chamberlain's descriptions were based on Cope's (1889) monograph, which explains his listing of the distribution of the frog he termed the "Western Frog (*R. pretiosa*)" as being from Montana to southern California, including (from Cope's listing) specimens currently classified as *R. aurora aurora*, *R. aurora draytonii*, *R. boyllii*, *R. muscosa* and *R. pretiosa* (Camp, 1917; Jennings, 1984; Linsdale, 1940; Zweifel, 1955). Furthermore, little doubt exists that Chamberlain's illustration of "*R. pretiosa*" is *R. a. draytonii* and his "Western Bullfrog (*R. aurora*)" strongly resembles the frog currently classified as *R. a. aurora*.

Similarly, Smith's (1895a) comments about *R. pretiosa* in San Francisco markets referred to *R. a. draytonii*. In contrast, Coombes (1902) cited no scientific names, but his comments on spawn that requires fastening (to vegetation) to keep it from sinking and January–February spawning months affirm that his California edible frog is *R. a. draytonii*. Dickerson (1906) concurred with this view because her life history account of *R. draytonii* [= *R. a. draytonii*] was based in part on Coombes' information.

HISTORY OF THE FROG INDUSTRY

Frog harvesting in California dates back to the gold rush of 1849. In a chronicle of California's resources, Cronise (1868) reported that "many species of frogs are eaten when large enough for their hind legs to furnish an adequate meal." Lockington (1879), however, was the earliest author to comment specifically on California's frog industry by noting that: "The large frog (*Rana temporaria* var. *aurora*), sometimes called 'bullfrog,' of this coast is eaten in considerable quantity in San Francisco." His comments are interesting because he noted a growing frog market at an early date and indicated that the San Francisco frog supply was already coming from sites as distant as Tulare County in the San Joaquin Valley, which was later

to become one of the three areas in the state heavily exploited by commercial frogging interests (Collins, 1892).

The growth which California and its fisheries experienced during this period was rapid (Smith, 1895b). California's human population quadrupled in size from 1860–1900 (Salitore, 1973) and this growth, coupled with increased demands for fishery products, was a factor that prompted the U.S. Bureau of Fisheries to begin detailed periodic censuses of Pacific fisheries beginning in 1888. Fishery data for the years prior to 1888 are limited and include no frog data (see Jordan, 1887). However, subsequent censuses showed not only a substantial frog harvest but a steady increase in harvests through 1895 (Table 1). Smith (1895a) noted this increase and identified the frog harvested as "*R. pretiosa*" (= *R. a. draytonii*). Chamberlain (1898), summarizing information up to 1897, listed California as one of the states supplying the largest quantities of frogs for markets and identified the marshes of the Sacramento and San Joaquin valleys as one of the major frog-producing regions in the United States.

Tabulation of the 1895 California frog harvest by county shows that most frogs came from counties adjacent to San Francisco with extensive marsh areas (Table 2). However, increased harvests were short-lived as 1899 figures show a marked decrease (Table 1). Those counties showing large harvests in 1895 decreased in 1899, and increased harvests in counties more distant from San Francisco or with more limited frog habitat are indicated (Table 2).

Because minimum age at reproductive maturity for *R. a. draytonii* is 2 yr for males and 3 yr for females (Storer, 1925; Hayes, unpublished data), yearly harvests of the magnitude indicated by pre-1900 figures could not continue indefinitely, even with the maximum replacement potential indicated by the minimum reproductive ages. However, the number of kilograms of frogs taken in 1895 (Table 1) permits further insight. These data allow

TABLE 2.—California frog harvest by county in 1895 and 1899. Data from Wilcox (1898, 1902).

