

CHRONIC ORGANOCHLORINE CONTAMINANTS, ENVIRONMENTAL VARIABILITY, AND THE DEMOGRAPHICS OF A BURROWING OWL POPULATION

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Abstract. We studied a population of Burrowing Owls whose eggs contained the organochlorine compound *p,p'*DDE and traces of other organochlorine contaminants to determine if the levels of contamination were associated with survival or reproduction when nonanthropogenic environmental and biological variables were also considered. Demographic data were collected in conjunction with sampling eggs for contaminants and analyzing pellets for dietary information. Levels of *p,p'*DDE in eggs varied over four orders of magnitude during the study but were not by themselves associated with reproductive failure. However, contaminant concentrations in combination with low rodent abundance in the diet were related to reduced productivity. The variation within and among years in egg contaminants suggests that patterns of egg contaminants are the result of immigrating owls from more contaminated sites, and to a lesser extent, to annual patterns in prey availability. Even low levels of chronic pesticide exposure may be detrimental when combined with other stressors, and documentation of the existence of a persistent pesticide in a biotic system is not enough to either infer the origin of the contamination or its potential effects.

Key words: *Athene cunicularia*; Burrowing Owls; DDE; egg contaminants; interactive effects; persistent pesticides; productivity; reproductive success; San Joaquin Valley, California.

INTRODUCTION

Decades have passed since the organochlorine pesticide DDT (dichlorodiphenyltrichloroethane) and its metabolite *p,p'*DDE (dichlorodiphenyldichloroethylene) were first recognized as bioaccumulating to levels causing reproductive harm in many species of birds (Hickey and Anderson 1968, Potts 1968, Heath et al. 1969, Porter and Wiemeyer 1969, Enderson and Berger 1970, Cade et al. 1971). Many studies have also documented the presence of DDT, and particularly *p,p'*DDE, in the eggs of these species and their prey, such as small birds or fish (e.g., Enderson et al. 1982, Anthony et al. 1999). Contaminant loads frequently have been correlated to eggshell thinning and reduced reproductive success (Klaas et al. 1978, Enderson et al. 1982, Wiemeyer et al. 1984, 1993, Anthony et al. 1993, 1999). Other persistent organochlorine residues such as polychlorinated biphenyls (PCBs) have also been linked to reproductive abnormalities and population declines in birds (e.g., Heath et al. 1972, Kubiak et al. 1989, Tillitt et al. 1992, Mora et al. 1993). However, many natural processes also affect survival and productivity, and these processes may strongly influence the uptake, toxicity, and movement of persistent

pollutants in biotic systems. Despite this, few studies have followed individual free-ranging organisms to examine the relative effects of both natural processes and pesticides on either individuals or populations. Consequently, we do not have a comprehensive understanding of the effects of persistent contaminants relative to natural processes.

Although the effects of *p,p'*DDE and PCBs on avian reproduction are clear both from experimental work and from field studies documenting consistently high levels of the compounds, the effects of low and variable levels of exposure to persistent organochlorine residues consistent with declining environmental concentrations are much less obvious. As persistent contaminant levels decline, the relative importance of natural environmental processes on individual animal fate and population dynamics will increase. Ecological complexity and environmental stochasticity suggest that persistent contaminant effects are likely to be variable across both space and time, contingent upon other processes also affecting productivity and survival.

Most terrestrial organisms are exposed to persistent contaminants through their diet. In addition to being a potential source of bioaccumulated contaminants, food abundance and quality greatly impact reproductive effort and success in many predatory bird species (Saurola 1989, Korpimäki and Norrdahl 1991, Rohner 1996). While abundant food resources may mitigate contaminant exposure effects, *p,p'*DDE may act synergistically with food shortage to reduce reproduction,

Manuscript received 17 June 2002; revised 7 February 2003; accepted 11 February 2003. Corresponding Editor: D. J. Levey.

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as was experimentally demonstrated in Ringed Turtle Doves (*Streptopelia risoria*; Keith and Mitchell 1993). The doves' body burdens of contaminants were below those causing negative effects without the added stress of starvation. Contaminant burdens may also be mobilized from fat stores during high stress periods in the life cycle such as breeding or post-fledging dispersal, thus reducing survival; this has been demonstrated with great-horned owls contaminated with the organochlorine pesticide dieldrin (Frank and Lutz 1999).

Furthermore, patterns of exposure may vary substantially among individuals of a species with a varied diet. Persistent contaminants are unlikely to be evenly distributed throughout a food web; short-lived consumer species will bioaccumulate lower levels of persistent contaminants than longer lived predators. Depending on prey choice, higher order predators will have variable dietary exposure. In addition, contaminants are often patchily distributed, potentially leading to "hot spots" where contamination levels are particularly concentrated in a prey species that may be relatively uncontaminated elsewhere.

Contaminant burdens in individual organisms may also act synergistically with environmental stress, such as cold weather, further compromising survival or the ability to reproduce. This has been demonstrated experimentally with American Kestrels (*Falco sparverius*; Rattner and Franson 1984). Climatic conditions alone may affect productivity and survival directly, or through impacts on food availability or habitat suitability (Steenhof et al. 1997, Franklin et al. 2000). For example, cold wet conditions may be detrimental to prey populations, whereas dry conditions may inhibit vegetation growth and limit forage and protective cover for prey. Alternatively, warm wet weather might benefit prey populations, but inhibit hunting success of predatory birds through increased vegetation density and interference with locating and capturing prey.

Other natural factors influencing productivity include intraspecific interactions and prior breeding effort. For example, the proximity of conspecific nest burrows influenced productivity in Burrowing Owls (*Athene cunicularia*; Green and Anthony 1989). Burrowing Owls defend the area immediately adjacent to their nest burrow, and antagonistic interactions with neighboring nesting pairs may negatively influence productivity through reduced predator vigilance or time spent foraging. In addition, prior reproductive effort may impose a penalty on future reproduction and survival (Nur 1988, Golet et al. 1998). Contaminants act within the scope of the life history of the species, and without an adequate understanding of natural processes and their effects on both individuals and populations, contaminant impacts are unlikely to be accurately assessed, and the pathways of exposure impossible to trace.

