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Authors: Burnett, L. Joseph, Sorenson, Kelly J., Brandt, Joseph, Sandhaus, Estelle A., Ciani, Deborah, et al.

EGGSHELL THINNING AND DEPRESSED HATCHING SUCCESS OF CALIFORNIA CONDORS REINTRODUCED TO CENTRAL CALIFORNIA

L. Joseph Burnett[1], Kelly J. Sorenson[1], Joseph Brandt[2], Estelle A. Sandhaus[3],
Deborah Ciani[4], Michael Clark[4], Chandra David[4], Jenny Theule[4],
Susie Kasielke[4], and Robert W. Risebrough[5,6]

[1]*Ventana Wildlife Society, 19045 Portola Dr., Ste. F1, Salinas, CA 93908*
[2]*United States Fish and Wildlife Service, Hopper Mountain National Wildlife Refuge Complex,*
P. O. Box 5839, Ventura, CA 93005
[3]*Santa Barbara Zoo, 500 Niños Drive, Santa Barbara, CA 93103*
[4]*Los Angeles Zoo and Botanical Gardens, 5333 Zoo Drive, Los Angeles, CA 90027*
[5]*The Bodega Bay Institute, 2711 Piedmont Avenue, Berkeley, CA 94705*

Abstract. From 1997 through 2010, in collaboration with the National Park Service, we released 84 captive-reared California Condors (*Gymnogyps californianus*) to the wild in central California; from 2006 through 2010 we recorded 16 nestings by nine pairs and recovered eggs or eggshell fragments from 12 nests. Mean thickness of shell fragments, without membrane, was 0.46 mm, 34% lower than the average thickness of 0.70 mm of fragments recovered from nine successful nests in interior southern California, 2007–2009. Hatching success in central California was 20–40%, significantly lower than the 70–80% recorded in southern California. The outer crystalline layer was absent or greatly reduced, as in thin-shelled condor eggs laid in southern California in the 1960s. Shell thickness was not related to egg size. Weight/water loss during incubation in the wild averaged three times greater than the normal rate associated with successful hatching; the rate of loss increased significantly with decreasing shell thickness. At least four failures, three from death of the embryo, we attribute to excessive weight/water loss; two other eggs losing substantial weight hatched successfully after artificial incubation at elevated humidities. DDT/DDE from wastes of a DDT factory discharged into the Southern California Bight had previously caused extensive eggshell thinning and reproductive failures of fish-eating and raptorial birds. Feeding on carcasses of California sea lions (*Zalophus californianus*), reintroduced condors now occupy a higher level of the food web. Like that of other species previously affected, the thickness of condor eggshells should recover as DDE contamination continues to decline.

Key words: California Condor, DDE, eggshell thinning, Gymnogyps californianus.

Adelgazamiento de la Cáscara del Huevo y Disminución del Éxito de Eclosión de Individuos de *Gymnogyps californianus* Reintroducidos en el Centro de California

Resumen. Desde 1997 hasta 2010, en colaboración con el Servicio de Parques Nacionales de los Estados Unidos, liberamos 84 individuos criados en cautiverio de *Gymnogyps californianus* en ambientes silvestres en el centro de California; desde 2006 al 2010 registramos 16 anidaciones por parte de nueve parejas y recuperamos huevos o fragmentos de cáscara de 12 nidos. El espesor medio de los fragmentos de la cáscara, sin la membrana, fue de 0.46 mm, 34% menos que el espesor medio de 0.70 mm de fragmentos recuperados de nueve nidos exitosos en el interior del sur de California, entre 2007 y 2009. El éxito de eclosión en el centro de California fue 20–40%, significativamente menor que el 70–80% registrado en el sur de California. La capa exterior cristalina estuvo ausente o muy reducida, como en los huevos de cóndor de cáscara fina puestos en el sur de California en los 1960s. El espesor de la cáscara no estuvo relacionado al tamaño del huevo. La relación peso/pérdida de agua durante la incubación en estado silvestre promedió tres veces más que la tasa normal asociada con el éxito de eclosión; la tasa de pérdida aumentó significativamente con la disminución del espesor de la cáscara. Al menos cuatro fracasos, tres debidos a la muerte del embrión, los atribuimos al exceso de peso/pérdida de agua; otros dos huevos que perdieron un peso substancial eclosionaron exitosamente luego de la incubación artificial realizada a humedades elevadas. DDT/DDE proveniente de desechos de una fábrica de DDT descargado en la Ensenada Sur de California había causado anteriormente el adelgazamiento generalizado de la cáscara del huevo y fracasos reproductivos de rapaces y aves alimentadas con peces. A partir de la ingestión de cadáveres de leones marinos de California (*Zalophus californianus*), los cóndores reintroducidos ocupan ahora un nivel más elevado en la red trófica. Al igual que el de otras especies afectadas previamente, el espesor de la cáscara de los huevos de cóndor debería recuperarse a medida que la contaminación con DDE continúa disminuyendo.

INTRODUCTION

In 1982, the California Condor (*Gymnogyps californianus*) was on the brink of extinction. At the end of that year, the total population consisted of 19 birds in the wild and four in captivity (Snyder and Johnson 1985, Mace 2010). In 2010, as a result of successful captive-breeding programs, the total number of California Condors reached 370 (U.S. Fish and Wildlife Service [USFWS] 2011). Reintroductions of California Condors to the wild began in 1992 with the release of two captive-reared birds in the Sespe Sanctuary in southern California (Kiff 2000), where Koford (1953) had undertaken his historic studies of this species in the 1930s and 1940s. At the end of 2010, there were 181 condors in the wild in southern and central California, Arizona, and Baja California, Mexico (USFWS 2011).

Of particular historical significance among the reintroduction sites has been Monterey County in coastal central California. The first recorded observations of California Condors were made in 1602 by a Carmelite friar, Fr. Antonio de la Ascension, from a Spanish ship anchored in Monterey Bay. He described them in his diary as birds in the shape of turkeys, the largest birds he had seen on the voyage (Wagner 1929, Harris 1941). Friar Antonio also wrote of the carcass of a large whale on the beach; although he did not mention that condors were feeding on the whale, the carcass was surely the reason for their presence. Almost 200 years later, in December 1792, Archibald Menzies collected the type specimen in the Monterey area (Grinnell 1932). The first descriptions of an egg and a chick of a California Condor, both obtained from tree nests in the vicinity of Carmel Valley in Monterey County in late April 1859, were published by A. S. Taylor (1859a). In 1994, USFWS invited the Ventana Wildlife Society (VWS), then known as the Ventana Wilderness Society, to submit a proposal for a condor-reintroduction program in the Big Sur area of Monterey County. In reviewing the proposal on behalf of USFWS, the California Condor Recovery Team noted that on the Big Sur coast condors would be expected to accumulate organochlorine contaminants from carcasses of marine mammals, possibly affecting reproduction. Fragments of condor eggshells recovered from nest sites in southern California in the 1960s were thin with structural abnormalities characteristic of shell thinning induced by DDE [p,p'-DDE, 1,1-dichloro-2,2-bis(p-chlorophenyl)ethylene], a derivative of the insecticide DDT [p,p'-DDT, 1,1,1-trichloro-2,2-bis(p-chlorophenyl)ethane]; thickness was inversely correlated with concentrations of DDE in the membrane's lipid (Kiff et al. 1979). Contamination of the coastal zone of southern California by DDT compounds and PCBs (polychlorinated biphenyls), however, had been declining (Anderson et al. 1975, Risebrough et al. 1980), and in the absence of new sources of these contaminants the decline was expected to continue, posing a diminishing threat to a reintroduced condor population. The team's recommendation that the project be approved was accepted by USFWS in 1995; releases in Big Sur by VWS began in 1997. The reintroduction program in central California was expanded in 2003 to include releases in the Pinnacles National Monument, 45 km east of Big Sur in Paicines, by the National Park Service (NPS). In this paper, we report severe thinning of eggshells and a depression of hatching success in the reintroduced population that is linked with high rates of weight/water loss.

METHODS

MANAGEMENT OF THE REINTRODUCED POPULATION

Whenever possible, LJB and assistants located individual condors daily to confirm survival and to locate incapacitated birds, nests, and feedings on nonproffered carcasses (Grantham 2007, Sorenson and Burnett 2007). Initially he used VHF radio transmitters attached to each condor in combination with visual confirmations of individual identity. Beginning in 2003, LJB used GPS transmitters in conjunction with the radio transmitters and, beginning in 2006, deployed them by priority to the most reproductively active condors.

To minimize exposure to lead in carcasses of animals shot but not retrieved by hunters, VWS and NPS placed carcasses of dairy calves, domestic rabbits, and domestic rats at feeding/baiting stations as sources of reliably lead-free food. Staff personnel supplied the stations with food every 3–4 days in amounts proportional to the population size. In 1999, LJB observed two condors feeding on the carcass of a California sea lion (*Zalophus californianus*) on the beach at Grimes Point on the Big Sur coast (36° 12′ N, 121° 44′ W); this was the first documented natural feeding on a nonproffered carcass. Thereafter, we monitored feeding on sea lion carcasses on the Grimes Point beach periodically and documented feeding on other nonproffered carcasses of both marine and terrestrial mammals opportunistically while monitoring condors. In each case, we noted the species of the carcass, location, and the date and time individual condors fed.