County	1895		1899	
	Harvest* (kg)	Value (\$)	Harvest* (kg)	Value (\$)
Contra Costa	—	—	987.9	2178
Humboldt	—	—	1814.4	4000
Marin	3470.0	1912	1451.5	3200
Monterey	—	—	45.4	60
Napa	7257.5	4000	1632.9	3600
San Mateo	—	—	1769.0	3880
Santa Clara	7937.9	4375	1542.2	3400
Santa Cruz	66.2	40	149.2	320
Sonoma	3674.0	2075	—	—
Totals	22,405.6	12,402	9383.5	20,638

* Converted from data presented in pounds.

calculation of the mean WT of frogs harvested in 1895. Regressions of WT on SVL for present-day, non-exploited populations of *R. a. draytonii* show that frogs with a WT equal to the 1895 mean are not only well within the range of adult females, but also correspond to a body size significantly larger than the largest males (Fig. 1). This suggests that females may have represented much of the 1895 harvest, a factor probably influenced by the largest frogs bringing the best price (Chamberlain, 1898; Heard, 1904; Herri-man, 1933; Schorsch, 1933; Storer, 1933). Because female *R. a. draytonii* typically reproduce only once a year (Storer, 1925; Hayes, unpublished data), such harvests would have depleted local populations even more rapidly than sex-unbiased harvests. Furthermore, this estimate is conservative, because frogs of the mean size harvested in 1895 represent individuals considerably larger than the minimum reproductive size for females (approximately 85 mm SVL) (Hayes, unpublished data).

For frogs to have been harvested at pre-1900 levels, a substantial demand must have existed. Lockington (1879) implies that such a demand for frogs existed at an early date and True (1884) discussed an Oakland firm that handled thousands of frogs per year for local markets. During the 1890's, several "frog farms" were established to supply *R. a. draytonii* for San

Francisco markets (Heard, 1904; Storer, 1933). In 1895, Coombes (1902) noted: "The demand for frogs proving to be so great, I was obliged to get a staff of men to catch them and also have the frogs shipped to me from all parts of the state to supply the growing and pressing wants and to supply the pressing orders daily coming in."

Changes in the market value of frogs also suggest a heavy demand. Lockington (1879) found San Francisco market prices for *R. a. draytonii* varied between \$1.75 and \$4.00 per dozen depending on frog size. Prices of \$3.00 and \$4.00 per dozen for frogs in San Francisco were the highest quoted by Chamberlain (1898) when he compared the market value of frogs across the United States. After 1900, frogs were selling for prices as high as \$8.00 per dozen in California (Heard, 1904). However, frog harvest data and the dollar value of those harvests allow a better comparison of the changes in the value of frogs (Table 1). Frog market value apparently increased little between the late 1880's and the early 1890's. In 1895, the value of frogs dropped to one-third the early 1890's level for reasons we were unable to determine. Because 1895 was the year of the largest harvest for which data are available, it may be that the drop in value was influenced by the abundant frog harvest. Also, because these data are based on the value per frog, which does not consider frog size, differences in value might also be explained by unknown size differences between years. Nevertheless, in 1895 frogs ranked second in value (55¢/kg) among the over 60 California fisheries products, surpassed only by "whalebone." After 1895, a per kilogram assessment of frog market value, data independent of size, shows that frogs increased in value more than any other fishery commodity between 1895 and 1899. Notably, frog value continued to increase until after frog harvests had declined (Table 1).

Demand for frogs was also influenced by local attitudes during the heavy exploitation period of the late nineteenth

century. In California, frogging was associated with French emigrants and sophisticated French cuisine (Lockington, 1879). This association was exploited by dealers claiming that frogs had been imported from abroad (Storer, 1922, 1933), and the name "French frog" became associated with *R. a. draytonii* (Grinnell and Storer, 1924; Storer, 1933; Camp, unpublished field notes, 1910). Furthermore, this association was often coupled with the assertion that *R. a. draytonii* was a more palatable frog (Coombes, 1902; Dickerson, 1906; Storer, 1933).