Although it has not been used in the United States in nearly 30 years, DDT and its metabolites have re-

mained widespread in California's agricultural soils at least through the mid-1980s (Mischke et al. 1985). Populations of Burrowing Owls appear to be declining in many parts of the species' range (Sheffield 1997), although they still remain at relatively high densities in agricultural systems in California (DeSante et al. 1997; Rosenberg and Haley, *in press*). Concern over the potential for pesticides to cause declines in Burrowing Owl populations in agricultural areas led to preliminary work in 1996 in the San Joaquin Valley of California. This work indicated that *p,p'*DDE contamination in Burrowing Owl eggs occurred at levels great enough to cause reproductive impairment in many other predatory birds (Gervais et al. 2000). In addition, low levels of PCBs were found in two of the eggs collected in 1996. We tested hypotheses on multiple interactions between environmental factors and spatial and temporal patterns of contamination to better understand how contaminants might impact the demographic performance of Burrowing Owl populations in agricultural ecosystems.

Burrowing Owl life history characteristics make them good subjects for examining the interplay of both environmental and anthropogenic stressors. Burrowing Owls in the San Joaquin Valley of California are year-round residents. They are highly opportunistic foragers, and their diet includes small mammals, insects (primarily crickets, grasshoppers, and beetles), toads, other invertebrates (spiders, centipedes), and passerine birds (Gervais et al. 2000). We predicted that levels of contaminants in eggs would be negatively correlated with the prevalence of mammalian prey in the diet. Voles in particular are selected by owls when available (Silva et al. 1995), but they are unlikely bioaccumulation candidates; California voles (*Microtus californicus*) often live less than one year (Batzli 1974) and are herbivorous (Gill 1977). We expected that productivity of nests would decline as contaminant loads increased, although it was unlikely to be the sole factor in determining productivity. The interaction between lack of vertebrate prey availability and greater concentrations of *p,p'*DDE contamination in particular should have a particularly negative impact on productivity, consistent with earlier experimental work examining diet quality and contaminants (Keith and Mitchell 1993). In addition, we predicted that overwinter survival of owls with the greatest contaminant levels would be reduced compared to those with lower contaminant body burdens as indicated by egg contaminant levels (Enderson and Berger 1970, Vermeer and Reynolds 1970, Henny 1977), particularly in years with low rodent abundance when food stress may act synergistically with contaminant loads. We assumed that the source of the contaminants was locally contaminated agricultural soil. We tested these predictions with field investigations on a population of Burrowing Owls in an intensively farmed region in the San Joaquin Valley of California.



PLATE 1. (Left) We used an infrared burrow probe to examine burrows to determine if the Burrowing Owls had initiated nesting. (Right) Burrowing Owl young were observed at the next burrow 12–28 days after hatching in order to estimate productivity. Both photos are by Daniel K. Rosenberg.

METHODS

Study site

Fieldwork was conducted on an 80-km² section of Naval Air Station (NAS) Lemoore (36°18' N, 119°56' W), 50 km southwest of Fresno, California, which supports a population of 63–85 breeding pairs of Burrowing Owls annually. These owls appear to remain on the site year round, and frequently use the same nest burrows from year to year (Rosenberg and Haley, *in press*). Nest burrows are scattered throughout fallow areas and the runway and taxiway easements of the station. The dominant land use is intensive row-crop agriculture (Gervais et al. 2003), composed primarily of cotton, with some tomatoes, alfalfa, corn, wheat, onion, and safflower. Crops are interspersed and rotated throughout the station. Despite extensive searches each year, we never found nest burrows in crop fields or along irrigation canals.

Field methods

Contaminant sampling of eggs was conducted from 1998 to 2001. A demographics study of Burrowing Owls at NAS Lemoore was initiated in 1997. Consequently, most individuals were marked, and many were known from previous years. Owls were captured on the site using a variety of burrow traps and mouse-baited spring nets. They were banded with U.S. Fish and Wildlife Service (USFWS) aluminum bands and riveted color bands with unique alpha-numeric codes. Nest burrows were located by walking transects in potential nesting habitat and revisiting burrows used in previous years. Nesting activity was assessed from owl behavior and the presence of pellets and nest material at the burrow entrance. We used an infrared burrow probe (Sandpiper Technologies, Manteca, California, USA) to determine if eggs were present (see Plate 1, left).

We collected eggs from the same or adjacent nest burrows each year, which increased the likelihood of sampling the same individual females in subsequent years due to their strong nest-site fidelity (Rosenberg and Haley, *in press*).

One egg was removed per nest, and at least one nest was sampled each year from all parts of the study site. Although egg contaminant levels have been shown to vary among eggs within a clutch, the variation is usually small compared to inter-clutch differences, and trends are not consistent within clutches in many cases (Snyder et al. 1973, Newton and Bogan 1978, Custer et al. 1990). Accordingly, we made no effort to systematically identify and remove eggs laid in any particular sequence. Eggs were refrigerated whole until contents were removed from the shells, whereupon they were stored in chemically clean glass jars on ice and delivered to the laboratory within 12 h. Eggshells were rinsed with tap water, air dried, and kept for later measurement of shell thickness.

We defined productivity as the number of owlets surviving per nest to 21–28 d of age (see Plate 1, right). We estimated productivity using a standardized system of nest watches. The maximum number of young seen during five 30-min watches conducted at least 12 h apart and within 1 wk was used as the estimate of productivity (Gervais 2002; Gorman et al., *in press*).

We collected regurgitated pellets of indigestible prey remains and recorded prey remains from each nest approximately every two weeks throughout the breeding season (late March through August). A sample was defined as all the pellets collected at a burrow on a given date. We identified invertebrates in pellets to order or family when possible, and vertebrates were identified to genus or species. Rodent remains were estimated as numbers of individuals based on dentary

bones. We calculated a dietary index by multiplying the number of individual rodents per sample by their mean mass based on freshly killed prey found at nest burrows. We then summed the estimated biomass of all species in each sample and divided it by the number of pellets in the sample to estimate the mean biomass of rodent prey per pellet for each sample collection for each nest. The mean value of all samples per year per nest was used in the analyses.