EGG EXCHANGES AND COLLECTION OF EGGSHELL FRAGMENTS

From 28 March 2006 to 6 April 2006 we observed condor pair 167/190 (studbook numbers 167 and 190, Mace 2010) occupying a cavity in a redwood tree in the Big Sur region (Fig. 1), but on 7 April 2006 they had abandoned the site. On 8 April 2006 JB recovered from the cavity an eggshell fragment of approximately 1 cm^2 (BS106), which we later concluded was from a thin-shelled condor egg (below, Fig. 2). Thereafter, to minimize breakage and maximize productivity, LJB, JB, and other personnel removed all accessible wild-laid eggs for artificial incubation at the Los Angeles Zoo and replaced them with captive-laid eggs approaching the pipping stage, or with dummy eggs, until a captive-laid egg was available. We measured the length and maximum breadth of wild-laid eggs to the nearest

FIGURE 1. Condor 167 at the nest site in a cavity of a redwood tree in Big Sur, 28 March 2006. Eggshell fragment BS106 was recovered from this cavity on 8 April 2006. Photo by Joseph Brandt.
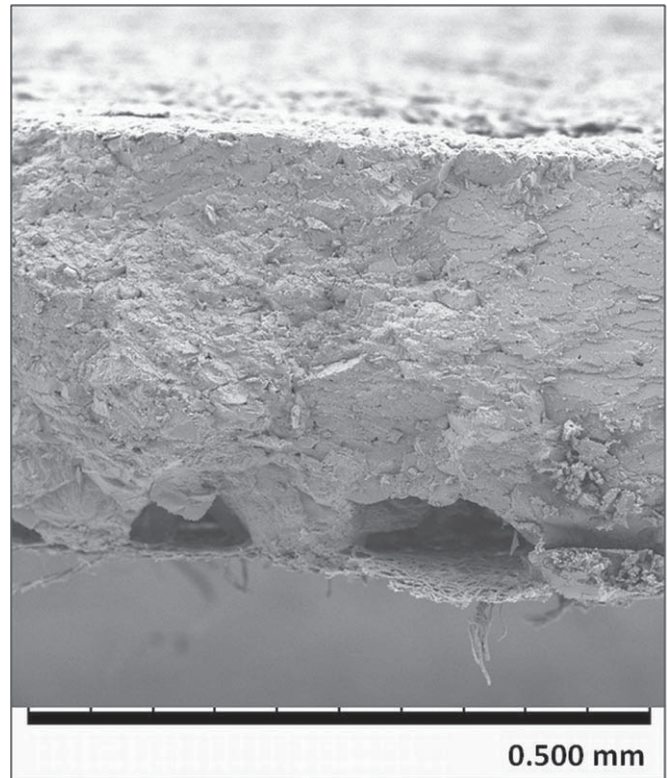

FIGURE 2. Photomicrograph of California Condor eggshell BS106 (thickness 0.35 mm), recovered from redwood nest cavity of Fig. 1 on 8 April 2006. The outer crystalline layer is absent and there are wide spaces between the mammillary cones.

tenth of a millimeter with digital calipers and weighed to the nearest tenth of a gram with a electronic balance (400 g), either at the time of collection from the nest or shortly after at the zoo. Staff personnel observed an egg or the pair's behavior indicating egg laying and/or incubation and entered nest sites between 10 and 44 days after an egg was laid.

During visits to nest sites after eggs had hatched in the wild, the southern California program routinely searched for and collected eggshell fragments. From 2007 to 2009 JB provided shell fragments from nine nests occupied by six pairs in southern California for comparison with shell thickness and structure of central California eggs.

STATISTICAL ANALYSES

For statistical tests we used SYSTAT 13 (2009), and we accepted significance when $P < 0.05$ (two-tailed). To determine the significance of differences in eggshell-fragment thicknesses between southern and central California, we applied the Mann–Whitney U-test and the two-sample t-test,

assuming unequal variances (Microsoft Excel). For the former we used the average of the three measurements taken from the first photomicrograph of the first fragment analyzed of each egg as a random sample of the shell thickness of that egg. For the central California data set we used the means of fragment thicknesses of each egg. We applied the Fisher exact test to determine significance of differences in hatching success between southern and central California; we used Spearman's correlation analysis and regression analysis to determine significance of the relationship between the rate of water loss and shell thickness. We obtained critical values of r_s from Johnson (1992). Mean values reported are arithmetic means ± SD. We use CV, the coefficient of variation, to express the magnitude of variation within a data set.

MEASUREMENTS OF EGGSHELL THICKNESS

Using a modified Federal P61 dial indicator (0.01 mm) mounted on a Federal 35B-21 comparator stand, C. Sumida, who had made the earlier measurements of condor eggshell thickness reported by Kiff et al. (1979), recorded a mean thickness of 0.41 ± 0.02 mm (without membrane) from a total of 22 measurements among eight fragments derived from the original single fragment obtained from the redwood cavity,
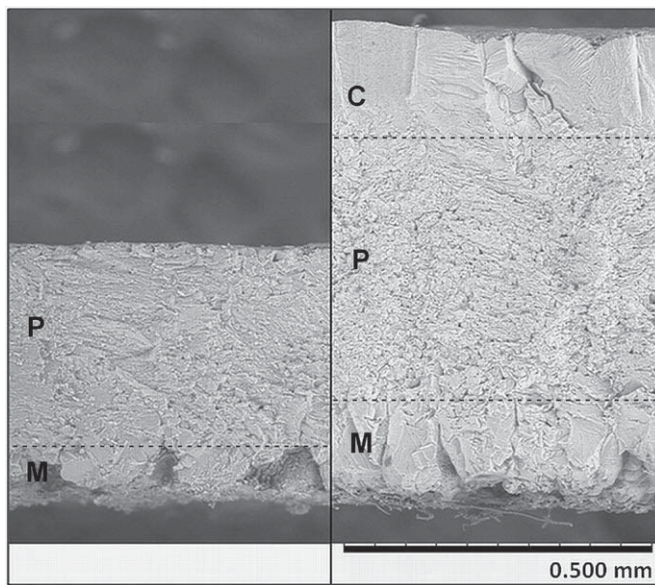
FIGURE 3.   SEM photomicrographs of BS208 (left), thickness 0.47 mm, from central California and FW609 (right), thickness 0.75 mm, from southern California. The central California eggshells have a lower density of cones in the mammillary layer (M), the palisade layer (P) is reduced, and the outer crystalline layer (C) is lacking.

range 0.39–0.45 mm. The mean of the eight fragments' means was also 0.41 ± 0.02 mm (C. Sumida, pers. comm.). RWR then measured the thickness of one of these fragments from photomicrographs obtained with scanning electron microscopy (SEM), using an ISI WB-6 Scanning Electron Microscope at 10 kV in the Microscopy & Imaging Laboratory, University of California, Santa Cruz. The fragment was mounted on a stub with silver paint, which was then coated with gold/palladium with a Polaron E5300 sputter coater. Images were collected on a 4Pi image-capture system (Bewersdorf et al. 2006). The measured thickness was 0.35 ± 0.02 mm (5 photomicrographs, 21 measurements; Fig. 2), a value lower than the mean thickness of 0.41 ± 0.02 mm obtained previously by Sumida. RWR concluded that it was from a condor egg on the basis of a comparison with the structure of the shell fragments obtained in southern California in the 1960s (Kiff et al. 1979). Also, shells of eggs laid after 2006 in the same cavity by the same parents and eggshells from elsewhere in central California after 2006 had structural features identical to those of the 2006 fragment, including the absence of, or a much reduced, outer crystalline layer and the spacing of the mammillary cones (Figs. 2, 3), providing additional support for the conclusion that the 2006 fragment was from a condor egg.

The Santa Cruz laboratory closed in 2007. Thereafter LJB, RWR, and JB measured the thickness and examined structural features of the shells of eggs from central and southern California from photomicrographs taken in the Robert D. Ogg Electron Microscope Laboratory, University of California, Berkeley. We placed eggshell fragments 5–7 mm long vertically on a mounting stub and viewed them with a Hitachi TM-1000 Tabletop Scanning Electron Microscope with a resolution of 30 nm. The photomicrographs, taken at 100–250× magnification, of cross-sections of the eggshells and their component layers were enlarged for measurement with hand-held digital calipers. We determined shell thickness by calibration with the image scale of the photomicrograph. Using the same mounted subfragment of BS106 that RWR measured in the Santa Cruz laboratory, we obtained in the Berkeley laboratory the same mean thickness (0.35 mm $\pm$ 0.01 mm, 10 micrographs, 30 measurements). We made three measurements from each photomicrograph and took at least three photos of most of the fragments. From the 10 central California eggshells that were recovered intact, we sampled fragments from the equatorial region in addition to several fragments from undetermined areas; from BS308 and a captive-laid egg from the Los Angeles Zoo we also measured fragments from the large and small ends. The areas of eggs BS106 and BS210, which had broken into many pieces during incubation, could not be determined. To obtain a thickness value for each egg, we averaged the three measurements from each photomicrograph and then averaged the means from all of the photomicrographs of each fragment to obtain a fragment value. When more than one fragment was measured, we averaged the fragments' means (Table 1). An intercalibration between SEM and the method of Sumida is currently underway to resolve the difference in the thicknesses yielded by the two methods. Because SEM measures the thickness of a smaller area of the eggshell, this method would most likely produce lower values.

