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SCAVENGING OF SEABIRD CARCASSES AT TWO OIL SPILL SITES IN CALIFORNIA AND OREGON

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SUMMARY

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After the *M/V Kure* oil spill in California and the *M/V New Carissa* spill in Oregon, we studied the removal of seabird carcasses by scavengers. The experimental design consisted of placing carcasses in randomized locations along the shoreline and returning at daily intervals to evaluate their condition. Twenty-five carcasses were placed at each of 4 sites in Oregon near Coos Bay and Waldport and 6 sites in California in and around Humboldt Bay, for a total of 250 carcasses distributed along 25 km of coastline. Small birds (<=521g) disappeared significantly faster than large birds (>521g), especially at the California sites where 66% to 78% of the carcasses were removed over the first 24 hours. Carcass removal rates varied significantly among sites in California, but not in Oregon. The daily rate of carcass removal tended to change over time, decreasing for small birds but increasing for large birds. Domestic waterfowl (mallard ducks) were removed more rapidly than seabirds, but wild passerines did not differ from seabirds in this regard. After six days, 16% of the small carcasses and 49% of the large carcasses remained at the California sites, while in Oregon 50% of the small carcasses and 56% of the large carcasses remained.

Key words: scavenging, carcass removal, carcass persistence, Weibull distribution, Kure, New Carissa, beached bird model

INTRODUCTION

Seabird carcasses are often reduced to unrecognizable fragments or removed entirely by scavengers soon after being beached. The rapidity of the process varies widely, ranging from only a few percent removal per day to nearly complete removal over a 48 hour period (Camphuysen 1989 cited in VanPelt and Piatt 1995, Ford et. al 1996). The number of carcasses found when searching a beach is determined by a balance between the rate of carcass deposition and the rate of carcass removal. If surveys of beached birds are used to infer the actual number of birds that were killed by natural die offs (Piatt and VanPelt 1997), oil spills (Page et al. 1990), or chronic pollution (Wiese and Ryan 2003), the carcass removal rate is a critical parameter that determines how many carcasses remain on the beach where searchers can find them

Beached bird monitoring surveys usually involve repeated visits to the same site at varying intervals, commonly ranging from daily to monthly. Searches tend to be more frequent during oil spill response activities and less frequent during long term monitoring programs (Camphuysen and Huebeck 2001). When scavenging activity is intense and the interval between searches is large, most of the beached carcasses are removed before they are found by searchers.

Several studies have estimated carcass persistence based on the monitoring of naturally deposited carcasses (Fowler and Flint 1997, VanPelt and Piatt 1995), experimentally placed marked carcasses (Wiese and Ryan 2003), or radio-tagged carcasses (Ford et. al 1996). The different methodologies have different advantages in that naturally deposited carcasses may be more “realistic” in their placement, but experimentally placed carcasses allow more control over sample size, make it possible to separate the effects of wave action and scavenging, and simplify comparison of the factors influencing carcass persistence.

Carcass removal is important to estimating mortality rates in terrestrial as well as in marine habitats. Wind farm development, with the associated risks to birds and bats, have resulted in several studies that quantify the rate at which carcasses are removed by scavengers in various terrestrial habitats (Osborne et al. 2000, Barrios and Rodriguez 2004, Johnson et al. 2004). Scavenging rates tend to be higher on beaches than in terrestrial environments, probably because the coastline is a rich and relatively predictable food source that many scavengers rely on. Because of their linearity and relatively open nature, beaches may also be easier for scavengers to search than vegetated two dimensional habitats such as grasslands, croplands, or marshes.

The experiments described here were carried out as part of the damage assessments for the 1997 *M/V Kure* oil spill (Ford et. al 2001a) in California and the 1999 *M/V New Carissa* oil spill (Ford et. al 2001b) in Oregon. Carcasses of a range of different species were placed along beaches in different locations so that we could separate the effects of scavenging from the effects of rewash. The purpose of these experiments was to estimate the rate at which seabird carcasses are removed by scavengers, and to determine which factors (carcass size, location, age, etc.) significantly affect those rates.

METHODS

Data Collection

Studies were carried out at two locations: (1) near the *M/V Kure* spill site in Humboldt Bay and on the adjacent coast in northern California, and (2) in areas affected by the *M/V New Carissa* spill on the coast of Oregon near Coos Bay and Waldport. We selected sites that were typical of the coastline affected by each of the spills. Sites selected for the New Carissa study were generally similar in structure, consisting entirely of sandy bluff backed beaches which is the most common beach type in Oregon. The *Kure* study sites included two bluff backed beach sites, South Coast Spit and North Coast Spit, as well as two marsh sites, South Bay Spit and Indian Island, and two dune grass backed sites, Mad River and Clam Beach, associated with the outflow of small rivers. A summary of the sites and their characteristics are shown in Table 1.