Laboratory analyses

All eggs were analyzed for a suite of organochlorine compounds and metabolites by the California Animal Health and Food Safety Laboratory System (formerly California Veterinary Diagnostics Laboratory System) at the University of California, Davis. The 30 compounds in the scan included DDT and metabolites, aldrin, dieldrin, BHC, endosulfan, heptachlor, lindane, toxaphene, and PCBs (Arochlor 1016, 1221, 1232, 1242, 1254, 1260, 1262; tested for as "mixed PCBs," and Arochlor 1260 was analyzed separately in 1998–2000). Detection limits were compound-specific, but ranged from 0.05 to 0.25 $\mu\text{g/g}$ with the exception of PCBs, with detection limits of 0.5 $\mu\text{g/g}$, and toxaphene, with a detection limit of 2 $\mu\text{g/g}$. A complete list of compounds and their detection limits is given in Gervais et al. (2000). Burrowing Owl eggs were analyzed individually. Whole egg contents were homogenized and extracted with 5% ethanol in ethyl acetate and cleaned up with automated gel permeation chromatography. They were then analyzed with gas chromatography with an electron capture detector (Perkin-Elmer Model Sigma 2000, Perkin-Elmer, Norwalk, Connecticut, USA). Mass spectrometry was used to confirm all detected residues. Every fourth sample was duplicated, and all sample runs were bracketed with control solutions of known analyte concentrations. Analyte spike recoveries were 70–110%. Full details of the chemical analyses are reported by Holstege et al. (1994).

All eggshells were air dried for several weeks, and the shells measured using a Starrett digital thickness indicator (Model 2500, Athol, Massachusetts, USA) mounted on a Federal bench comparator. The same investigator measured all shells, taking five measurements from around the equator. The mean value for each egg was used for statistical analyses. We measured shell mass using a Cahn TA 450 digital balance (Thermo Cahn, Madison, Wisconsin, USA).

Statistical analyses

Eggshells.—Contaminant concentrations reported by the laboratory were adjusted to account for egg water loss during incubation; freshly-laid egg concentrations (FEC) were calculated using the equation $\text{FEC}_{\text{DDE}} = (\text{DDE}) \times (\text{sample mass}) / (\text{egg volume} - \text{shell mass})$. To estimate egg volume, we used the equation $K \times L \times B^2$, where K is a dimensionless constant of 0.00051,

TABLE 1. Models tested by multiple regression and Akaike's Information Criterion (AIC) exploring the relationship among contaminant levels in Burrowing Owl eggs from Naval Air Station (NAS) Lemoore in California, 1996–2001, and various independent variables.

Model	ΔAIC_c	AIC_c weight
Year	0	0.630
Year + biomass [†]	2.324	0.197
Year + region [‡]	3.251	0.124
Year + region + biomass	5.234	0.046
Biomass	12.629	0.001
Intercept only [§]	13.081	0.001
Region	19.937	0.000
Region + biomass	20.302	0.000

Notes: Models represented hypotheses to account for patterns of egg contamination. The ΔAIC_c scores indicate relative fit to the data (the lower the score, the better the model), and AIC_c weights indicate the proportional weight of evidence for each model.

[†] Defined as the mean mass of rodents per owl pellet as an indicator of diet.

[‡] Delineated as distinct clusters of Burrowing Owl nests separated from all others by at least 600 m.

[§] Model containing no explanatory variables; used to evaluate relative explanatory power of models containing biological explanatory variables.

and L and B are length and breadth of the eggshell in millimeters, respectively (Gervais et al. 2000). We assumed a specific gravity of 1.0, so 1 cm^3 is equivalent to 1 g. The contaminant concentrations corrected to fresh egg mass were used in all analyses. Geometric mean concentrations of contaminants were calculated for each year, and Ratcliffe's shell index (Ratcliffe 1967) was estimated for each egg. We used an analysis of variance (ANOVA) followed by Ryan's Q multiple comparison procedure (Day and Quinn 1989) to compare annual contaminant levels. We also compared levels of egg contaminants between years for females from whom >1 egg was collected with a matched-pairs t test. We examined relationships between log-transformed p,p' DDE concentration and eggshell thickness using regression analysis (Graybill and Iyer 1994). Values of egg contaminant concentrations were log transformed prior to all analyses to better meet the assumptions of normality for parametric statistical analysis.

Egg contaminants.—We examined factors that may be linked to egg contaminant levels using a modeling approach with multiple regression. We formulated a number of a priori models that linked p,p' DDE and other contaminants in eggs to region of the study area and diet, reflecting the hypothesis that contamination would be patchily distributed and that diet influenced uptake and accumulation (Table 1). Due to the patterns in contamination in the eggs collected in 1996, we examined the relationships using three different dependent variables: The first analysis used the concentration of p,p' DDE in each egg as the dependent variable. The second analysis used a dependent variable

of the total additive concentrations of all detected organochlorine compounds in the eggs. The third analysis modeled a synergistic effect, whereby we multiplied the concentration of *p,p'*DDE in the egg by a factor of 1.5 if any other organochlorine compound was present. Diet was estimated using the mean biomass of rodents per pellet. The study site was broken up into nine regions based on distinct clusters of nests separated from other clusters by distances >600 m; 80% of all foraging observations made on breeding male owls were within 600 m of the nest burrow (Gervais et al. 2003). We examined the potential for these models to account for individual egg contaminant loads using multiple regression and Akaike's Information Criterion (AIC; Burnham and Anderson 1998, Franklin et al. 2001).

AIC is based on maximum likelihood theory and allows the simultaneous consideration of a suite of hypotheses represented as models by objectively selecting the model that best fits the available data as a compromise between model variance and bias. The greater the number of parameters, the less the bias in parameter estimates, but the greater the variance in those estimates; AIC therefore does not automatically select the model with the most parameters as the most appropriate for the data at hand (Burnham and Anderson 1998:23, Franklin et al. 2001). The model that is most appropriate for the data is the one with the lowest AIC score relative to the other models in the set, all of which are tested with the identical data set. The scores are typically standardized by subtracting the smallest score from all others, so that the model that best fits the data has the adjusted score of zero. The adjusted scores are commonly referred to as the Δ AIC scores. Models whose adjusted score values are <4 can be considered competitive with the top model (Burnham and Anderson 1998). This method of data analysis provides a means of assessing the strength of evidence for one hypothesis over another, as opposed to the consideration of one alternative hypothesis at a time using conventional tests of statistical significance. An intercept-only model can be included in the set of regression models to allow evaluation of biologically based parameters relative to the intercept-only model, which contains no explanatory variables. Likewise, an r^2 statistic can be calculated with regression-based models for a general indication of how well the models do in explaining variation in the data. We used AIC_c , which includes a correction for small sample sizes (Burnham and Anderson 1998:221). We also evaluated the relative importance of each model and each parameter in our models by examining the Akaike weights (AIC_c weights), which are measures of relative likelihood for each of the models in a set (Burnham and Anderson 1998, White 2001). Weights are calculated as follows:

$$w_i = \frac{\exp(-0.5 \times \Delta AIC_{c_i})}{\sum \exp(-0.5 \times \Delta AIC_{c_i})}$$

where the summation occurs over all models' ΔAIC_c

scores. The weights for a set of models therefore sum to unity. Weights can also be used to evaluate parameter importance by summing model weights for all models containing each parameter (Burnham and Anderson 1998).