We estimated fresh weights as $g = K_W \times$ length (mm) $\times$ breadth^2 (mm^2) (Hoyt 1979). From the USFWS data base of 431 captive-incubated eggs at all facilities from 1983 through 2004, RWR derived a value for K_W of 0.000564 ± 0.000015, CV = 2.7, which we used to estimate the original fresh weight and weight reduction during incubation of eggs taken from the wild (Table 2). In the USFWS data base, the average fresh weight is 268.1 ± 22.0 g, CV = 8.2; the average weight loss of a subsample for which weights at pipping were available over an average of 54.2 ± 1.2 days of incubation until pipping is 13%, $n = 259$. In this sample the number of incubation days until pipping was significantly ($P < 0.001$) dependent on fresh weight: pipping day = 48.4 + 0.022 × fresh weight (SYSTAT 13, regression analysis). The extremes were three eggs with average weight of 240 g that pipped at day 51 and the heaviest egg at 288 g that pipped at day 59 (RWR, unpubl. data).

For captive incubation, MC, CD, JT, and DC maintained an incubator temperature of 36.8 ºC and initiated incubation at a relative humidity between 59 and 64%. After establishing an initial weight-loss trend (WLT), MC, CD, JT and DC adjusted humidity settings to increase or decrease the daily rate of weight loss to achieve a total reduction of approximately 14%

TABLE 1. Nestings from 2006 to 2010 of California Condors reintroduced to central California, eggshell thickness, and productivity.

Sire/dam[a]	Year	Egg[b]	Nest site	Productivity Wild-laid	Productivity Captive-laid	Shell thickness	No. fragments
167/190[c]	2006	BS106	Redwood cavity I	Failed	—	0.35 ± 0.01	2
167/190	2007	BS107	Redwood cavity I	Failed	Foster SB444	0.47	1
167/190	2009	BS109	Redwood cavity I	Failed	Foster SB499	0.41 ± 0.00	2
168/208	2007	BS207	Cave I	SB431[d]	Foster SB429	0.50 ± 0.01	2
168/208	2007	BS309	Redwood cavity III	SB 530[d]	Foster SB503[e]	0.56	1
168/208	2007	BS310	Redwood cavity IV	Failed	—	—	—
204/222	2008	BS208	Cave II	Failed	Foster SB470	0.47 ± 0.05	3
204/222	2010	BS310	Cave II	Failed	—	0.32 ± 0.04	3
194/171	2008	BS308	Cliff ledge I	Failed	Foster SB475	0.46 ± 0.06	5
194/171	2009	BS209	Cliff ledge I	Failed	Foster SB501	0.42	1
194/171	2010	BS110	Cliff ledge I	Failed	Foster SB567	0.49 ± 0.01	2
199/231	2008	BS108	Redwood cavity II	SB477	—	—	—
313/303	2009	PN109	Cave III	SB522[d]	Foster SB514	0.49 ± 0.06	3
209/236	2009	BS409	Cave IV	SB538	—	—	—
219/310	2010	PN210	Cave V	SB574	—	—	—
318/317	2010	PN110	Cave VI	Failed	Foster SB550[f]	0.61 ± 0.02	3

[a]Studbook numbers (Mace 2010).
[b]Two-letter location code (BS, Big Sur; PN, Pinnacles), single-digit egg number, two-digit year.
[c]Possibly laid by pair 164-171 in 2005, see text.
[d]Successfully hatched in captivity from wild-laid egg.
[e]Died prior to fledging from ingesting trash.
[f]Removed prior to fledging for treatment of lead toxicosis.

TABLE 2. Observed vs. predicted rates of weight loss at time of collection of eggs of California Condors reintroduced to central California, 2006–2010; projected percentages of weight loss at 54 days.

Egg identity	Calculated fresh weight[a] (g)	Estimated time in wild nest at collection[b] (days)	Predicted weight at collection[c] (g)	Weight at collection[d] (g)	Predicted weight loss day^{-1} (g)	Observed weight loss day^{-1} (g)	Observed/ predicted weight loss[e]	Weight loss projected at 54 days[f] (%)
BS106	—	—	—	—	—	—	—	—
BS107	—[g]	32	—[g]	238.5	—[g]	—[g]	—[g]	—
BS109	—[g]	14	—[g]	246.0	—[g]	—[g]	—[g]	—
BS207	310.8	23	292.3	277.4	0.81	1.45	1.8	25.2
BS309	279.9	15	269.0	267.8	0.73	0.81	1.1	15.6
BS310	—	20	—	—	—	—	—	—
BS208	292.3	35	—	—[h]	—	—	—	—
BS210	—	—	—	—	—	—	—	—
BS308	260.9	29	241.3	198.2	0.68	2.16	3.2	44.7
BS209	264.2	10	257.4	218.0	0.68	4.62	6.7	94.4
BS110	279.5	14	269.4	229.0	0.72	3.61	5.0	69.7
BS108	—	—	—	—	—	—	—	—
PN109	265.4	44	235.1	210.9	0.69	1.24	1.8	25.2
BS409	—	—	—	—	—	—	—	—
PN210	—	—	—	—	—	—	—	—
PN110	267.9	20	254.0	249.6	0.69	0.91	1.3	18.4

[a]Fresh weight of egg with normal thickness and weight from formula: fresh weight = length × breadth^2 × K_W, K_W = 0.000564, see text.
[b]Visual observations of behavior and GPS data.
[c]Based on 14% weight loss over 54 days incubation.
[d]Includes both water loss and reduction in shell weight resulting from thinning.
[e]Average 3.0 ± 2.1.
[f]Weight-loss trends (WLTs).
[g]Excluded from statistical analyses because of abnormal shape.
[h]Weight at collection not available.

at the average time of pipping at 54 days. The initial WLT, WLT = {[($F_W − C_W$)/D_C] × 54}/F_W × 100, provides the projected percentage weight loss at 54 days, where F_W = fresh weight, C_W = current weight and D_C = current number of days of incubation. This water loss is a physical rather than a metabolic process and is independent of the metabolism of the embryo (Kasielke 2007).

Currently, the data base is not sufficient to determine the initial component of weight reduction that is a consequence of shell thinning. Although the CV of the value of K_W derived from fresh egg weights is relatively small, 2.7, the CV of fresh egg weights, 8.2, was three times higher. We have not therefore been able to assign an error range in our estimates of fresh egg weights derived from K_W and the egg dimensions.

For embryos that died, we determined stages of embryonic development by reference to Hamburger and Hamilton (1951).

RESULTS

POPULATION GROWTH AND NESTINGS

Through 2010, VWS and NPS released 84 captive-reared condors in the Big Sur region and in the Pinnacles National Monument. The two groups have extensively co-mingled. Twenty-one captive-reared birds had died as of 31 December 2010, five from lead poisoning and five after colliding with power lines. Two of the females released in Big Sur have become members of breeding pairs in southern California; 12 condors in central California were permanently removed from the wild because of behavioral problems. On 31 December 2010, 49 of the original released birds remained in the wild in central California with nine wild-fledged birds. Twenty-four were 7 years old or older (eighth year or more); nine were 7 years, none was 8, three were 9, three were 10, four were 11, two were 12, and three were 13 years old. All of the 12 birds 9 years old or older had mated; seven of the 24 birds 7 years or older remained unmated at the end of 2010 (LJB, unpubl. data).

In 2005, condors 164 and 171, both 8 years old, formed a pair bond and occupied a territory on the Big Sur coast. We were unable to locate the pair's nest site or confirm behavior indicative of egg laying. In September 2005, male condor 164 died of lead poisoning in southern California; the territory was taken over by pair 167/190 in late 2005 and was occupied into the spring of 2006. As noted above, we observed the pair occupying a redwood cavity from 28 March 2006 to 6 April 2006, but on 7 April 2006 they had abandoned the site. The possibility that the shell fragment recovered from the cavity on the following day came from an egg laid in 2005 by pair 164/171 cannot be excluded. Through 2010 there was a total of 16 nestings by nine pairs (Table 1), not including pair 164/171. Six were in cavities of redwood trees, occupied by three pairs in a total of four trees (Table 1).