Twenty five carcasses were set out at each of the 10 sites for a total sample size of 250 carcasses. Each carcass was placed between zero and 200 meters from the previous carcass based on a uniform random distribution, so that the mean distance between carcasses was 100 meters. Occasionally, we could not place carcasses in the randomly selected position because of obstacles such as a river mouth or a rock outcropping, and in these cases we continued to the first position where it could be placed. Carcasses were placed in randomized location between the wrack line and the top of the beach. In a few cases, waves came all the way to the base of the low, sandy bluffs that formed the beach back, and we placed carcasses on the bluff face or on the bluff top above the reach of the tide. In order to avoid providing inadvertant cues to the scavengers, we set out carcasses during a rising tide, walking below the wrack line whenever possible so that any tracks would be washed away by the waves. The total length of all study beaches was about 25 km. The *M/V Kure* study took place in November 1998, and the *M/V New Carissa* study in March and April of 2000.

Latitude, longitude, time, carcass identification number, and species were recorded at the time of placement. A small block of wood, about 10 cm x 10 cm, with the carcass identification number was placed under each carcass, and a matching tag with the same number was fastened to one leg. The wooden blocks, which were light and easily shifted by wave action, were used to differentiate between the removal of carcasses by scavengers and the removal of carcasses by waves. If a carcass was missing but the wooden block was still present, we assumed that the carcass was taken by scavengers: if both carcass and block were missing, we assumed that the carcass was washed out. Although it possible for carcasses to wash out and to later beach again, we never encountered this situation.

Carcasses were obtained from a variety of sources, but all were formerly frozen and unoiled at the time of placement. Some of the carcasses were originally oiled, but were cleaned by washing them in Dawn liquid detergent based on the protocols recommended for the cleaning and rehabilitation of live oiled birds (Newman et al. 2003) since the Oil Pollution Act of 1990 (OPA 90) prohibits the introduction of oiled material (i.e oiled birds) into the environment. A range of species were used, consisting primarily of seabirds, but the *Kure* study in California also included some wild passerines and domestic mallard ducks. A list of the various species used in the studies is given in Tables 2a and 2b.

Carcasses were checked on a daily basis to determine if they had been removed, washed away, or scavenged. Carcass condition was scored as follows:

Unscavenged	Carcass intact and in place
Disturbed	Carcass moved but unscavenged
Partially scavenged	Less than half of carcass removed
Heavily scavenged	More than half of carcass removed
Removed	Only feathers, bones, or scraps of skin remain
No Trace	No sign of carcass remains

All sites excepting Indian Island were checked for six consecutive days. Because of the difficulty of access (which required an airboat), Indian Island was checked for four consecutive days.

Analysis

Carcass persistence as a function of time was calculated separately for each site and for each size class (large or small) of bird carcass. We chose the weight of a Rhinoceros Auklet (521 grams) as the upper limit of the ‘small’ bird category because it was the median weight of the specimens used in the two studies. Additionally, Rhinoceros Auklets are small enough to be carried short distances by ravens, one of the most common coastal scavengers in both Washington and Oregon, an event which was observed twice during the study.

The process of changing from one scavenging state to another was analyzed by computing transition matrices for each size class and study area. Each carcass was placed into one of four categories on each day: *Unscavenged, Partially Scavenged, Heavily Scavenged, and Removed*. The *Unscavenged* state included carcasses that were classified in the field as either *Unscavenged* or *Disturbed*. The *Removed* state included carcasses that were originally classified as either *Removed* or as *No Trace*.

We used a statistical model that could examine multiple factors simultaneously to determine how study site, carcass type, and carcass size affected the rate at which scavengers remove seabird carcasses. Because carcasses were checked on a daily basis, the exact time of carcass removal was not known, a phenomenon referred to as censoring. We therefore used a Weibull parametric survival model which accounts censored data on the dependent variable (carcass persistence time). This model allows the use of left censored removal times (i.e., removeal before the first daily observation), right censored removal times (i.e., the carcass was not removed), and interval censored removal times (i.e., removed sometime between two daily observations). All three of these situations occurred in our dataset. The Weibull model is parametric in that it specifies a functional form of the survival distribution, but it is sufficiently general for carcasses to be removed from the beach at either increasing or decreasing rates relative to the constant rate exponential model. Estimation was performed using the *censorReg* function in S-Plus (Insightful Corporation, 2006).