Productivity.—To investigate the effects of *p,p'*DDE and other organochlorine contaminants on owl productivity, we examined 13 models representing alternative hypotheses explaining productivity (Table 2). We used multiple regression with a negative binomial distribution for the response variable of numbers of owlets per nest (White and Bennetts 1996), and $QAIC_c$, a quasi-likelihood adjustment in AIC for overdispersion in the data (Anderson et al. 1994). A maximum rescaled adjusted r^2 value (Nagelkerke 1991, Allison 1999) was also calculated for the most appropriate model in addition to the AIC_c statistic. These are likelihood-based and can be interpreted as the amount of information gained when predictors are included in a model as compared to the intercept-only model. All models containing the variable of contaminant concentration in eggs were analyzed three times: first, with the variable equal to the concentration of only *p,p'*DDE in the eggs; second, with the additive total of all organochlorine contaminants; and finally, 1.5 multiplied by *p,p'*DDE concentrations if any other organochlorine contaminant was present. Habitat adjacent to the nest was quantified as the percentage of grass and amount of edge within a radius of 400 m of the nest; 400 m was used because it was the mean distance traveled from the nest during breeding season foraging trips (Gervais et al. 2003). We postulated that the amount of grass should be correlated positively with rodent abundance and hence, diet quality. Rodents are considered high-quality food due to their mass and both the functional and numerical responses of Burrowing Owl populations to rodent abundances (Silva et al. 1995; J. A. Gervais and D. K. Rosenberg, *unpublished data*). Although rodents were possibly present in crop fields as well, frequent field operations and the use of flood irrigation would prevent populations in the crop fields from reaching high densities. Edges of roads, drainage ditches, and the interface between cover types (defined in Gervais et al. 2003) also appeared to provide good foraging opportunities (J. A. Gervais, *personal observation*). Edge was quantified as the total linear distance of roads and ditches within 400 m of the nest burrow. We defined neighbors as the number of breeding pairs nesting within 400 m of the focal nest.

To further explore the potential for a negative interaction between diet and *p,p'*DDE on productivity, we compared mean reproductive output of owls with greater levels of *p,p'*DDE in eggs (>4.0 μ g/g) and lower rodent biomass in their diets (<3 g/pellet) to the rest of the population. Monte Carlo simulation analysis was conducted to determine the likelihood of the outcome (Manly 1991). We used this approach because the spe-

TABLE 2. Productivity of Burrowing Owls at NAS Lemoore, California (1998–2000), as a function of habitat characteristics near the nest, diet as measured by mean grams of rodent biomass per owl pellet, number of neighboring conspecifics, and organochlorine contamination loads in eggs.

Model	ΔQAIC_c	QAIC_c weight
Intercept only†	0	0.569
Organochlorine contaminants (OCs)	2.192	0.190
Biomass‡	3.454	0.101
Edge§ + grass	4.467	0.061
Neighbors¶ + biomass	6.423	0.023
OCs + grass + OCs \times grass#	6.835	0.019
OCs + biomass + OCs \times biomass	7.750	0.012
Biomass + grass + edge	8.228	0.009
Neighbors + OCs + biomass	8.784	0.007
Year	9.469	0.005
OCs + biomass + grass + edge	10.486	0.003
OCs + neighbors + biomass + grass + edge	14.135	0.001
Region††	19.847	0.000

Notes: Relationships were modeled using multiple regression with a negative binomial distribution for the response variable and QAIC_c . QAIC_c is a quasi-likelihood adjustment of Akaike's Information Criterion for overdispersed data (Anderson et al. 1994). Contaminant concentrations were log-transformed for the analysis. The ΔQAIC_c scores indicate relative fit to the data (the lower the score, the better the model), and QAIC_c weights indicate the proportional weight of evidence for each model.

† Model containing no explanatory variables; used to evaluate relative explanatory power of models containing biological explanatory variables.

‡ Mean mass of rodents per owl pellet as an indicator of diet.

§ Total linear distance of roads, ditches, and field edges within 400 m of the nest burrow.

|| Percentage of grass cover within 400 m of the nest burrow.

¶ Number of other Burrowing Owl pairs within 400 m of the nest burrow.

Interaction of egg contaminants and amount of grass cover within 400 m of the nest.

†† Delineated as distinct clusters of Burrowing Owl nests separated from all others by at least 600 m.

cific interaction of relatively high body burdens of contaminants with lower rodent biomass in the diet was of interest. We did not attempt to model a generalized interaction between *p,p'*DDE and food because we hypothesized that this relationship will vary widely over different levels of the two variables, and we have insufficient information to justify any nonlinear model form over any other in this two-variable system. Therefore, we split the observations into two groups. We chose the 4 $\mu\text{g/g}$ *p,p'*DDE concentrations in eggs as a threshold value because this is the lowest concentration associated with reproductive failure in any avian species (Blus 1996, Gervais et al. 2000). A majority of pellet samples (60%) had >3 g of rodent biomass per pellet. We defined our limits to ensure a sample size sufficient, albeit small, to allow an evaluation of the detection of effects of a *p,p'*DDE and food limitation interaction. The analysis was then repeated, using 4 $\mu\text{g/g}$ of total egg contamination as the threshold value.