EGGSHELL THINNING

We did not obtain eggshell fragments from the three nestings that fledged young without manipulation. Nor did we recover an egg or eggshell fragments from the apparent nesting in 2010 of pair 168/208, which had appeared to be incubating an egg but then abruptly abandoned the site, an inaccessible cavity in a redwood. We recovered eggs or eggshell fragments from all of the other 12 nestings by five pairs from 2006 to 2010 (Table 1). The mean of the 12 means of shell-fragment thicknesses was 0.46 ± 0.08 mm, range 0.32–0.61 mm, $n = 73$ photomicrographs, 34% thinner than the mean of 0.70 ± 0.05 mm (range 0.62–0.76, 29 photomicrographs) of the thickness of shell fragments from nine wild-hatched eggs of six pairs in southern California 2007–2009 (Fig. 3). The difference in shell thickness between the two areas is highly significant ($P < 0.001$, two-sample t-test assuming unequal variances and the Mann–Whitney U-test using the means derived the first three measurements of the first fragment of each egg). The value of 0.70 mm obtained for the southern California eggs from 2006 to 2009 is equivalent to the value of 0.69 ± 0.05 mm for the thickness of seven pre-1944 eggshells, without an estimated value for the membrane of 0.10 mm, obtained by Kiff et al. (1979). As noted above, an intercalibration between the two methods is underway but incomplete at this time. Mean CV of thickness measurements of single fragments from BS208 and BS308 was 2.8, range 1.0–7.1 ($n = 8$ fragments, 30 photomicrographs, three measurements per micrograph), providing an estimate of the component of variance derived from measurements of a single fragment. Coefficients of variation among fragments of a single egg averaged 6% ($n = 8$, Table 1). The two highest values of 13% were among fragments of BS308, which included a fragment from both the large and small ends, and of the shell of BS210, the egg with the thinnest shell, which had broken into many small fragments in the nest. Means of the thickness of five fragments of BS308 were 0.37 ± 0.01 (broad end), 0.49 ± 0.00 and 0.46 ± 0.04 (equator), 0.53 ± 0.00 (small end), and 0.47 ± 0.01 (area not determined), indicating a large variance within this egg; thickness at the small end was 43% higher than at the broad end. The trend in egg LA907, laid at the Los Angeles Zoo in 2007, was similar, with thicknesses of 0.50 ± 0.01, 0.61 ± 0.03, and 0.63 ± 0.01 at the broad end, equator, and small ends, respectively, two fragments from each area. We are undertaking follow-up studies to determine whether this pattern is typical of condor eggs. Snyder and Meretsky (2003) stated, without supporting data, that eggshell thickness is usually "greater at the equator than at the poles." Although shell fragments were taken from the equatorial region of the intact eggs from central California, it was not possible to determine the area of the egg from which the relatively small southern California fragments had come. The coefficient of variation, however, is relatively small, 7.1, when compared with the value of 13 obtained from the two shells from which fragments were obtained from several areas.
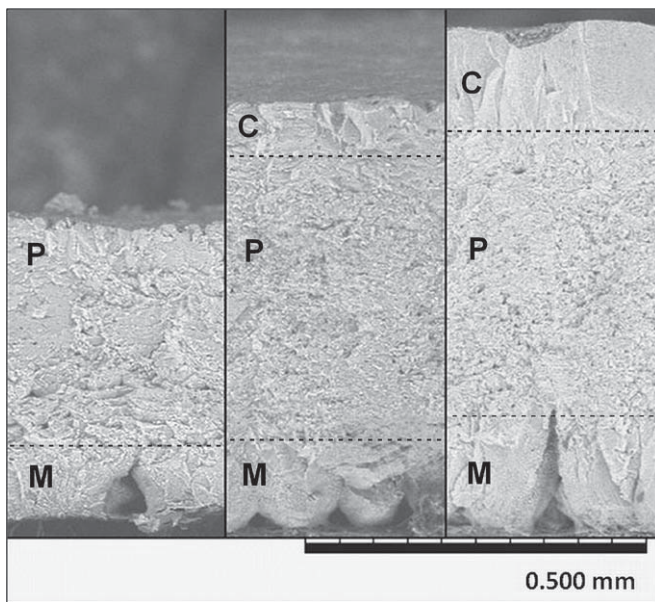
FIGURE 4. SEM photomicrographs of BS308 (left) and PN110 (center) from central California and FW509 (right) from southern California. The outer crystalline layer (C) is lacking in BS308, greatly reduced in PN110, and intact in FW509. The palisade layer (P) is reduced in BS308. The cones in the mammillary layer (M) are reduced in BS308 and PN110. Compare with Figure 2 in Kiff et al. (1979).

Only two of the 12 central California eggs had a visible portion of the outer crystalline layer (Fig. 4). For statistical analysis KJS assigned a thickness of 0.005 mm to the others. The significance of the difference in thickness of this layer between central and southern California is high: 0.011 ± 0.013 mm, $n = 12$, vs. 0.144 ± 0.027 mm, $n = 9$, $P < 0.001$ (Mann–Whitney U test). The outer crystalline layer occupies $21 \pm 4\%$ and $2 \pm 3\%$ of the thicknesses of the southern and central California eggshells, respectively.

EGGSHELL THINNING AND WATER LOSS

From the dimensions of eggs taken from the wild we calculated fresh weights by the formula of Hoyt (1979) and the value of K_W derived from the fresh weights and dimensions of 431 captive-incubated eggs (above, Table 2). Assuming a weight loss of 14% over the average incubation period of 54 days, we calculated for each egg a predicted weight loss day^{-1}. This we compared with the weight loss in the field day^{-1} derived from the total weight loss over the estimated number of days between laying and collection (Table 2). The ratio of the field to the predicted weight losses day^{-1} averaged 3.0 ± 2.1. Weight/water loss increased with decreasing shell thickness ($r_s = -0.85$, $P < 0.05$, $n = 7$; $r = -0.76$, $F_{1,5} = 6.74$, $P = 0.05$, $n = 7$).

The WLTs used at the Los Angeles Zoo to estimate the percentage total weight loss at day 54, which can be derived from the ratio of field to predicted rates of water loss, ranged

from 16% for egg BS309 (ratio 1.1) to 94% for BS209 (ratio 6.7, Table 2). BS309 was one of three apparently healthy eggs that were removed for artificial incubation at the Los Angeles Zoo, following the established protocol. It hatched successfully with a total weight loss of 14%. We conclude that BS309 would have hatched successfully in the wild. BS207 and PN109, also brought in from the wild for captive incubation, both had WLTs of 25%. Relative humidity was increased to 73–76% within the first week of captive incubation to lower the rate of weight loss; both eggs hatched with weight losses of 18 and 23%, respectively. We conclude that this adjustment of humidity prevented failure from excessive water loss that would have occurred in the wild.

HATCHING SUCCESS

In southern California, 22 eggs were laid in the wild from 2006 to 2010. Two disappeared during incubation, probably because of predation, and were excluded from statistical analyses. When the hatching success of two eggs appeared to be threatened by parental factors, they were removed for artificial incubation at the Los Angeles Zoo. One was returned to the wild where it hatched; the other showed a normal pattern of water loss and hatched in captivity. We conclude that it would have hatched in the wild. Of the remaining 18 eggs, 14 hatched successfully. None of the four failures could be attributed to a factor that was not intrinsic to the egg. We therefore used the resulting failure/success ratio of 4/16 for comparison with the success of hatching of the central California eggs.

Of the 16 eggs laid in the wild in central California, three hatched in the wild without any manipulation or other interference and three hatched after artificial incubation at the Los Angeles Zoo (above). We replaced 10 wild-laid eggs with zoo-laid eggs, all of which hatched in the wild. All of the other ten eggs failed (Table 3). We attribute at least four of these failures to excessive weight loss (Table 3) and conclude that without artificial incubation six eggs would have failed to hatch from this cause.

A careful examination of the surface of both eggs revealed no visible cracks. Water loss therefore resulted from a modification of the eggshell structure not yet characterized (below).

Egg BS210, with 54% thinning, was the thinnest-shelled of the central California eggs and was found crushed in the nest. Its membrane was mostly intact, the shell broken into many small pieces. We attribute crushing of the egg to the extreme thinning and weakness of the shell, similar to that of the eggs of Brown Pelicans (*Pelecanus occidentalis*) on Anacapa Island in 1969 (Risebrough et al. 1971), and not to predation. The breakage of BS106, the second thinnest-shelled with 50% thinning, however, cannot conclusively be attributed to thinning; predation of eggs by Common Ravens (*Corvus corax*) was a major cause of failure of nests in southern California (Snyder 1983) and must therefore be considered a possible cause of the

TABLE 3.   Success and failure of hatching of eggs of California Condors reintroduced to central California, 2006–2010.

Egg identity	Success/failure; comments	Cause of failure
BS106	Failure; shell fragment recovered, unknown fertility and weight reduction	Shell thinning or predation
BS107	Failure; abnormal shape[a], decomposition, unknown fertility	Undetermined[b]
BS109	Failure; abnormal shape[a], embryonic death at mid-development H & H[c] stage 27, abnormal gas bubble in albumen	Undetermined[b]
BS207	Successful captive hatch; artificially incubated at elevated humidity; WLT 25.2	Excessive weight loss; failure if left in wild
BS309	Successful captive hatch after artificial incubation; WLT 15.2	—
BS310	Failure during early incubation, no egg or egg fragments recovered	Undetermined[e]
BS208	Failure: embryonic death at mid-to-late development, H & H stage 39-40; abnormally large air cell, advanced state of decomposition	Excessive weight loss
BS210	Failure; crushed egg recovered from nest, 54% shell thinning	Extreme shell thinning
BS308	Failure: embryonic death at mid-development, H & H stage 37, large air cell, high weight/water loss; WLT 44.7	Excessive weight loss
BS209	Failure: decomposition, unknown fertility, high weight/water loss. WLT 94.4	Excessive weight loss
BS110	Failure: embryonic death at mid-development, H & H stage 27, high weight/water loss; WLT 69.7	Excessive weight loss
BS108	Successful wild hatch	—
PN109	Successful captive hatch; artificially incubated at elevated humidity; WLT 25.2	Excessive weight loss, failure if left in wild
BS409	Successful wild hatch	—
PN210	Successful wild hatch	—
PN110	Failure: embryonic death at early development, H & H stage 7–12; WLT 18.4	Undetermined[f]

[a]Curvature less on one side.
[b]Absence of outer crystalline layer may have facilitated entry of bacteria.
[c]Hamburger and Hamilton (1951).
[d]Excessive water loss, a possible cause, could not be determined because of the abnormal shape of the egg.
[e]Predation or egg breakage because of thinning are possible causes.
[f]Natural cause or unidentified contaminant.