Oregon and Northern California study sites were treated as completely separate datasets in the statistical analysis. When building a statistical model for each site, carcass weight was considered in two separate manners: (1) as a continuous covariate; and (2) as a dichotomy whereby all relationships between dependent and independent variables could vary depending on whether the carcass is "small" (>=521g) or "large" (>521g). The use of both dichotomous and continuous treatments of weight as a predictor allowed us to explore whether the effect of weight on scavenging rates is best modeled as a step-function or as a continuous factor. Dummy (0/1) variables were used to identify individual sites within each study area and, in the case of the Northern California datset, to identify whether a carcass was a seabird or a non-seabird.

RESULTS

Carcass persistence varied widely among sites for both the Kure and the New Carissa studies. At the Kure sites around Humboldt Bay, some of this variation was clearly related to carcass size (Figures 1 and 2). With the exception of Indian Island, only 22% to 44% of the small carcasses remained after the first 24 hours compared to 77% to 100% of the large carcasses. On Indian Island, a marsh island in upper Humboldt Bay, carcass removal proceeded slowly for both size classes, where 75% and 77% of the small and large carcasses respectively still remained after four days on the beach.

The relationship between size class and persistence was less distinct in the *New Carissa* study where both large and small size classes had persistence rates comparable to the large size class in the *Kure* study. At the *New Carissa* site, small birds were removed more rapidly than large birds during the first day, but the proportion of the of the two size classes remaining converged thereafter (Figure 3). The proportion of carcasses that were no longer intact or had disappeared showed a pattern similar to that of persistence, with only 15% to 20% of the carcasses still intact by the end of the study.

Transition matrices for scavenging state (partioned by study area and carcass size) are shown in Tables 3a through 3d. Each matrix cell contains the probability that a carcass will change from one scavenging state to another state over a 24 hour period. The matrix diagonal represents the probability that a carcass will remain in the same state. Since *Removed* is an absorbing state (i.e. once *Removed*, a carcass remains *Removed*) , the probability that a carcass will remain *Removed* from one day to the next is always 1.0. The matrix is triangular because it was since carcasses did not change back to a less scavenged state or reappear after being removed.

For the *New Carissa* study sites in Oregon, transition matrices for both size classes are generally similar. Excepting the transition from *Removed* to *Removed*, the most likely transition was *Heavily Scavenged* to *Heavily Scavenged,* indicating that carcasses tend to remain in that state rather than changing to the *Removed* state. Small birds at the Humboldt Bay site differed from the other three site x size class combinations in that the transition probability from *Not Scavenged* to *Removed* was greater. In other words, small birds in the *Kure* study were more likely to change directly from a *Not Scavenged* state to a *Removed* state than were large birds. Small *Kure* birds also differed in that carcasses in the *Heavily Scavenged* state were more likely to change to the *Removed* state. Aside from small *Kure* birds, carcasses typically passed through *Partially Scavenged* or *Heavily Scavenged* states before coming to rest in the *Removed* state, and tended to remain in the *Heavily Scavenged* state.

In estimating the survival model, multiple explanatory factors were included in order to protect against systematic biases associated with omitting variables. We evaluated the decision to separate the dataset into large birds and small birds based on a 521g weight breakpoint using likelihood ratio tests that compared the relative fit of (1) combining large and small bird categories for the analyses versus (2) estimating separate models with different coefficients for birds in each size category. The likelihood ratio tests support the separation of the data sets into large and small categories around this breakpoint. Size class differences were stronger in the *Kure* data set ($\chi^2[9] = 51.5$, $p < 0.001$) than the *New Carissa* dataset ($\chi^2[6] = 12.8$, $p < 0.05$).

Tables 4a through 4d present the results of the survival analysis partitioned by study area and carcass size. The dependent variable is the (censored) time at which the carcass is removed from the beach. Positive coefficients indicate that an independent variable is associated with increased persistence once other variables in the model are considered, and negative coefficient values imply decreased persistence. For example, in the case of large birds in the Kure study area (Table 4b), the negative coefficient on the non-seabird indicator variable is -1.398, implying that non-seabird carcasses (mallards) have decreased persistence time compared to seabird carcasses ($p < 0.01$). The non-seabird coefficient was also negative for small passerine birds in the Kure study area (-0.982), but this relationship was not statistically significant. The coefficients on the continuous bird weight variable were statistically significant only for large birds in the *New Carissa* study. This relationship was positive, indicating that marginal increases in weight for larger bird species were associated with longer carcass persistence times. The fact that this weight variable was not significant for any of the other models indicates that much of the impact of weight on carcass persistence was captured by the discrete separation of small and large bird categories.