After 1900, data are meager, but those available indicated limited frog harvests (Table 1) and increased importation of frogs from sources outside California (Alexander, 1905; Bryan, 1915; Bryant, 1917; Conner, 1937; Heard, 1904; Louisiana Department of Conservation, 1935; Storer, 1922, 1925, 1933). Although frogs continued to be listed among fishery products for the period from 1900–1935, most years show no figures. The lack of consistency in those counties that report frog harvests is attributed to the fact that dealers only handled frogs incidentally with regard to the fish trade (Conner, 1937), so the absence of reported data is consistent with the idea that frog populations were too depleted to support commercial harvests, and as a result were of too limited economic importance to report. After 1900, most frog harvests were apparently conducted by part-time frog collectors or owners of "culture operations" who sold their small catches directly in the market (Cort, 1919; Heard, 1904). In just 8 yr, California went from being the leading supplier of market frogs in the United States to that of a supplier of quantities too small to report (Wright, 1920). Of the 10 states that supplied most of the frogs for commercial markets in 1900, only California and New York were not listed as major suppliers in 1908 (Wright, 1920), and New York is known to have later supplied many frogs for commercial froggers during 1915–1916 (Adams and Hankinson, 1916).

BULLFROG INTRODUCTION

The initial date of the introduction of the bullfrog into California is vague. Although Cope (1889), True (1884) and Yarrow (1882) reported an early collection of *R. catesbeiana* from "San Diego, California," they all apparently listed the wrong state in spite of the original United States National Museum catalogue entry (USNM 3340) to the contrary (R. McDiarmid, personal communication). Kellogg (1932) correctly stated that this specimen was taken in San Diego, Nuevo Leon, Mexico. The California Acclimatization Society, which was responsible for many successful and unsuccessful introductions of fishes, turtles and invertebrates into California waters, seriously contemplated introducing bullfrogs just prior to 1900 (Anonymous, 1898). However, because their meeting notes were destroyed in the San Francisco earthquake of 1906, it is not known if any specimens were purchased and released. Stebbins (1951) stated that introduction occurred around 1905. However, when recently questioned about this date, he was unable to recall the basis for the statement and thought it might be a misprint (R. Stebbins, personal communication). Storer and Usinger (1963) gave the dates 1905–1914 without supporting information. Moyle (1973) quoted Storer's (1922, 1925) comments of several introductions between 1914 and 1922, but he did not specify an initial date.

The earliest introduction of *R. catesbeiana* is reported in a previously uncited paper by Heard (1904) who described a "frog farm" at Stege (= El Cerrito), Contra Costa County, California (see also Storer, 1933), where 36 bullfrogs were stocked in four artificial ponds in 1896. The bullfrogs are reported to have originated from "Baltimore," Maryland, and "Florida" (Heard, 1904). A shipment of 72 frogs sent to Hilo, Hawaii from Contra Costa County, California in October of 1897 (see Appendix I) is known to have had bullfrogs from the Stege "farm" (Cobb, 1902; Heard, 1904). The probable descendants

from this introduction resulted in 172 kg of bullfrogs harvested in Hawaii in 1900 (Cobb, 1902). Some of these "Hawaiian bullfrogs" were later shipped to the San Francisco markets for sale (Alexander, 1905; Bryan, 1915; Storer, 1922). Storer (1925) also reported that Albert W. C. T. Herre (an ichthyologist at Stanford University) told him that bullfrogs were present in a creek at Los Gatos, Santa Clara County, California prior to 1910.

DISCUSSION

It seems a bit incongruous that herpetologists in California during the early part of the twentieth century were unaware of the extensive commercial utilization of *R. a. draytonii* during the late 1800's. However, only John Van Denburgh and Joseph Grinnell were active in the state in the 1890's and neither mentioned the commercial utilization of native frogs in their extensive publications (see Grinnell, 1940; Slevin and Leviton, 1956 for complete bibliographies). Dickerson (1906) and Wright (1920) mention the utilization of frogs in California based on limited observations made after 1900. Only Storer collected extensive information about California anurans during the early part of the twentieth century. However, Storer's experience dates back to only 1911 (Storer, unpublished field notes), and he was apparently unaware of the pre-1900 data on frog harvest collected by the U.S. Commission of Fish and Fisheries, because he stated: "No figures are available regarding the quantities of frogs used commercially in California; in fact there are very few reliable statements anywhere concerning the numbers of these animals sold or the prices received, since data on frogs are not ordinarily included in the statistical reports on fisheries compiled by the Federal government or the states" (Storer, 1933). Thus, he concluded that *R. a. draytonii* was never abundant, a conclusion made evident by his statements: "The supplies of red-legged frogs, the only native species used commercially to any extent, were never large . . . Much of the