breakage of BS106. In both cases the nest site was abruptly abandoned by the pair following egg breakage early in the incubation period. Egg breakage, whether by crushing or from predation, is therefore a plausible explanation for the sudden abandonment of the nest site of pair 168/208 in 2010 (Table 1). The failure of BS107, with undetermined fertility and decomposed contents, may have resulted from entry of bacteria in the absence of an outer crystalline layer. None of the failures could with certainty be attributed to an extrinsic factor such as predation. The ratio of failure to success would therefore be 8/3 if the artificially incubated eggs, the apparent failure of BS310 from undetermined cause, and BS106, the nesting from which only the fragment of the shell was recovered, are not included, 10/4 if the three artificially incubated eggs are added, and 12/4 if all nestings are included. The probability that any of these ratios can be considered to be from the same distribution as the ratio of 4/16 from the southern California nestings is <0.001 (two-tailed Fisher exact test). In addition to the four demonstrated and two hypothetical failures caused by weight losses associated with thinning, breakage associated with thinning accounted for at least one and up to three additional failures. Thinning may also have facilitated entry of bacteria into an egg
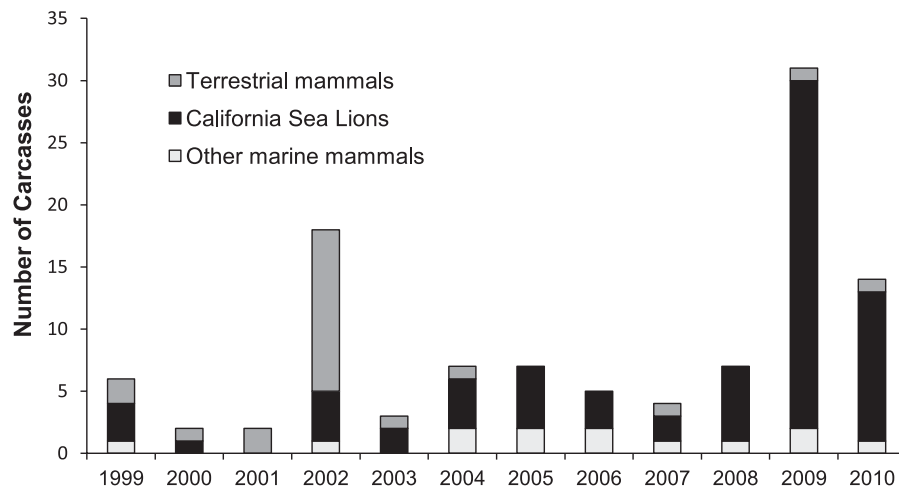
FIGURE 5.   Observed feedings on non-proffered carcasses of terrestrial mammals, California sea lions, and other marine mammals by California Condors from 1999 through 2010.

that failed. Without manipulation, therefore, thinning would have caused at least seven failures and up to 10 or even 11 of the 12 failures.

FEEDINGS ON MARINE MAMMAL CARCASSES

From 1999 to 2010, in addition to the continuing use of the proffered food supply, we documented feedings on 83 marine and 23 terrestrial nonproffered mammal carcasses (Fig. 5). Carcasses of California sea lions constituted 84% of the marine-mammal carcasses fed upon by condors, 93% of which were at Grimes Point. Other identified marine-mammal carcasses included those of two gray whales (*Eschrichtius robustus*) and a southern sea otter (*Enhydra lutris nereis*). Terrestrial mammals included the mule deer (*Odocoileus hemionus*), tule elk (*Cervus canadensis nannodes*), domestic animals (cattle, horse, and cat), ringtail (*Bassariscus astutus*), and northern raccoon (*Procyon lotor*). In 2002, condors fed on 10 deer carcasses, accounting for most of the carcasses other than sea lions in that year (Fig. 5), but thereafter deer carcasses were much less common. Feeding on nonproffered carcasses was highest in 2009, when condors fed on the carcasses of 28 sea lions (Fig. 5) at Grimes Point.

DISCUSSION

Our findings appear to be inconsistent with the conclusion of Snyder and Meretsky (2003) that a reduced thickness of California Condor eggshells is an association with smaller eggs rather than an effect of an environmental factor. We have, however, demonstrated very significant differences in both eggshell thickness and structure between recent eggs laid in central and southern California; we now show that there is no relationship between eggshell thinning of the central California eggs and egg size.

The mean shell thickness of eggs laid in central California from 2006 to 2010, 0.46 ± 0.08 mm, is equivalent to 0.45 ± 0.07 mm, the mean thickness of shell fragments recovered from 13 condor nests in southern California from the 1960s through 1973 (Kiff et al. 1979); we subtracted 0.10 mm from each of the values published by Kiff et al. (1979) to obtain estimates of thickness without membrane. These means are 33 and 35% lower than the mean shell thickness of 0.69 ± 0.05 mm of seven eggs laid before 1944 (Kiff et al. 1979). The mean shell thickness of eggs laid in the wild in southern California from 2007 to 2009, 0.70 ± 0.05 mm, is equivalent to the mean of eggs laid before 1944 and may therefore be considered "normal."

One outlier eliminated, the average shell thickness of 30 eggs laid in the wild in the 1980s was 0.61 ± 0.10 mm (Snyder and Meretsky 2003), 12% lower than the pre-1944 mean of Kiff et al. (1979). Twenty six of these eggs were produced by only three females, the Santa Barbara female, TAMA, and AC8 (Adult Condor 8) (studbook numbers 10, 11, and 12, respectively, designated by Snyder and Meretsky (2003) as SBF, CCF, and SSF. An additional egg reported by Snyder and Meretsky (2003) to have been laid in 1980 by AC8 is attributed by the studbook (Mace 2010) only to a "wild" female and is not included. In this sample, a high variability of shell thickness was associated with variation in egg size among individual females. The mean shell thickness of the eggs laid by TAMA (0.77 ± .06 mm, *n* = 8), was 12% higher than the pre-1944 mean and 54% higher than the mean shell thickness of eggs laid by AC8 in the wild in the 1980s (0.50 ± 0.04 mm, *n* = 8). The mean shell thickness of eggs of the Santa Barbara female was intermediate (0.60 ± 0.04 mm, *n* = 10, Snyder and Meretsky 2003).

Sixteen of these eggs laid in the wild in the 1980s were removed for artificial incubation. The fresh weights of eggs of
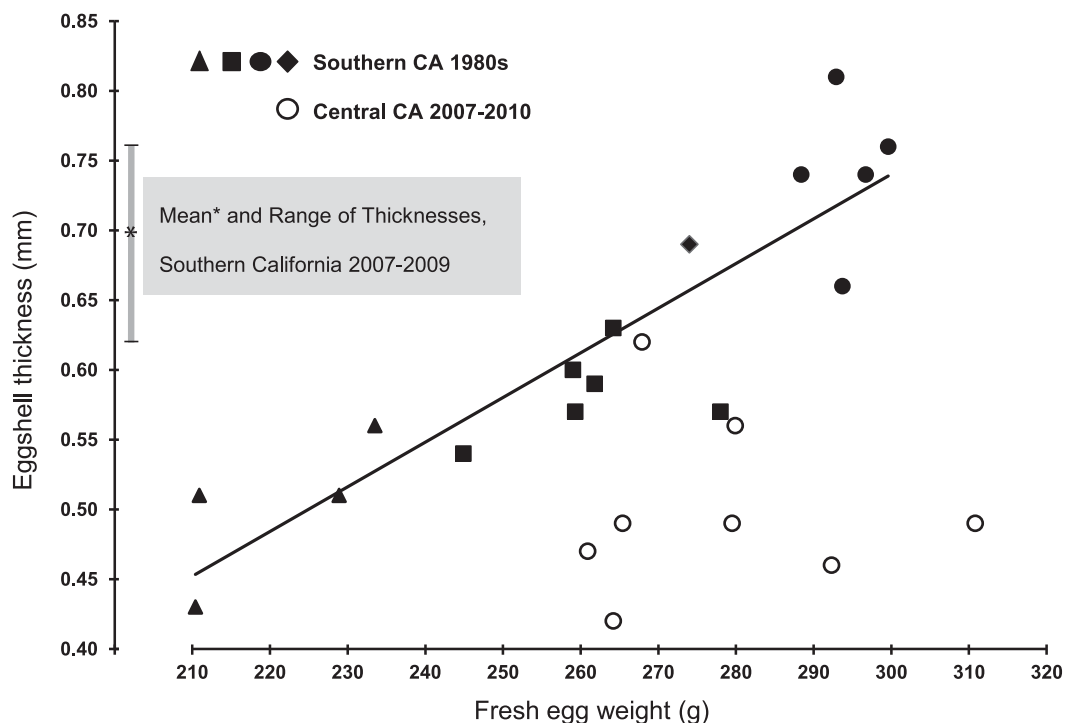
FIGURE 6.   Relationship and lack of relationship between measured or calculated fresh egg mass and eggshell thickness (without membranes) of eggs of California Condors in southern California in the 1980s and in southern and central California 2007–2010. Eggs from the 1980s shown as black symbols (AC8, triangles; Santa Barbara female, squares; CVF [studbook number 8], diamond; TAMA, circles, Snyder and Meretsky 2003). Eight eggs from central California 2007–2010 shown as white circles; eggs BS107 and BS109 are excluded because of their abnormal shape. Mean and range of thicknesses of nine southern California eggs 2007–2009 shown as vertical line, egg masses not available.

AC8, the Santa Barbara female, and TAMA also varied widely, averaging 220.9 ± 12.0 ($n = 4$), 261.2 ± 10.6 ($n = 6$), and 294.3 ± 4.2 ($n = 5$) g, respectively. In this sample, the correlation between fresh weight and thickness was highly significant ($r = 0.90$, $P < 0.001$, $n = 16$, Snyder and Meretsky 2003, Fig. 6). However, without supporting evidence, Snyder and Meretsky (2003) furthermore concluded that all variation in shell thickness of condor eggs, including all eggs laid in the 1960s for which no size data are available, is a consequence of variation in egg size.