Tables 4a through 4d also include variables that identify the location of each carcass in terms of study site. Models were estimated multiple times, each time suppressing a different site. The interpretation of the signs and the significance of the coefficients on the remaining "Contrast Variables" are indicative of pairwise comparisons between the effects of the included site and the excluded site in terms of carcass persistence. For example, in the case of small birds in the Kure study area, the positive coefficient (3.455) on the *Indian Island* Contrast Variable (table row) under the *Mad River* baseline variable (table column) denotes that birds at the Indian Island site persisted longer than birds at the *Mad River* site ($p < 0.01$).

While there were almost no statistically identifiable differences in carcass persistence rates among sites in the *New Carissa* study area, there were distinct patterns in the *Kure* study area. The greater persistence of small birds at *Indian Island* (Table 4a and Figure 1) is statistically significant relative to all other sites. For large birds in the *Kure* study area (Table 4b), carcass removal was most rapid at the Mad River site as evidenced by the positive pairwise comparisons with all other locations that were highly significant ($p < 0.001$) for three of the 5 sites. With the exception of the South Spit Coast site, every site in the *Kure* study area was statistically distinguishable from at least one other site for large birds at a significance level of $\alpha = 0.05$ or smaller. Although no single site was statistically different from all other sites, considering all sites simultaneously indicated that site was a significant factor in predicting persistence rates ($\chi^2[5] = 22.9$, $p < 0.001$ for small birds; $\chi^2[5] = 22.3$, $p < 0.01$ for large birds) in the *Kure* study. Site was not a statistically significant factor in the *New Carrisa* study.[1]

The dispersion paramater shown in Tables 4a through 4b describes the shape of the carcass persistence curve. When the dispersion parameter equals one, the average rate at which carcasses are removed from the beach is constant over time (i.e, an exponential decay model). When the dispersion parameter is less than one, carcasses are removed at an increasing rate over time, and when the parameter is greater than one, carcasses are removed at a decreasing rate. In both the *Kure* and *New Carissa* studies, small birds were removed at a decreasing rate over time, and large birds were removed at an increasing rate. While the form of the persistence function is consistent for large and small birds in both studies, only the large birds in the *Kure* study ($p < 0.05$) and the small birds in the *New Carissa* study ($p < 0.01$) were significantly different from the exponential model.

DISCUSSION

Different sites in the two study areas varied widely regarding carcass persistence. In general, small birds at the *Kure* site disappeared very quickly compared to either large birds at the *Kure* site or both size classes at the *New Carissa* site. The low persistence of small birds at the *Kure* site resulted primarily from very rapid removal during the first 24 hours after carcass placement.

Small bird carcasses at the *Kure* site tended to remain longest in the *Partially Scavenged* state, whereas large *Kure* carcasses and *New Carissa* carcasses remained longest in the *Heavily Scavenged* state. The relatively rapid disappearance of small carcasses at the *Kure* site occurred regardless of carcass condition. As with overall disappearance rates, the transition probabilities for large *Kure* birds and both size classes of *New Carissa* birds are similar among themselves, but differ markedly from the transition probabilities for small *Kure* birds.

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[1] We also explored including variables in the statistical model based upon the Akaike Information Criterion (AIC). This produced results that were qualitatively similar to those presented in Tables 4a-d. Variables that were significant in the full model in 4a-d were also retained in the "best models" based upon AIC. For the Northern California dataset, these were the seabird dummy variable, the site location factor, and the dichotomous treatment of carcass weight. For the Oregon dataset, these were the dichotomous treatment of carcass weight combined with continuous effects of carcass weight within the dichotomous categories. The signs of the coefficients were the same in the AIC-based models, and the significance levels were similar.

Although ocean beaches are populated by both invertebrate and vertebrate scavengers, we saw little evidence that carcass removal was caused by invertebrate activity. Invetebrate scavengers undoubtedly speeded up the decomposition process, but the invertebrate species present in the upper beach were too small to disarticulate or remove even a small bird carcass. The apparently minor role of invertebrates may have resulted from placing the carcasses above the tideline, or because the duration of the studies was only one week.

Sightings of avian scavengers were common, and they were often observed clustered around carcasses. Similarly, large numbers of bird tracks were often observed around scavenged or dismembered carcasses. Mammalian scavengers (aside from domestic dogs) were never observed, but their tracks were frequently associated with large heavily scavenged or missing carcasses. In the latter case, we often observed drag marks in the sand which led into the vegetated back beach. In four instances at the *Kure* site, we were able to follow the drag marks to locations where carcasses had been cached.