Adult female survival.—Body burdens of contaminants such as *p,p'*DDE may affect the survival of adult owls. The likelihood that an individual would be recaptured in the following year was modeled using logistic regression as a function of productivity (number of owlets raised to 21–28 d of age in a nesting attempt), mean biomass of rodents per pellet as an indicator of diet quality, whether the previous nesting attempt was successful at raising any owlets to 21–28 d of age, and

contaminant concentrations in the owls' eggs as an indicator of body burden of the contaminants. All models containing the variable contaminant concentrations in eggs were run three times: first with the variable equal to the concentration of only *p,p'*DDE in the eggs, second with the additive total of all contaminants, and finally, 1.5 multiplied by *p,p'*DDE concentrations if any other contaminant was present. A maximum rescaled adjusted r^2 value (Nagelkerke 1991, Allison 1999) was also calculated for the most appropriate model in the set. Because we did not have all the covariate information for all years, we first examined whether owls were seen again or not as a function of contaminants and year (Table 3), and then as a function of contaminants, biomass, productivity, year, and nest success to maximize the sample sizes available (Table 4). For individuals sampled in more than one year, the year of the maximum egg level of *p,p'*DDE was used in the analysis. We used whether individuals were seen again or not as a relative index of survival, recognizing that this index is lower than actual survival rates due to the potential confounding effect of emigration, or failure to identify an owl that was in fact present on the study site. Because even owls with high contaminant body burdens attempted to breed, there should be little difference in detection probability among individuals due to contaminant loads. Survival estimates for individual owls were not determined because co-

TABLE 3. Survival rates of Burrowing Owls at NAS Lemoore, California, 1996–2000, as a function of year and contaminant levels in eggs.

Model	ΔAIC_c	AIC_c weight
Year	0	0.3845
Intercept only†	0.6687	0.2752
OCs‡	1.1029	0.2215
OCs + year	2.3473	0.1189

Notes: Models were evaluated using logistic regression and Akaike's Information Criterion adjusted for small sample sizes. The ΔAIC_c scores indicate relative fit to the data (the lower the score, the better the model), and AIC_c weights indicate the proportional weight of evidence for each model. OCs = organochlorine contaminants.

† Model containing no explanatory variables; used to evaluate relative explanatory power of models containing biological explanatory variables.

‡ Log concentrations of organochlorine contaminants in eggs.

variate information was not available for all owls in all years.

To better examine the potential for greater contaminant loads to impair apparent survival, we examined survival solely as a function of body burden of contaminants as indicated by egg contamination. Nine of the most contaminated eggs were collected in 1996, when we were unable to collect productivity or detailed diet data. These individual female owls could not be included in the previous survival analysis. Therefore, we compared the percent of owls surviving with >4 $\mu\text{g/g}$ of total contaminants in their eggs at any time to

the percentage of owls surviving with less than that level of contaminant in their eggs. These comparisons were done using a Monte Carlo randomization approach using 1000 replications to obtain a distribution of percentages of survivorship against which the observed rates could be compared (Manly 1991:21). The analysis was repeated using the threshold of 4 $\mu\text{g/g}$ *p,p'*DDE in eggs.

We examined the potentially negative impact of greater *p,p'*DDE body burdens and low biomass of rodents in the diet on survival by comparing our index of survival of owls with >4 $\mu\text{g/g}$ *p,p'*DDE in their eggs and <3 g/pellet biomass to the apparent survival of all other owls in the population during that time period. As with the productivity effects analysis, we chose to examine this question using a Monte Carlo randomization because we were interested in this specific interaction of high *p,p'*DDE and low dietary biomass. These comparisons also were done using a Monte Carlo randomization approach using 1000 replications. We repeated the analysis using a threshold value of 4 $\mu\text{g/g}$ of total egg contaminants and <3 g/pellet biomass.

RESULTS

Egg contaminant levels

We collected 16–26 eggs/yr between 1998–2001, in addition to the nine eggs collected in 1996, for a total of 92 eggs (Table 5). Of the 30 compounds included in the laboratory analyses, only *p,p'*DDE was found in all eggs. Mixed PCBs or Arochlor 1260 were detected

TABLE 4. Survival rates of Burrowing Owls at NAS Lemoore, California, 1997–2000, as a function of various independent factors.

Model	ΔAIC_c	AIC_c weight
Biomass† + year + productivity‡	0.0000	0.4254
Biomass + year + success§	1.4089	0.2103
Biomass + year + OCs¶ + productivity	1.8523	0.1685
Biomass + year	4.0567	0.0560
Year + productivity	4.4237	0.0466
Biomass + year + OCs + success	5.9973	0.0212
Biomass + year + OCs	6.0660	0.0205
Year + OCs + productivity	6.3190	0.0181
Year + success	7.6587	0.0092
Year	7.8263	0.0085
Year + OCs + biomass + OCs \times biomass	8.4923	0.0061
Year + OCs	9.6337	0.0034
Year + OCs + success	9.9040	0.0030
Intercept only#	11.0071	0.0017
OCs + biomass + OCs \times biomass	11.3267	0.0015

Notes: Models were evaluated using logistic regression and Akaike's Information Criterion adjusted for small sample sizes. The ΔAIC_c scores indicate relative fit to the data (the lower the score, the better the model), and AIC_c weights indicate the proportional weight of evidence for each model. OCs = organochlorine contaminants.

† Mean mass of rodents per owl pellet as an indicator of diet.

‡ Number of owlets raised to 21–28 d of age per nest.

§ Whether or not the nesting attempt raised any owlets to 21–28 d of age.

|| Log concentrations of organochlorine contaminants in eggs.

¶ Interaction between egg concentrations of organochlorine contaminants and mean mass of rodents per owl pellet.

Model containing no explanatory variables; used to evaluate relative explanatory power of models containing biological explanatory variables.

TABLE 5. Total number of active nests on site, number of Burrowing Owl nests sampled for egg *p,p'*DDE per year, geometric means and ranges of *p,p'*DDE contamination in $\mu\text{g/g}$, productivity, and biomass from NAS Lemoore, California, 1996–2001.

Year	No. nests	Nests sampled	DDE	Ryan's Q †	DDE range	Productivity‡	Biomass§
1996	...	9	8.83	A	4.16–32.82
1998	63	21	2.60	B	0.90–10.11	1.6 (0.2)	3.75 (0.54)
1999	85	26	0.74	C	0.06–3.11	3.9 (0.3)	8.37 (0.47)
2000	63	20	1.00	C	0.20–25.56	1.8 (0.2)	2.35 (0.51)
2001	...	16	1.14	C	0.61–3.71	...	2.77 (0.63)

Notes: Ellipses indicate that data were not available for that year. Values given in productivity and biomass are means with 1 SE in parentheses.