This conclusion of Snyder and Meretsky discounts the major changes in eggshell structure that were characteristic of the eggs from the 1960s and that is a prominent feature of the recent central California eggs. Snyder and Meretsky (2003) attributed an absent or a reduced outer crystalline layer of at least two of "three especially thin shells of the 1980s and 1960s" to "nutritional stress." One of these from the 1980s is clearly an outlier (RWR, unpubl. data); no supporting evidence is provided for another egg from either decade. The SEM photomicrographs of four condor eggshells from the 1960s show no outer crystalline layer at all in two and a reduced layer in the other two (Kiff et al. 1979). Similarly, as reported above, ten of the 12 central California eggs had no outer crystalline layer, which was present but reduced in the other two eggs with thicker eggshells, and which was well defined in the shells of all of the southern California eggs (Figs. 3, 4). Nutritional stress has not been documented or suspected in the central California population and cannot be considered to be a cause of the structural changes without supporting evidence.

From 2006 to 2010, the fresh weights of the central California eggs, calculated from their dimensions with the K_W value of 0.000564 (above), averaged 277.6 ± 17.0 g, $n = 8$ (Table 2); the range of values was 260.9–310.8, in the middle and upper range of the fresh weights of the eggs laid in the 1980s and heavier than all of the eggs laid by AC8 in the wild in the 1980s. This value of K_W is identical to that derived by Snyder and Meretsky (2003) from the 16 eggs removed from the wild in the 1980s. Comparison of the shell thicknesses and the fresh weights of both the eggs of the 1980s and the eggs from central California, 2006–2010 (Fig. 6), clearly shows that the reduction of shell thickness of the central California eggs is associated with a factor other than egg size. Snyder and Meretsky (2003) failed to distinguish thinning induced by an environmental factor such as DDE from the naturally thinner eggshells of smaller eggs of a species with a wide range of egg sizes.

Beginning in 1947, the weight and thickness of eggshells of the Peregrine Falcon (*Falco peregrinus*) were reduced in both Great Britain and North America (Ratcliffe 1967, Hickey and Anderson 1968). Eggshell thinning has since been documented in a large number of avian species (L. F. Kiff, unpubl. data). A review by Risebrough (1986) of all experimental and field studies of eggshell thinning up to that time concluded that only DDE could account for the thinning and that a contribution by any other factor, including one or more organic contaminants, would at most be minor. An update of this review, including a review of all California Condor data, has reached the same conclusion and specifically concluded that thinning of the eggshells of the central California birds is caused by DDE in their diet (RWR and L.F. Kiff unpublished).

Concentrations of DDE in five failed eggs ranged from 170 to 500 parts per million lipid weight (D. Crane, K. Regalado, LJB, and RWR, unpubl. data), levels associated with reproductive failures of other species, including the Bald Eagle (*Haliaeetus leucocephalus*; Wiemeyer et al. 1984, 1993). The sample size and the ranges of DDE concentrations and of thicknesses, however, are as yet insufficient to determine the relationship between DDE and thickness. A significant negative correlation between shell thickness and DDE concentration, however, has been demonstrated in many other species (Risebrough 1986), including Brown Pelicans on Anacapa Island and other west coast and Florida colonies in 1969 (Risebrough 1972, Schreiber and Risebrough 1972). Shell thinning and/or structural abnormalities associated with high concentrations of DDE have been well documented in other species in the Southern California Bight, including the Double-crested Cormorant (*Phalacrocorax auritus*; Gress et al. 1973), Bald Eagle (Bland 1990), Ashy Storm-Petrel (*Oceanodroma homochroa*; Carter et al. 2008), and Peregrine Falcon (Latta 2012).

Egg breakage has been the conspicuous and best documented effect of eggshell thinning (Ratcliffe 1958, Risebrough et al. 1971) and has been assumed hypothetically to be the principal effect of DDE on condors (Snyder 1983). At most only three of the failures to date in central California were caused by breakage of eggs, two with extreme shell thinning on the order of 50% (Table 1). Embryonic mortality associated with the PCBs and related compounds was a principal cause of failures of hatching of fish-eating birds in the Great Lakes (Gilbertson et al. 1991). Concentrations of PCBs in the central California eggs measured to date, however, have been below threshold levels of effect (D. Crane, K. Regalado, and RWR, unpubl. data). During artificial incubation, rates of water loss from thinner-shelled Peregrine Falcon eggs laid in the wild were higher but variable; successful hatching was dependent on regulation of the rate of water loss (Linthicum et al. 1994). Survival and growth of California Condor embryos and chicks during artificial incubation and brooding is also highly dependent on the rate of water/weight loss (D. Ciani, M. Clark, C. David, and J. Theule, unpubl. data).

Our demonstration that failure to hatch is significantly correlated with rate of water loss during incubation in the wild is consistent with these observations.

Water loss associated with eggshell thinning, however, has apparently yet to be shown to cause death of early avian embryos such as the embryo of PN110. Residues of antibiotics in the stillborn dairy calves that are routinely supplied as lead-free supplemental food are a possible cause yet to be investigated. Fluoroquinolone antibiotics have been detected in vultures breeding in Spain and have been linked with failure of eggs to hatch and with deaths of chicks of the Bearded Vulture (*Gypaetus barbatus*). All of four dead nestlings and three of five embryos in unhatched eggs contained from two to six veterinary drugs. Major histopathological lesions, including glomerulonephritis and/or glomerulonephrosis, were observed in the kidneys of all nestlings with fluoroquinolones. All nestlings with fluoroquinolones also showed lesions of the joints, including arthritis and/or arthrosis of the long bones' articulations, as well as massive osseous stroma of the spongeous bones (Lemus et al. 2008, 2009, Blanco and Lemus 2010). Comparable studies have not yet been undertaken in North America.

The carcasses of sea lions and lesser numbers of other marine mammals are the only component of the condor's diet in central California that is not present in the diet of those in interior southern California and must therefore be associated with the thinning. California sea lions rarely breed north of San Miguel Island in southern California (Peterson and Bartholomew 1967) but have recently done so on the Grimes Point beach and on the Farallon Islands (R. L. Delong, pers. comm.). Adult male sea lions from the Channel Island colonies migrate north after the breeding season to northern California, Oregon, Washington, and British Columbia (R. L. Delong, pers. comm.). Adult females from San Miguel Island alternate marine foraging trips and terrestrial nursing of the pup for up to 11 months of each year, foraging along the central California coast from Point Conception to Monterey (Melin 2002, Melin et al. 2008). Along the central California coast strandings of adult females are more frequent during El Niño events (Gulland 2000, Greig et al. 2005). Except for the occasional local births, all of the California sea lions available to condors in central California have spent at least a portion of their lives in the highly contaminated Southern California Bight. Northward movements of the sea lions thereby provide a vehicle of transport of DDE and other contaminants to condors in central California.

In the early 1970s, exceptionally high concentrations of the totals of the several DDT compounds (ΣDDTs), principally DDE, were recorded in the blubber and tissues of California sea lions in both southern and central California (Le Boeuf and Bonnell 1971, Delong et al. 1973, Gilmartin et al. 1976). Le Boeuf and Bonnell (1971) reported an arithmetic mean concentration of 1452 parts per million (ppm) lipid weight of total DDTs

in the blubber of 25 animals, mostly males. Lieberg-Clark et al. (1995) reported a geometric mean concentration of 5.0 ppm wet weight in the blubber of seven male sea lions stranded in central California 1988–1992, 150 times lower than concentrations recorded 20 years earlier. A variable not taken into account, however, was the relative amount of exposure of each group to the higher levels of contamination in the Southern California Bight. The mean concentration of ΣDDTs in the blubber of 92 California sea lions stranded in the Southern California Bight from 1994 through 2006 was 594 ppm (Blasius and Goodmanlowe 2008). Their sample consisted of pups, yearlings, subadults, and adults of both sexes with a wide range of lipid content. In their sample, on a lipid-weight basis, concentrations of organochlorines were higher in adult males than in adult females by a factor of 18; the mean concentration of ΣDDTs in the blubber of five males was 2270 ppm. These data are sufficient to support the conclusion, still to be fully confirmed, that the condors ingest an amount of DDE in carcasses of sea lions sufficient to induce the eggshell thinning we report here.

The Southern California Bight has experienced the world's highest level of coastal DDE/DDT contamination. The National Mussel Watch Program (Goldberg et al. 1978, Farrington et al. 1983) determined that contamination of the Southern California Bight by ΣDDTs in the 1970s exceeded by an order of magnitude or more that of any other coastal environment in the USA; a review of the global literature indicated that this comparison applied also to the rest of the world (RWR, unpubl. data). The contamination was first documented in 1965 when high concentrations of ΣDDTs were recorded in northern anchovies (*Engraulis mordax*) from Los Angeles Harbor (Risebrough et al. 1966, Risebrough 1969). In 1969, the arithmetic mean concentration of DDE in 65 crushed and broken eggs of Brown Pelicans on Anacapa Island was 1176 ppm lipid weight and the average reduction in shell thickness was 44% (Risebrough et al. 1971, Risebrough 1972). In the absence of any evidence that the DDT contamination resulted from domestic, public health, or agricultural uses, the Los Angeles County Sanitation Districts searched for a source among the industries discharging into their wastewater-treatment system and tracked the contamination to the Montrose Chemical Corporation, then the world's largest manufacturer of DDT. Complying with a directive issued by the sanitation districts in 1970, the Montrose Corporation began measures to end the discharges, which terminated in 1971 (Carry and Redner 1970, Redner and Payne 1971). DDE contamination of the local marine environment began to decline immediately. By the mid-1970s the average shell thickness of Brown Pelican eggs had increased and thicker-shelled eggs were hatching (Anderson et al. 1975). Monitoring of California mussels (*Mytilus californianus*) showed that the decline continued through the 1970s (Risebrough et al. 1980), justifying an attempt to reintroduce Bald Eagles to Santa Catalina Island in the Southern California Bight.