Larid gulls, Common Ravens (*Corvus corax*), and Turkey Vultures (*Cathartes aura*) were common at both sites. At the *Kure* site, we also observed two instances of Northern Harriers (*Circus cyaneus*) feeding on carcasses, and at the *New Carissa* site we observed American Crows (*Corvus brachyrhynchos*) and Bald Eagles (*Haliaeetus leucocephalus*). Large carcasses that were partially or heavily scavenged, were often surrounded by hundreds of bird tracks, whereas small carcasses often disappeared completely with no visible trace or with only a few footprints left in the immediate vicinity of the marker. We assume that many of the birds categorized as small were carried away by avian scavengers. In one instance, R. Hewitt (pers. comm) videotaped an American Raven flying off with a Rhinoceros Auklet in its beak. In another instance, we found part of a Rhinoceros Auklet carcass surrounded by feathers and fresh bird droppings atop a large log near the original carcass location.

Domestic dogs were often seen investigating carcasses, but they were never observed scavenging or removing carcasses. Tracks at the *Kure* site indicated that the principal mammalian scavengers were racoons (*Procyon lotor*) skunks (*Mephitis mephitis*), and to a lesser extent gray foxes (*Urocyon cinereoargenteus*, Halfpenny 1986). River otter (*Lutra canadensis*) scat was commonly observed at the Indian Island site in Humboldt Bay. Tracks were more difficult to identify at the *New Carissa* site because of blowing sand, but similarity in habitat and species composition suggest that the mammalian scavenger fauna was probably comparable at both sites. Our subjective impression is that mammal tracks and/or drag marks were usually associated with complete carcass removal rather than with progressive scavenging.

Although the avian scavenger communities were similar at the two sites, differences in weather conditions may have led to decreased levels of avian scavenging activity at the *New Carissa* sites. Avian scavengers were frequently seen on the beach at the *Kure* sites, but they were much less common at the *New Carissa* sites where they were regularly observed hovering a short distance inland, shielded from the onshore wind by the sand bluffs and rarely venturing onto the beach. The difference in the removal rate of small carcasses at the two sites may have resulted from lower rates of avian scavenging activity during the *New Carissa* study due to the windy conditions.

While statistical analysis of carcass persistence data demonstrated differences between small and large birds in both the *Kure* and *New Carissa* studies, the magnitude of these differences varied. In the Kure study, there were striking differences between the persistence of small birds and large birds, especially within the first few days (Figure 3), and the difference between small and large bird carcass persistence is highly significant. Conversely, in the *New Carissa* study, carcass persistence was less variable between size classes and the differences were not as significant. The difference between the persistence of large and small observed during the *Kure* study may have resulted from higher rates of avian scavenging compared to the *New Carissa* study. These results emphasize the potential importance of conducting site-specific scavenging studies when estimating avian mortality based on the collection of beached bird carcasses.

Analysis of both the *Kure* and *New Carissa* data sets indicated that the rate of small and large bird carcass removal changed over time. In both cases, small birds were removed at decreasing rates relative to large birds as the carcasses aged (see the dispersion parameter in Table 4). At the *Kure* site, survival modeling showed that the removal rate of small birds decreased significantly as they aged, whereas the removal rate of large carcasses was not significantly distinguishable from a constant rate model. At the *New Carissa* site, the removal rate of small birds could not be distinguished from a constant rate model, whereas the removal rate of large birds increased significantly as they aged. A possible explanation for this phenomenon can be found in the transition matrices, where large birds were more likely than small birds to be progressively scavenged while remaining on the beach in an identifiable form (i.e. *Partially scavenged* and *Heavily scavenged* states). This resulted in a slower initial rate of removal, which increased as carcasses became progressively dismembered and fragmentary. By comparison, small carcasses that were scavenged were more likely than large birds to transition directly from an *Unscavenged* to a *Removed* state.

In three out of the four combinations of body size and study site, the relationship between body weight and persistence appeared to be based on a threshold rather than a continuous relationship, implying that scavengers respond in a qualitatively different manner to small and large carcasses. The associated transition matrices suggest that this difference is related to the tendency for smaller carcasses to be removed suddenly and completely, whereas larger carcasses are often dismemembered and scattered in place. In cases such as this, different persistence functions should be estimated for different size classes of carcasses.

Although estimates of carcass persistence have shown wide variation in various studies (Ford 2006), this variability was not apparent among the sites at each of the two study areas. We found no significant differences between sites within the *New Carissa* study area, and at the *Kure* study site only the marsh site on Indian Island differed significantly from all the other sites(Tables 4a and 4b). Small birds showed no significant differences in persistence rates among the remaining *Kure* sites, but large birds did. Large carcasses were removed most rapidly at the Clam Beach and Mad River sites, both wide sandy beaches associated with the outflow of small rivers, and all sites showed significant or marginally significant differences compared with other sites. This pattern suggests that the distribution of scavengers capable of removing large carcasses intact, probably medium size mammals, was more variable than the distribution of scavengers capable of removing smaller carcasses.