area now inhabited by the bullfrog was previously unoccupied by any frog whatsoever so that the species constitutes a distinct addition to the fauna of the State" (Storer, 1933).

These comments, coupled with Storer's first-hand knowledge of many so called "frog farms" and the relatively small harvests (approximately 40,000 frogs per year) in the state during the 1920's and 1930's, helps us understand why Storer believed that *R. a. draytonii* was never utilized in large quantities. Because Storer was such a careful worker, there was no reason for subsequent workers to question his statements.

Besides commercial exploitation, habitat alteration probably contributed to the early decline of populations of *R. a. draytonii* in parts of the Central Valley. According to Collins (1892), Jordan (1887) and Lockington (1879), both Tulare and Kern counties supplied commercial quantities of *R. a. draytonii* to San Francisco markets prior to 1890. During this period these two counties were the center of major efforts to create vast areas of irrigated farmlands (Brown and Richmond, 1940; Newell, 1894; Preston, 1981). An extensive network of canals was dug and much of the swampland in the vicinity of Tulare Lake was drained between 1860 and 1900 (Brown and Richmond, 1940; Preston, 1981). Such extensive alterations undoubtedly had a negative impact on local *R. a. draytonii* populations as human-altered habitats in the San Joaquin Valley are known to be generally unfavorable to native anurans (Moyle, 1973).

We cannot be certain of the identity of all frogs represented by harvest figures. Wright (1920) reported that *Rana boylei* was also utilized for food, although much less so due to its smaller size and irritating skin secretions. Some of the 1899 harvest came from Humboldt County, California (Table 2), part of the putative interface zone between *R. a. draytonii* and *R. a. aurora* (Hayes and Miyamoto, 1984). Furthermore, because the earliest date of bullfrog presence in the state was 1896,

bullfrogs may be represented in some of the 1899 harvest. However, this does not diminish the fact that if the 1895–1899–1904 harvest figures reflect a decline in wild populations, then *R. a. draytonii*, as the only significantly exploited endemic taxon (Storer, 1933), was the prominent component of this decline.

However, it is surprising that harvests of tens of thousands of adult frogs each year (Table 1) continued for as long as they did before a decline occurred. The first year for which data exist is 1888, but Lockington's (1879) comments suggested that large harvests may have occurred for an undetermined number of years prior to that date. In view of the probable female harvest bias, for harvests not to show a decline for the time period indicated suggests that historical populations were very large. Indeed, Yarrow and Henshaw (1878) listed *Rana temporaria aurora* (= *R. a. draytonii*) as "abundant in California." Furthermore, we find it curiously coincidental that the period of initial bullfrog introduction is bracketed by the years indicating decline. This suggests that depletion of wild stocks (namely *R. a. draytonii*) was sufficient to import bullfrogs as substitutes, because the demand for frogs is known to have persisted (Heard, 1904; Storer, 1933).