That program began in 1980 (Garcelon et al. 1989). The first egg in 1987 and a second in 1988 broke soon after being laid; thereafter all eggs were removed as soon as possible for artificial incubation. Hatchlings were later returned to the wild to be raised by their natural parents. In 2007, four eggs were left in the nests and successfully hatched without human assistance (Sharpe 2008). In 2008, six chicks hatched in five wild nests (Sharpe 2009). There were six known attempts at nesting on Santa Catalina Island in 2009; eggs were left in all. One failed, but a total of eight chicks hatched and fledged successfully from the other five nests (Sharpe 2010). Productivity therefore is now in the range typical of healthy Bald Eagle populations (Sprunt 1969). On the basis of both the well-established relationship between depressed productivity and DDE concentrations in unhatched eggs (Wiemeyer et al. 1984, 1993, Nisbet 1989, Nisbet and Risebrough 1994) and of DDE concentrations in unhatched eggs from Santa Catalina Island from 1987 to 2007 (D. K. Garcelon and P. Sharpe, unpubl. data), DDE levels fell by a factor of 2–3 in the food web supporting the Bald Eagles on the Channel Islands over the 20 years from 1987 to 2007.

Although many of A. S. Taylor's accounts of the condor in Monterey County in the mid-1850s (Taylor 1859a, b) are second hand and lack credibility (Harris 1941), we give credence to his reports in 1859 of many condors feeding on the carcasses of sea lions killed for their oil and of condors feeding on the carcass of a whale (Taylor 1859b). Carcasses of the California sea lion, northern elephant seal (*Mirounga angustirostris*), harbor seal (*Phoca vitulina*), several species of whales, and other marine mammals were surely significant historical sources of food for condors along the coast, particularly after the extinction of the Pleistocene megafauna (Koford 1953), until populations were decimated by commercial overharvesting after the arrival of Europeans. Moreover, collagen in the bones of ten condors trapped in the Rancho La Brea tar pits during the Pleistocene contained a marine component (Chamberlain et al. 2005), indicating that condors in coastal areas at that time were exploiting both marine and terrestrial food sources. Koford (1953) and Collins et al. (2000) reported finding shells of marine mollusks at nest sites, indicating that condors had been recently foraging on the coast. In his *Ornithology of California*, Cooper (1870) wrote that condors had been reported feeding on dead seals and whales, but he had not observed many "Californian Vultures" along the coast, noting that at that time condors were "most abundant in the hot interior valleys of California, where the large herds of cattle furnish an abundance of food". Twenty years later, however, he wrote (Cooper 1890) that since 1855 he had "seen fewer every year …in localities the most suitable for them." He attributed the decline in part to the poisoning of carcasses, in part to indiscriminate opportunistic shooting, and in part to "the much less abundance of cattle, sheep, etc.… where grazing is giving way to agriculture and fruit-raising."

He was apparently the first ornithologist to relate the condor's distribution to the abundance and availability of food. There are now many fewer carcasses of livestock and of native ungulates available to condors, but the recovery of marine mammal populations has restored a traditional food source in protected areas of the coast of western North America, assuring a dependable food supply in the foreseeable future.

Since the food web that supports the Bald Eagles of the Southern California Bight and the species previously affected by eggshell thinning also supports the sea lions that provide carcasses for the condors in central California, we predict that the condors' DDE accumulation will continue the decline observed in the Southern California Bight over the past 41 years. We therefore also predict that eggshell thickness and productivity of the central California condors will increase to normal levels but at a rate that cannot be estimated with any certainty at this time.

We shall continue, however, the current intensive management program in both central and southern California until we have shown that exposure to fragments of lead ammunition in nonproffered carcasses (Sorenson and Burnett 2007) is at a level that does not threaten the self-sustaining status of a future population.

ACKNOWLEDGMENTS

LITERATURE CITED

ANDERSON, D. W., J. R. JEHL JR., R. W. RISEBROUGH, L. A. WOODS JR., L. R. DEWEESE, AND W. G. EDGECOMB. 1975. Brown Pelicans: improved reproduction off the southern California coast. Science 190:806–808.

BEWERSDORF, J., A. EGNER, AND S. W. HELL. 2006. 4Pi Microscopy, p. 561–570. *In* J. Pawley [ED.], Handbook of biological confocal microscopy, 3rd ed. Springer, New York.

BLANCO, G., AND J. A. LEMUS [ONLINE]. 2010. Livestock drugs and disease: the fatal combination behind breeding failure in endangered Bearded Vultures. <http://www.plosone.org/article/info%3Adoi%2F10.1371%2Fjournal.pone.0014163>.

**BLAND, D. 1990. The relationship of organic and inorganic components of eggshells to DDE content in eggs of California Brown Pelicans and Bald Eagles. M.Sc. thesis, University of California, Santa Cruz, CA.

BLASIUS, M. E., AND G. D. GOODMANLOWE. 2008. Contaminants still high in top-level carnivores in the Southern California Bight: levels of DDT and PCBs in resident and transient pinnipeds. Marine Pollution Bulletin 56:1973–1982.

**CARRY, C. W., AND J. A. REDNER. 1970. Pesticides and heavy metals: progress report, December, 1970. County Sanitation Districts of Los Angeles County, P.O. Box 4998, Whittier, CA 90607.

CARTER, H. L., J. L. LEE, D. WELSH, AND D. W. ANDERSON [ONLINE]. 2008. Organochlorine contaminants in Ashy Storm-Petrel eggs from Santa Cruz Island, California, in 1992–2008: preliminary findings. <http://www.montroserestoration.gov/wp-content/uploads/2011/08/ASSP_preliminary_report_2007.pdf> (25 September 2012).

CHAMBERLAIN, C. P., J. R. WALDBAUER, K. FOX-DOBBS, S. D. NEWSOME, P. L. KOCH, D. R. SMITH, M. E. CHURCH, S. D. CHAMBERLAIN, K. J. SORENSON, AND R. RISEBROUGH. 2005. Pleistocene to recent dietary shifts in California Condors. Proceedings of the National Academy of Sciences USA 102:16707–16711.

COLLINS, P. W., N. F. R. SNYDER, AND S. D. EMSLIE. 2000. Faunal remains in California Condor nest caves. Condor 102:222–227.

**COOPER, J. G. 1870. Ornithology. Volume I: land birds. State Geological Survey of California, Sacramento, CA.

**COOPER, J. G. 1890. A doomed bird. Zoe 1:248–249.

DELONG, R., W. G. GILMARTIN, AND J. G. SIMPSON. 1973. Premature births in California sea lions: association with high organochlorine pollutant residue levels. Science 181:1168–1170.

FARRINGTON, J. W., E. D. GOLDBERG, R. W. RISEBROUGH, J. H. MARTIN, AND V. T. BOWEN. 1983. U.S. "Mussel Watch" 1976–1978: an overview of the trace metal, DDE, PCB, hydrocarbon and artificial radionuclide data. Environmental Science and Technology 17:490–496.

**GARCELON, D. K., R. W. RISEBROUGH, W. M. JARMAN, A. B. CHARTRAND, AND E. E. LITTRELL. 1989. Accumulation of DDE by Bald Eagles *Haliaeetus leucocephalus* reintroduced to Santa Catalina Island in southern California, p. 491–494. *In* B.-U. Meyburg and R. D. Chancellor [EDS.], Raptors in the modern world. World Working Group on Birds of Prey and Owls, Berlin.

GILBERTSON, M., T. KUBIAK, J. LUDWIG, AND G. FOX. 1991. Great Lakes embryo mortality, edema, and deformities syndrome (GLEMEDS) in colonial fish-eating birds: similarity to chick-edema disease. Journal of Toxicology and Environmental Health 33:455–520.

GILMARTIN, W. G., R. L. DELONG, A. W. SMITH, J. C. SWEENEY, B. W. DE LAPPE, R. W. RISEBROUGH, L. A. GRINER, M. D. DAILEY, AND D. B. PEAKALL. 1976. Premature parturition in the California sea lion. Journal of Wildlife Diseases 12:104–115.

GOLDBERG, E. D., V. T. BOWEN, J. W. FARRINGTON, G. HARVEY, J. H. MARTIN, P. L. PARKER, R. W. RISEBROUGH, W. ROBERTSON, E. SCHNEIDER, AND E. GAMBLE. 1978. The Mussel Watch. Environmental Conservation 5:1–25.

GRANTHAM, J. 2007. Reintroduction of California Condors into their historic range: the recovery program in California, p. 123–138. In A. Mee and L. S. Hall [EDS.], California Condors in the 21st Century. Series in Ornithology 2.

GREIG, D. J., F. M. D. GULLAND, AND C. KREUDER. 2005. A decade of live California sea lion (Zalophus californianus) strandings along the central California coast: causes and trends, 1991–2000. Aquatic Mammals 31:11–22.

GRESS, F., R. W. RISEBROUGH, D. W. ANDERSON, L. F. KIFF, AND J. R. JEHL, JR. 1973. Reproductive failures of Double-crested Cormorants in southern California and Baja California. Wilson Bulletin 85:197–208.

GRINNELL, J. 1932. Archibald Menzies, first collector of California birds. Condor 34:243–252.

GULLAND, F. [ONLINE]. 2000. Domoic acid toxicity in California sea lions (Zalophus californianus) stranded along the central California coast, May–October 1998. Report to the National Marine Fisheries Service Working Group on unusual marine mammal mortality events. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-OPR-17. <http://www.nmfs.noaa.gov/pr/pdfs/health/domoic_acid_california.pdf> (25 September 2012).