Obtaining seabird carcasses for persistence studies is sometimes difficult, and in many instances it would be convenient to use the carcasses of domestic fowl or wild passerines. The dataset for the *Kure* study site allowed us to determine whether (small) passerines or (large) domestic mallards were scavenged in a manner comparable to seabirds. The persistence of small passerine carcasses was comparable to that of seabirds, but domestic mallard ducks persisted for less time than did wild seabirds. While not conclusive because the test included only one type of domestic fowl, the results suggest that scavengers may prefer the carcasses of domesticated farm reared birds to the carcasses of wild seabirds, and this should be taken into account when designing scavenging studies.

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Table 1. Characterization of ten sites used in scavenging studies.

Name	Incident	Latitude (N)	Substrate	Backing
South Spit Coast	*Kure*	40.7448	Sand	Bluff
South Spit Bay	*Kure*	40.7387	Marsh	Marsh
Indian Island	*Kure*	40.8146	Marsh	Marsh
Clam Beach	*Kure*	41.0214	Sand	Dune Grass
Mad River	*Kure*	40.9173	Sand	Dune Grass
North Spit Coast	*Kure*	40.7741	Sand	Bluff
Umpqua R. South (Hauser)	*New Carissa*	43.6042	Sand	Bluff
Umpqua R. North (Sparrow Pk)	*New Carissa*	43.7858	Sand	Bluff
Coos Bay North (Colorado St.)	*New Carissa*	44.3583	Sand	Bluff
Coos Bay South (Driftwood Way)	*New Carissa*	44.4733	Sand	Bluff

Table 2. Numbers and characteristics of carasses used for (a) the *Kure* scavenging study, and (b) the *New Carissa* scavenging study. Weights marked with asterisks are averages based on carcass measurements. All other weights are from Dunning (1984).

(a) Carcasses used in *Kure* study.

Species	**Number**	**Weight (g)**	**Category**
Oregon Junco	1	20	Passerine
Brown-headed Cowbird	5	44	Passerine
Varied Thrush	1	78	Passerine
Common Murre (juvenile)	13	200*	Seabird
Marbled Murrelet	1	220	Seabird
Pigeon Guillemot	1	487	Seabird
Rhinoceros Auklet	33	520	Seabird
Common Murre (sub-adult)	3	600*	Seabird
Sooty Shearwater	8	787	Seabird
Common Murre (adult)	46	993	Seabird
Western Gull	2	1011	Seabird
Mallard Duck	30	1082	Domestic
Common Loon	6	4134	Seabird

(b) Carcasses used in *New Carissa* study.

Species	**Number**	**Weight (g)**	**Category**
Fork-tailed Storm Petrel	1	55	Seabird
Cassins Auklet	4	188	Seabird
Common Murre (juvenile)	22*	200	Seabird
Ancient Murrelet	1	206	Seabird
Franklins Gull	1	281	Seabird
Common Murre (subadult)	38*	336	Seabird
Ring-billed Gull	1	519	Seabird
Rhinoceros Auklet	1	520	Seabird
Northern Fulmar	1	544	Seabird
American Coot	1	726	Seabird
Common Murre (adult)	25	993	Seabird
Unidentified Gull	3*	1000	Seabird
Glaucous-wing Gull	1	1010	Seabird
Western Gull	1	1011	Seabird

Table 3. Daily transition matrices for four carcass states: *Not Scavenged*, *Partially Scavenged*, *Heavily Scavenged*, and *Removed*. Each cell shows the probability that a carcass would change from one state to another over a 24 hour period. Separate matrices are given for small and large birds in the *Kure* and *New Carissa* studies.

(a) Transition matrix for small carcasses, *Kure* study.

		To			
		Not Scavenged	*Partially Scavenged*	*Heavily Scavenged*	*Removed*
From	*Not Scavenged*	0.443	0.093	0.082	0.381
	Partly Scavenged	0.000	0.737	0.105	0.158
	Heavily Scavenged	0.000	0.000	0.471	0.529
	Removed	0.000	0.000	0.000	1.000

(b) Transition matrix for large carcasses, *Kure* study.