† Results of one-way ANOVA followed by Ryan's Q multiple comparison procedure to examine differences in levels of egg *p,p'*DDE levels among years. Letters indicate statistically different groups.

‡ Number of owlets raised to 21–28 d of age per nest.

§ Mean mass of rodents per owl pellet as an indicator of diet.

|| Data from Gervais et al. 2000.

in 17 eggs (range: 0.5–2.9 $\mu\text{g/g}$, 1.2 ± 0.2 [mean \pm 1 SE]). Nine of these eggs (52%) were collected in 1998. DDT was detected in one egg (2.3 $\mu\text{g/g}$), and HCB was detected in two eggs (0.05 $\mu\text{g/g}$ and 0.11 $\mu\text{g/g}$). A total of 21% of all eggs contained compounds in addition to *p,p'*DDE. Regression analysis indicated no relationship between *p,p'*DDE and other contaminant concentrations ($F_{1,17} = 0.47$, $P = 0.503$, $n = 19$). Geometric mean concentrations of *p,p'*DDE detected in eggs changed substantially from year to year (Table 5). These fluctuations were statistically significant ($F_{4,87} = 18.58$, $P = 0.001$; Table 5). Two eggs in 2000 contained 25.56 $\mu\text{g/g}$ and 10.01 $\mu\text{g/g}$, respectively. The greater of these two concentrations of *p,p'*DDE was from a female banded as a fledgling from an uncontaminated clutch the year before; this egg also contained DDT. This indicates that free-ranging Burrowing Owls can accumulate substantial contaminant residues in less than a year. Contaminated eggs were collected from all regions of NAS Lemoore, but no region or location was a consistent source of eggs with high *p,p'*DDE levels. The length of the study area from which eggs were collected was 10 km, while Burrowing Owl breeding territories were generally <1 km in diameter (Gervais et al. 2003), suggesting that a local “hot spot” of *p,p'*DDE contamination was unlikely.

We resampled eggs from two females in three consecutive years, and 13 females in two consecutive years. Levels of *p,p'*DDE generally declined in eggs over time within individual birds, with decreases of 7.04 $\mu\text{g/g}$ over a 2-yr period in one individual to an annual gain of 0.52 $\mu\text{g/g}$ in another. The mean annual change in *p,p'*DDE levels per owl was -1.27 ± 0.40 $\mu\text{g/g}$ (95% CI = -0.49 – -2.05 , $t = 3.2$, $P = 0.006$, $n = 15$), where the mean annual decline was used for the two owls with three years of samples.

The Ratcliffe index was positively correlated with eggshell thickness ($r^2 = 0.31$, $\beta = 3.205$, 95% CI = 2.168–4.243, $F_{1,79} = 36.67$, $P = 0.001$, $n = 81$). Eggshell thickness was weakly correlated with log *p,p'*DDE concentrations in eggs ($r^2 = 0.09$, $\beta =$

-0.004 , 95% CI = -0.006 – -0.001 , $F_{1,88} = 9.31$, $P = 0.003$, $n = 90$). The Ratcliffe index and *p,p'*DDE were not strongly correlated to each other, with a slightly negative relationship ($r^2 = 0.09$, $\beta = -0.025$, 95% CI = -0.041 – -0.008 , $F_{1,79} = 8.64$, $P = 0.004$, $n = 81$). We did not observe any indication that eggshells were breaking under the weight of incubating female owls; only one damaged egg was found in any nest. The damage was a slight circular fracture.

None of our models accounted very well for individual levels of egg contaminant concentrations (Table 1); the r^2 value for the best model, that of year, was only 0.23. The three calculations of contaminant concentrations in eggs yielded nearly identical results (differences of <0.1 in AIC_c scores), suggesting that our data are insufficient to discriminate among them. Accordingly, we report the results for the additive contaminant concentrations. Of the models examined, the models containing year and region were over three times more likely than competing models based on the AIC_c weights. When model weights were summed over all models containing each factor to estimate the relative weights of evidence for the importance of individual factors, year and region were twice as important as biomass (summed AIC_c weights per parameter: 1.000, 0.999, and 0.449, respectively). There were indeed annual patterns in egg contaminant loads, but they were not well explained by either consistent spatial variation or by biomass of rodents in the diet as we measured them.

Productivity

Productivity varied widely from year to year (Table 5). Our a priori models did not explain the data very well, as indicated by the fact that the intercept-only model was selected as the best model for these data (Table 2). This model has an adjusted maximum rescaled r^2 value of zero, as it contains no explanatory variables. As before, the data were not sufficient to distinguish among the three calculations of contaminant concentrations (maximum AIC_c score differences

of <0.1), and the additive concentrations were used for calculations of AIC_c scores and weights. The intercept-only model was nearly three to five times more likely than the two closest competing models that contained biological effects, suggesting that the biological variables we measured had little or no association with observed productivity.

Although there did not appear to be a linear interaction between diet and p,p' DDE, owls with $>4 \mu\text{g/g}$ p,p' DDE in their eggs and a biomass of $<3 \text{ g/pellet}$ raised fewer owlets to fledging than did other owls in the population (mean = 2.0, 95% CI = 0.7–3.2, $n = 5$; mean = 3.8, 95% CI = 3.1–4.5, $n = 62$, respectively). Monte Carlo simulations composed of random draws of five productivity estimates were repeated 1000 times. When all estimates were sampled with replacement, the outcome of 2.0 or fewer mean owlets occurred in 10.5% of the simulations. When estimates excluded the owls with $>4 \mu\text{g/g}$ p,p' DDE and $<3 \text{ g/pellet}$ biomass, the outcome of 2.0 or fewer owlets occurred in 9.1% of simulations. This suggests that our results were unlikely at the $P = 0.10$ level.

Owls with $>4.0 \mu\text{g/g}$ total contaminants in their eggs and $<3 \text{ g/pellet}$ rodent biomass in their diet raised an average of 2.1 owlets (95% CI = 0.8–3.5, $n = 7$), whereas owls with lower total contaminant loads raised an average of 3.8 owlets (95% CI = 3.1–4.5, $n = 60$). Monte Carlo simulations composed of random draws of seven productivity estimates were repeated 1000 times. When all estimates were sampled with replacement, the outcome of 2.1 or fewer mean owlets occurred in 10.5% of the simulations, but when the seven owls with the combined egg contaminant loads $>4.0 \mu\text{g/g}$ and $<3 \text{ g/pellet}$ biomass were excluded from the sample pool, the outcome of 2.1 or fewer mean owlets occurred in only 2.3% of the simulations.