HAMBURGER, V., AND H. L. HAMILTON. 1951. A series of normal stages in the development of the chick embryo. Journal of Morphology 88:49–92.

HARRIS, H. 1941. The annals of Gymnogyps to 1900. Condor 43:3–57.

HICKEY, J. J., AND D. W. ANDERSON. 1968. Chlorinated hydrocarbons and eggshell changes in raptorial and fish-eating birds. Science 162:271–273.

HOYT, D. F. 1979. Practical methods of estimating volume and fresh weight of bird eggs. Auk 96:73–77.

JOHNSON, R. R. 1992. Elementary statistics, 6th ed. PWS-Kent, Boston.

**KASIELKE, S. 2007. Incubation of eggs, p. 39–54. In L. J. Gage and R. S. Duerr [EDS.], Hand-rearing birds. Blackwell, Ames, IA.

**KIFF, L. 2000. The California Condor recovery program, p. 307–319. In R. D. Chancellor and B.-U. Meyburg [EDS.], Raptors at risk. Hancock House, Surrey, B.C., Canada.

KIFF, L. F., D. B. PEAKALL, AND S. R. WILBUR. 1979. Recent changes in California Condor eggshells. Condor 81:166–172.

KOFORD, C. B. 1953. The California Condor. National Audubon Society Research Report 4.

LATTA, B. C. [ONLINE]. 2012. 2007 Channel Islands Peregrine Falcon study, final report. Report to U.S. Fish and Wildlife Service, Carlsbad, CA, project 9820002. <http://www.montroserestoration.gov/wp-content/uploads/2012/06/2007-Channel-Islands-Peregrine-Falcon-Study-Final-Report.pdf> (25 September 2012).

LE BOEUF, B. J., AND M. L. BONNELL. 1971. DDT in California sea lions. Nature 234:108–110.

LEMUS, J. A., G. BLANCO, J. GRANDE, B. ARROYO, M. GARCIA-MONTIJANO, AND F. MARTÍNEZ [ONLINE]. 2008. Antibiotics threaten wildlife: circulating quinolone residues and disease in avian scavengers. <http://www.plosone.org/article/info:doi/10.1371/journal.pone.0001444>.

LEMUS, J. A., G. BLANCO, B. ARROYO, F. MARTÍNEZ, AND J. GRANDE. 2009. Fatal embryo chondral damage associated with fluoroquinolones in eggs of threatened avian scavengers. Environmental Pollution 157:2421–2427.

LIEBERG-CLARK, P., C. E. BACON, S. A., BURNS, W. M. JARMAN, AND B. J. LE BOEUF. 1995. DDT in California sea lions: a follow-up story after twenty years. Marine Pollution Bulletin 30:744–745.

**LINTHICUM, J. L., W. M. JARMAN, B. J. WALTON, R.W. RISEBROUGH, L. F. KIFF, AND J. S. MINTON. 1994. Weight loss during artificial incubation vs. eggshell thinning of California Peregrine Falcon Falco peregrinus eggs brought from the wild, pp. 761–765. In B.-U. Meyburg and R.D. Chancellor [EDS.], Raptor conservation today. World Working Group on Birds of Prey and Owls, Berlin.

**MACE, M. 2010. California Condor international studbook. Zoological Society of San Diego, San Diego.

MELIN, S. R. 2002. The foraging ecology and reproduction of the California sea lion (Zalophus californianus californianus). Ph.D. dissertation, University of Minnesota, St. Paul, MN.

MELIN, S. R., R. L. DELONG, AND D. B. SINIFF. 2008. The effects of El Niño on the foraging behavior of lactating California sea lions (Zalophus californianus californianus) during the nonbreeding season. Canadian Journal of Zoology 86:192–206.

**NISBET, I. C. T. 1989. Organochlorines, reproductive impairment, and declines in Bald Eagle Haliaeetus leucocephalus populations: mechanisms and dose–response relationships, p. 483–489. In B.-U. Meyburg and R. D. Chancellor [EDS.], Raptors in the modern world. World Working Group on Birds of Prey and Owls, Berlin.

**NISBET, I. C. T., AND R. W. RISEBROUGH. 1994. Relationship of DDE to productivity of Bald Eagles Haliaeetus leucocephalus in California and Arizona, USA, p. 771– 773. In B.-U. Meyburg and R. D. Chancellor [EDS.], Raptor conservation today. World Working Group on Birds of Prey and Owls, Berlin.

**PETERSON, R. S., AND G. A. BARTHOLOMEW. 1967. The natural history and behavior of the California sea lion. American Society of Mammalogy Special Publication 1.

RATCLIFFE, D. A. 1958. Broken eggs in Peregrine eyries. British Birds 51:23–26.

RATCLIFFE, D. A. 1967. Decrease in eggshell weight in certain birds of prey. Nature 215:208–210.

**REDNER, J. A., AND K. PAYNE. 1971. Chlorinated hydrocarbons: progress report, 1971. County Sanitation Districts of Los Angeles County, P.O. Box 4998, Whittier, CA 90607.

**RISEBROUGH, R. W. 1969. Chlorinated hydrocarbons in marine ecosystems, p. 5–23. In M. W. Miller and G. G. Berg [EDS.], Chemical fallout. Charles C. Thomas, Springfield, IL.

**RISEBROUGH, R. W. 1972. Effects of environmental pollutants upon animals other than man, p. 443–463. In L. LeCam, J. Neyman and E.L. Scott [EDS.], Proceedings Sixth Berkeley Symposium Mathematical Statistics and Probability. University of California Press, Berkeley.

RISEBROUGH, R. W. 1986. Pesticides and bird populations. Current Ornithology 3:397–427.

**RISEBROUGH, R. W., D. B. MENZEL, D. J. MARTIN JR., AND H. S. OLCOTT. 1966. Chlorinated hydrocarbons in Pacific marine organisms. Report on grant no. EF-00600-02 to U.S. Public Health Service, Department of Health, Education and Welfare. Bodega Bay Institute, Berkeley, CA.

RISEBROUGH, R. W., F. C. SIBLEY, AND M. N. KIRVEN. 1971. Reproductive failure of the Brown Pelican on Anacapa Island in 1969. American Birds 25:8–9.

**RISEBROUGH, R. W., B. W. DE LAPPE, E. F. LETTERMAN, J. L. LANE, M. FIRESTONE-GILLIS, A. M. SPRINGER, AND W. WALKER II. 1980. California State Mussel Watch, vol. III. Organic pollutants in mussels, Mytilus californianus and M. edulis. California State Water Resources Control Board, Water Quality Monitoring Report 79-22.

SCHREIBER, R.W., AND R.W. RISEBROUGH. 1972. Studies of the Brown Pelican. Wilson Bulletin 84:119–135.

**SHARPE, P.B. 2008. Restoration and management of Bald Eagles on Santa Catalina Island, California, 2007. Institute for Wildlife Studies, Arcata, CA.

**SHARPE, P. B. 2009. Bald Eagle restoration on the California Channel Islands, January–December 2008, 7th annual report. Institute for Wildlife Studies, Arcata, CA.

**SHARPE, P. B. 2010. Bald Eagle restoration on the California Channel Islands, January–December 2009, 8th annual report. Institute for Wildlife Studies, Arcata, CA.

SNYDER, N. F. R. 1983. California Condor reproduction, past and present, p. 67–86. In S.A. Temple [ED.], Bird Conservation 1. University of Wisconsin Press, Madison, WI.

SNYDER, N. F. R., AND E. V. JOHNSON. 1985. Photographic censusing of the 1982–1983 California Condor population. Condor 87:1–13.

SNYDER, N. F. R., AND V. J. MERETSKY. 2003. California Condors and DDE: a re-evaluation. Ibis 145:136–151.

SORENSON, K. J., AND L. J. BURNETT. 2007. Lead concentrations in the blood of Big Sur California Condors, p. 185–195. In A. Mee and L. S. Hall [EDS.], California Condors in the 21st Century. Series in Ornithology 2.

**SPRUNT, A. IV. 1969. Population trends of the Bald Eagle in North America, p. 347–351. In J.J. Hickey [ED.], Peregrine Falcon populations: their biology and decline. University of Wisconsin Press, Madison, WI.

**TAYLOR, A. S. 1859a. The egg and young of the California Condor. Hutchings' California Magazine 36:537–540.

**TAYLOR, A. S. 1859b. The great condor of California. Hutchings' California Magazine 36:540–543, 37:17–22, 38:61–64.

UNITED STATES FISH AND WILDLIFE SERVICE (USFWS) [ONLINE]. 2011. Hopper Mountain National Wildlife Refuge Complex. California Condor recovery program, current population. <http://www.fws.gov/hoppermountain> (26 September 2012).

WAGNER, H. R. 1929. Father Antonio de la Ascension's account of the voyage of Sebastian Vizcaino, p. 180–272. In Spanish voyages to the northwest coast of America in the sixteenth century. California Historical Society Special Publication 4.

WIEMEYER, S. N., T. G. LAMONT, C. M. BUNCK, C. R. SINDELAR, F. J. GRAMLICH, AND J. D. FRASER. 1984. Organochlorine pesticide, polychlorobiphenyl, and mercury residues in Bald Eagle eggs—1969–79—and their relationships to shell thinning and reproduction. Archives of Environmental Contamination and Toxicology 13:529–249.

WIEMEYER, S. N., C. M. BUNCK, AND C. J. STAFFORD. 1993. Environmental contaminants in Bald Eagle eggs 1980–84 and further interpretations of relationships to productivity and shell thickness. Archives of Environmental Contamination and Toxicology 24: 213–227.