		To			
		Not Scavenged	*Partially Scavenged*	*Heavily Scavenged*	*Removed*
From	*Not Scavenged*	0.621	0.123	0.180	0.076
	Partly Scavenged	0.000	0.571	0.333	0.095
	Heavily Scavenged	0.000	0.000	0.822	0.178
	Removed	0.000	0.000	0.000	1.000

(c) Transition matrix for small carcasses, *New Carissa* study:

		To			
		Not Scavenged	*Partially Scavenged*	*Heavily Scavenged*	*Removed*
From	*Not Scavenged*	0.427	0.214	0.214	0.146
	Partly Scavenged	0.000	0.813	0.141	0.047
	Heavily Scavenged	0.000	0.000	0.863	0.137
	Removed	0.000	0.000	0.000	1.000

(d) Transition matrix for large carcasses, *New Carissa* study:

		To			
		Not Scavenged	*Partially Scavenged*	*Heavily Scavenged*	*Removed*
From	*Not Scavenged*	0.475	0.220	0.254	0.051
	Partly Scavenged	0.000	0.655	0.172	0.172
	Heavily Scavenged	0.000	0.000	0.903	0.092
	Removed	0.000	0.000	0.000	1.000

Table 4. Censored Weibull survival models for carcass persistence. The dependent variable is the time that the carcass is removed from the beach. Positive coefficients imply longer persistence times.

(a) Survival estimates for small carcasses, *Kure* study.

VARIABLE	**COEFFICIENT**					
Non-seabirds (0/1)	-0.982					
Bird Weight (grams)	0.000					
Site Contrasts (0/1)						
	Baseline Variable					
Contrast Variable	*Mad River*	*South Spit Beach*	*South Spit Coast*	*North Spit Coast*	*Clam Beach*	*Indian Island*
Mad River		-0.958	-0.214	-0.507	-0.352	-3.455**
South Spit Beach	0.958		0.744	0.451	0.606	-2.497*
South Spit Coast	0.214	-0.744		-0.294	-0.138	-3.241**
North Spit Coast	0.507	-0.451	0.294		0.156	-2.948*
Clam Beach	0.352	-0.606	0.138	-0.156		-3.103**
Indian Island	3.455**	2.497*	3.214**	2.948*	3.103**	
Intercept	-0.179	0.779	0.035	0.328	0.173	3.276**
Dispersion (Increasing Rate < 1)	1.238					

Note: #,*,**,*** denote significance at α = 0.1, 0.05, 0.01, 0.001

(b) Survival estimates for large carcasses, *Kure* study.

VARIABLE	**COEFFICIENT**					
Non-seabirds (0/1)	-1.398***					
Bird Weight (grams)	0.000					
Site Contrasts (0/1)						
	Baseline Variable					
Contrast Variable	*Mad River*	*South Spit Beach*	*South Spit Coast*	*North Spit Coast*	*Clam Beach*	*Indian Island*
Mad River		-0.315	-0.560$^{\#}$	-0.942**	-1.364***	-1.402*
South Spit Beach	0.315		-0.245	-0.627$^{\#}$	-1.049*	-1.087
South Spit Coast	0.560	0.245		-0.383	-0.804$^{\#}$	-0.842$^{\#}$
North Spit Coast	0.942**	0.627$^{\#}$	0.383		-0.421	-0.460
Clam Beach	1.364***	1.049*	0.804$^{\#}$	0.421		-0.038
Indian Island	1.402**	1.087*	0.842$^{\#}$	0.460	0.038	
Intercept	1.620***	1.935***	2.180***	2.562***	2.984***	3.022***
Dispersion (Increasing Rate < 1)	0.698*					

Note: #,*,**,*** denote significance at α = 0.1, 0.05, 0.01, 0.001

(c) Survival estimates for small carcasses, *New Carissa* study.

VARIABLE	COEFFICIENT			
Bird Weight (grams)	0.006			
Site Contrasts (0/1)				
	Baseline Variable			
Contrast Variable	*Site 1*	*Site 2*	*Site 4*	*Site 3*
Site 1		0.378	-0.340	-0.651
Site 2	-0.378		-0.718	-1.029
Site 4	0.340	0.718		-0.311
Site 3	0.651	1.029	0.311	
Intercept	0.269	-0.109	0.609	0.920
Dispersion (Increasing Rate < 1)	1.764**			

Note: #,*,**,*** denote significance at α = 0.1, 0.05, 0.01, 0.001

(d) Survival estimates for large carcasses, *New Carissa* study.