Adult female survival

Neither p,p' DDE nor year were influential in modeling survival over all individual female owls whose eggs had been sampled ($n = 68$). The model with only the factor year was the most parsimonious model for these data, but did not describe the data well ($r^2 = 0.15$), and the AIC_c weight was only 1.4 times greater than the no-effects model; differences in the AIC_c scores among models were also small (Table 3). The differences among the three contaminants calculations were all <0.3 , so the results of the models with additive concentrations of contaminants were used in the calculations. The index of survival of owls for whom covariate information for all measured factors was available ($n = 59$) was better accounted for with the a priori models than survival as a function of only year and p,p' DDE ($n = 67$). The best model included biomass, year, and productivity. However, the AIC_c weight for this model was only 2.0 and 2.5 times greater than the next two most competitive models, which when combined with the similarity in the ΔAIC_c values suggests

little difference in the level of support for each hypothesis (Table 4). The best model fit the data well (adjusted maximum rescaled r^2 value = 0.41). Parameter estimates for the model components indicated that biomass of rodents in pellets was positively related to apparent survival ($\beta = 0.3795$, $SE = 0.1557$). The number of owlets raised to fledging was also positively related to survival ($\beta = 0.4147$, $SE = 0.1881$), while year effects were variable. AIC_c weights summed over all models for each factor indicated that year and productivity contributed substantially to model fit (summed AIC_c weights: 0.9979 and 0.6585, respectively), but contaminant residues in eggs did not contribute nearly as much (summed AIC_c weight: 0.2423). Once again, the data were insufficient to discriminate among the three calculations of contaminant concentrations, and the results of the additive concentrations were used in the calculations of AIC_c scores and weights.

Of the 15 owls with $>4 \mu\text{g/g}$ total contaminants in their eggs, six were seen again in subsequent years. This outcome occurred in 88.9% of the Monte Carlo simulations when drawn from owls with egg contaminant levels below $4 \mu\text{g/g}$, demonstrating that the survival rate was not different than that expected by chance. Owls with greater levels of contamination in their eggs, and presumably with greater body burdens of p,p' DDE than the general population, did not appear to have reduced survival rates.

We were unable to examine the effects of a low biomass and high p,p' DDE interaction on survival because two of the five owls meeting our criteria were never individually identified, and consequently their survival could not be calculated. The effects of a low biomass and high total egg contaminant concentrations on survival were difficult to distinguish, as only four owls whose identity was known fell into this category. Of these four, only one was seen in a subsequent year, but this outcome occurred in 61.6% of simulations when all owls were included in the pool, and 52.8% of the simulations when the four owls were excluded from the pool. It does not appear that there is a synergistic effect between egg contaminants and low food on whether an owl is likely to be seen again in subsequent years, although sample sizes are too small to detect any but the most dramatic effects on survival.

DISCUSSION

The most significant result of this study is that levels of p,p' DDE that were not associated with reduced reproductive output by themselves were associated with reduced productivity when combined with reduced rodent biomass in the diet. The results found in experimental work demonstrating a negative synergistic relationship between food and p,p' DDE on avian reproduction (Keith and Mitchell 1993) apply to free-living birds as well.

Although many persistent organochlorine compounds such as DDT and PCBs have been banned in many if not all countries, lingering residues and global redistribution of low concentrations of these compounds may still have negative ecological effects when combined with other stressors. Monitoring residue levels alone will not be sufficient to determine whether negative impacts on free-living populations of organisms or ecological communities are likely to occur. Collecting biologically relevant information during contaminant sampling work will be necessary to interpret patterns of variation in demographic rates correctly, and in determining whether contaminant exposure is a contributing factor. Annual patterns of contaminant levels and demographic rates in exposed populations should be examined in light of factors such as fluctuating food availability or climate variables. Such investigations may suggest auxiliary variables that could be measured and used to infer fluctuating risk.

There is growing awareness that contaminants must be considered in total when exploring their potential effects on biota. Almost all of the organochlorine contamination we documented was *p,p'*DDE, and the low levels of PCBs, HCB, and DDT detected in 21% of the eggs did not appear to have any additional adverse impacts. However, the natural variability in biological processes such as productivity is large, and the small fraction of eggs with secondary compounds further reduces the ability to detect subtle effects. The particular pattern of contamination documented in this study does not allow elucidation of the potential interactions of other organochlorine residues with *p,p'*DDE. These interactions will be particularly hard to predict due to the fact that various planar halogenated hydrocarbons such as PCB congeners can interact, leading to synergistic, additive, or antagonistic interactions depending on the compounds involved (Birnbaum et al. 1985, Davis and Safe 1988).

The levels of *p,p'*DDE that we detected were not by themselves associated with lowered productivity or reduced apparent overwinter survival. Instead, overwinter survival was most strongly associated with a combination of biomass of rodents in the diet, the number of owlets produced that year, and annual environmental variation summed as "year" effects. However, there were insufficient data to entirely rule out the possibility that contaminants may also contribute, as indicated by the close AIC scores between the best model and one containing contaminants as a variable. Interestingly, productivity was positively associated with overwinter survival, in contrast to experimental work (Nur 1988, Golet et al. 1998). Apparently, good years for producing owlets were also good years for survival, although an alternative explanation is that successful breeders are more likely than failed breeders to remain on the same breeding territory the following year (Newton and Marquiss 1982, Hakkarainen et al. 2001; Rosenberg and Haley, *in press*). Due to incomplete banding data,

we were unable to examine survival rates for a negative interaction between high organochlorine body burdens and low dietary rodent biomass.

In contrast, none of the biological or environmental variables we measured accounted for productivity. Many factors influence productivity, and we may have failed to measure the appropriate variables in this case, or failed to model them correctly. In addition, sampling error associated with estimating productivity of this burrow-nesting species will make detecting patterns more difficult (Gorman et al., *in press*). Although *p,p'*DDE is best known for its impacts on shell formation and subsequent reproductive failure in birds (e.g., Blus 1996), we were unable to compare hatching rates among nests because they could not be accurately determined in the natural burrows most of our study owls used. Although productivity was not affected by contaminants or biomass of rodent prey when these were modeled as separate factors, the interaction of contaminants with low dietary biomass on productivity suggests that eggshell thinning is not the only biological endpoint of concern. The interactive combination may have reduced parental attentiveness, reducing food deliveries to the brood or increasing the likelihood of predation.