After 1910, introductions of bullfrogs were well documented (Storer, 1922, 1925, 1933). However, the extent of established bullfrog populations for the period 1910–1925 are not. The many introductions that occurred during this period imply that *R. catesbeiana* was not yet abundant in most areas. In fact, the inducement for Storer to write his 1933 paper [based on earlier mimeographed circulars written in 1930 and 1931 (Salt and Rudd, 1975)] was the increase in inquiries on the subject of rearing frogs not only in California (Storer, 1933) but in the rest of the United States as well (Fenton, 1932; Herriman, 1933; Louisiana Department of Conservation, 1935; Ruffner, 1933; Stoutamire, 1932; Van Alstine, 1983; Viosca, 1931, 1934). However, Storer's emphasis on the invari-

able failure of frog farming ventures suggests that only the establishment of sizable feral populations of *R. catesbeiana* would again allow heavy exploitation of frog resources. Although this condition eventually did occur in the early 1930's in limited parts of the Central Valley (Anonymous, 1933; Ingles, 1933; Storer, 1933), it was not until much later that widespread exploitation took place (Treanor, 1975; Treanor and Nicola, 1972).

We conclude that historical populations of *R. a. draytonii* were large, but that heavy exploitation occurred for an undetermined number of years before 1900. A decline in harvest began between 1895 and 1899, and the first introductions of *R. catesbeiana* occurred during this period, probably in response to this decline. Decline continued until commercial populations of *R. a. draytonii* were depleted, some time soon after 1900. Incognizance of the early exploitation and decline of *R. a. draytonii* resulted from the fortuitous combination of an absence of workers during this period, the interpretation that early post-1900 population conditions were similar to pre-1900 conditions, an ignorance of frog harvest literature, habitat alteration, and nomenclatural confusion. Subsequently, the period 1900–1930 saw many introductions of *R. catesbeiana* and numerous frog farming enterprises. The existence and eventual abandonment of these enterprises probably added to the establishment of feral *R. catesbeiana* populations (see especially Fenton, 1932; p. 71), but *R. catesbeiana* did not become abundant until after this period. The conclusion cannot be avoided that *R. catesbeiana* became established in many areas of California at a time when endemic *R. a. draytonii* populations were considerably diminished. Although these data do not permit evaluation of the recent effects bullfrogs may have on extant populations of *R. a. draytonii*, any consideration of such effects must recognize that populations of the former may have increased in the absence of substantial populations of the latter.

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APPENDIX I

This date was quoted as "1879" by Jordan and Evermann (1905), and Oliver and Shaw (1953), while Cobb (1902) stated that it is "1899." The actual date is probably October 1897, when a shipment of black bass (*Micropterus* sp.) and several other organisms were received at Hilo, Hawaii, from San Francisco, California (Cobb, 1902).

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EDITOR'S NOTE: This is the third in a series of "State-of-the-Art Book Reviews."

CONSERVING SEA TURTLES: CONSTRUCTIVE CRITICISM IS STILL NEEDED

C. KENNETH DODD, JR.

ABSTRACT: The recent publication of the book *Conserving Sea Turtles* presents a sharp criticism of programs and techniques developed for the management of these biologically and socio-economically valuable species. While many of the criticisms are valid, they are couched in terms that are unnecessarily acrimonious, and thus are likely to prolong heated debate rather than assist the understanding of the bases of particular techniques. This review analyzes the content of this book in light of both the accuracy and tone to determine if the criticism might result in more constructive programs, and concludes that it falls far short of its objectives. Constructive criticism of conservation programs is necessary to ensure a sound biological basis and ultimate success of such programs; emotional and inaccurate criticism may be more detrimental than beneficial.

THE biological characteristics of sea turtles (long life span, large number of eggs produced by a female during her reproductive life, migratory nature, temperature dependent sex determination, long amount of time until sexual maturity is reached, large aggregations of nesting females), the many unknowns concerning the biology of these species (such as survivorship rates, sex ratios, population estimates, movement patterns), coupled with a large number of threats, a complex sociocultural position in the lives of many

coastal peoples, and a great potential economic value, have combined to create some of the most difficult problems imaginable in terms of scientific study, conservation and management. As a result, many views and opinions have been expressed in many forums as to the "best" way to conserve as well as to allow controlled use of these species. Papers by Pritchard (1979, 1980), Ehrenfeld (1982) and many other papers in Bjorndal (1982), and the recent publication of a research and conservation techniques manual (Pritchard et al., 1983)