The pattern of highly variable contaminant levels among individuals and years in the population begs the question of the origin of contaminant exposure. Prey movements have long been recognized as a vector carrying contaminants far from their source; for example, insectivorous migratory birds may carry contaminant residues from Central and South America (Enderson et al. 1982, Fyfe et al. 1990). Presumably, the population of sedentary predators intercepting the cloud of contaminated migratory prey would be at roughly equal risk of contaminant exposure, depending on the individual variation in prey item selection. One therefore might predict that once a balance had been reached between consumption of contaminated prey and excretion rates, individuals would carry roughly equivalent body burdens after accounting for age, sex, and breeding effects. Similar patterns might be expected if contaminants are of local origin, and present in the local food web.

Residues in eggs were greatest in 1996, when the geometric mean of the sample exceeded the contaminant levels found in almost all eggs in any other year. Burrowing Owls eat a wide variety of prey taxa (e.g., Green et al. 1993, Gervais et al. 2000, York et al. 2002; Rosenberg and Haley, *in press*), although they do seem to select rodent prey when available (Silva et al. 1995; J. A. Gervais and D. K. Rosenberg, *unpublished data*). Limited contaminant sampling of prey items of Burrowing Owls at NAS Lemoore indicated that only low levels of *p,p'*DDE were present, and only in centipedes (Gervais 2002). This would suggest that some residual contamination still remains in the area. Other species of owls substitute avian prey into their diets when

mammalian prey are at low densities (Adamcik and Keith 1978, Wendland 1984, Korpimäki and Nordahl 1991), and Burrowing Owls at other sites appear to do the same (Rosenberg and Haley, *in press*). Avian prey consumption in particular has been linked to egg contaminant levels in raptors (e.g., Enderson et al. 1982, Custer and Meyers 1990, Kozie and Anderson 1991, Anthony et al. 1999). Although avian prey do not appear to be major dietary items for Burrowing Owls at NAS Lemoore, we did identify five species of passerines from prey remains (Loggerhead Shrikes, *Lanius ludovicianus*; Red-winged Blackbirds, *Agelaius phoeniceus*; Western Meadowlarks, *Sternella neglecta*; Horned Larks, *Eremophila alpestris*; and Savannah Sparrows, *Passerculus sandwichensis*). Contaminant residue patterns among years may be at least in part due to the extent to which the owls include voles, centipedes, or possibly birds in their diet with annual fluctuations of prey availability. Unfortunately, it was nearly impossible to quantify centipede and avian prey consumption, as these are very difficult to detect in pellet remains.

Although broad-scale changes in prey availability may explain variation in contaminant levels among years, it does not seem able to account for the wide variation in individual body burdens and egg loads. Burrowing Owls are extreme generalists in their diet, but it seems unlikely that individual owls' diets vary greatly enough to cause substantial bioaccumulation in the tissues of one owl, and nearly none in another individual living nearby. It is possible that differences were due to age, but Burrowing Owl females at this site rarely appear to live longer than 4–5 years (D. K. Rosenberg and J. A. Gervais, *unpublished data*).

Alternatively, the occurrence of a few highly contaminated owls in the population could result from the movements of owls themselves. Although this population of owls appears to be resident year-round, young owls may range widely in the months between fledging and settling to breed the following spring (D. K. Rosenberg and J. A. Gervais, *unpublished data*). In addition, failed breeders may relocate to a new area before attempting to breed again (Newton 1979, Newton and Marquiss 1982; Rosenberg and Haley, *in press*). Patterns of contamination at the population level are therefore likely to be the result of both prey selection and regional recruitment patterns. These two dynamics can result in variable contaminant levels in a population over time, but the original source of the contaminants may be very different. Such variable patterns of population-level residues suggest that potential effects may be quite variable as well.

It does not appear that the organochlorine contaminants we detected in individual Burrowing Owls are likely to have an impact on the demographic performance of this population of Burrowing Owls as a whole. However, residues may reach levels causing decreased reproduction or survival in some years, partic-

ularly when combined with other non-anthropogenic stressors such as food scarcity. Those effects will only be documented if data on these additional stressors are collected for a population as well as the contaminant samples. The established practice of sampling eggs from unmarked individuals whose geographic origin and movements are not known will be of limited value in either inferring potential demographic consequences of contaminant exposure or in identifying sites with potential contaminant problems. Studies that are not adequately replicated through time are also at risk of misidentifying the true extent and magnitude of the effects of contaminants, particularly if the species is capable of prey-switching behavior. Finally, a better understanding of metapopulation dynamics and how regional movements affect patterns of contaminant occurrence will be needed to both identify source areas and to interpret the demographic impacts of exposure.

ACKNOWLEDGMENTS

This work was supported by grants from the U.S. Navy EFA West and California Department of Fish and Game, and National Fish and Wildlife Foundation to D. K. Rosenberg and was conducted as a part of the Burrowing Owl Research Program, a collaborative research program including The Institute for Bird Populations, Oregon State University, and San Jose State University with assistance from the Oregon Cooperative Fish and Wildlife Research Unit. Cooperators of the Oregon Cooperative Fish and Wildlife Research Unit included the U.S. Fish and Wildlife Service, Oregon State University, Oregon Department of Fish and Wildlife, the Wildlife Management Institute, and the Biological Resources Division of the U.S. Geological Survey. Our thanks especially to Mr. John Crane of NAS Lemoore for his support and assistance. M. Abright, M. Anderman, M. Bond, C. Bailey, C. Dalton, V. Franke, T. Lanman, J. Podulka, and S. Solomon assisted with fieldwork. G. Santolo and J. Yamamoto provided technical advice and assistance in egg sample preparation. H. Packard and J. Rosier analyzed owl pellets. D. K. Rosenberg offered invaluable assistance both in the field and during statistical analyses. M. Ambrosino, J. Barth, M. Conner, E. Forsman, A. C. Hatch, P. C. Jepson, D. Levey, D. K. Rosenberg, I. Tinsley, and two anonymous reviewers provided comments on the manuscript. This project would not have been possible without the extensive collaboration and support that we received. This is publication number 203 of The Institute for Bird Populations.

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