VARIABLE	COEFFICIENT			
Bird Weight (grams)	0.010*			
Site Contrasts (0/1)				
	Baseline Variable			
Contrast Variable	*Site 1*	*Site 2*	*Site 4*	*Site 3*
Site 1		-0.921	-0.985	-1.711#
Site 2	0.921		-0.064	-0.790
Site 4	0.985	0.064		-0.726
Site 3	1.711#	0.790	0.726	
Intercept	-6.754#	-7.849	-7.784	-7.059#
Dispersion (Increasing Rate < 1)	0.836			

Note: #,*,**,*** denote significance at α = 0.1, 0.05, 0.01, 0.001

FIGURE CAPTIONS

Figure 1. The proportion of carcasses remaining on each day of the study at each sitea for the *Kure* study area around Humboldt Bay, California. Solid data points indicate small birds (<521g) and open data points denote larger birds.

Figure 2. The proportion of carcasses remaining on each day of the study at the *New Carissa* study area in Oregon. Solid data points indicate small birds (<521g) and open data points denote larger birds.

Figure 3. The proportion of carcasses remaining for each day of study at both the *Kure* and *New Carissa* study areas. Data points are averaged over all sites in each study area. Solid data points indicate small birds (<521g) and open data points denote larger birds.

Figure 1.

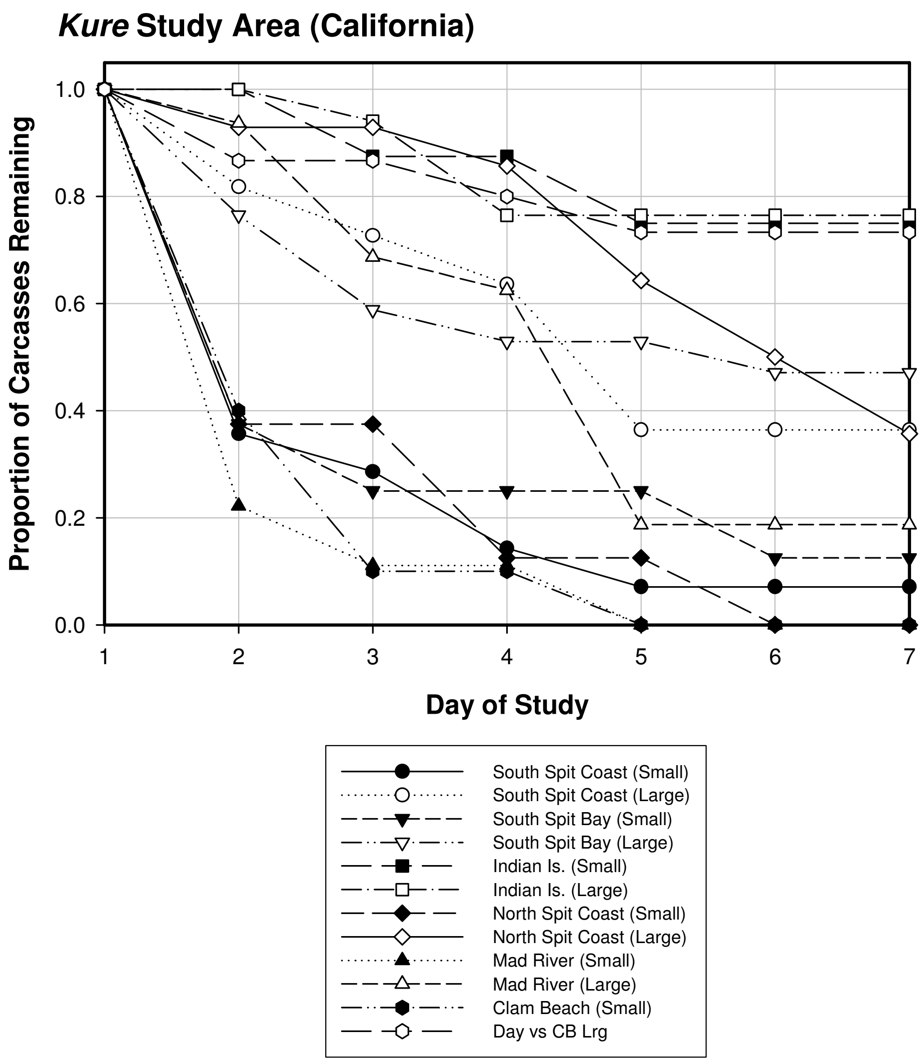

Kure Study Area (California)
Proportion of Carcasses Remaining
1.0
0.8
0.6
0.4
0.2
0.0
1
2
3
4
5
6
7
Day of Study
South Spit Coast (Small)
South Spit Coast (Large)
South Spit Bay (Small)
South Spit Bay (Large)
Indian Is. (Small)
Indian Is. (Large)
North Spit Coast (Small)
North Spit Coast (Large)
Mad River (Small)
Mad River (Large)
Clam Beach (Small)
Day vs CB Lrg

Figure 2.

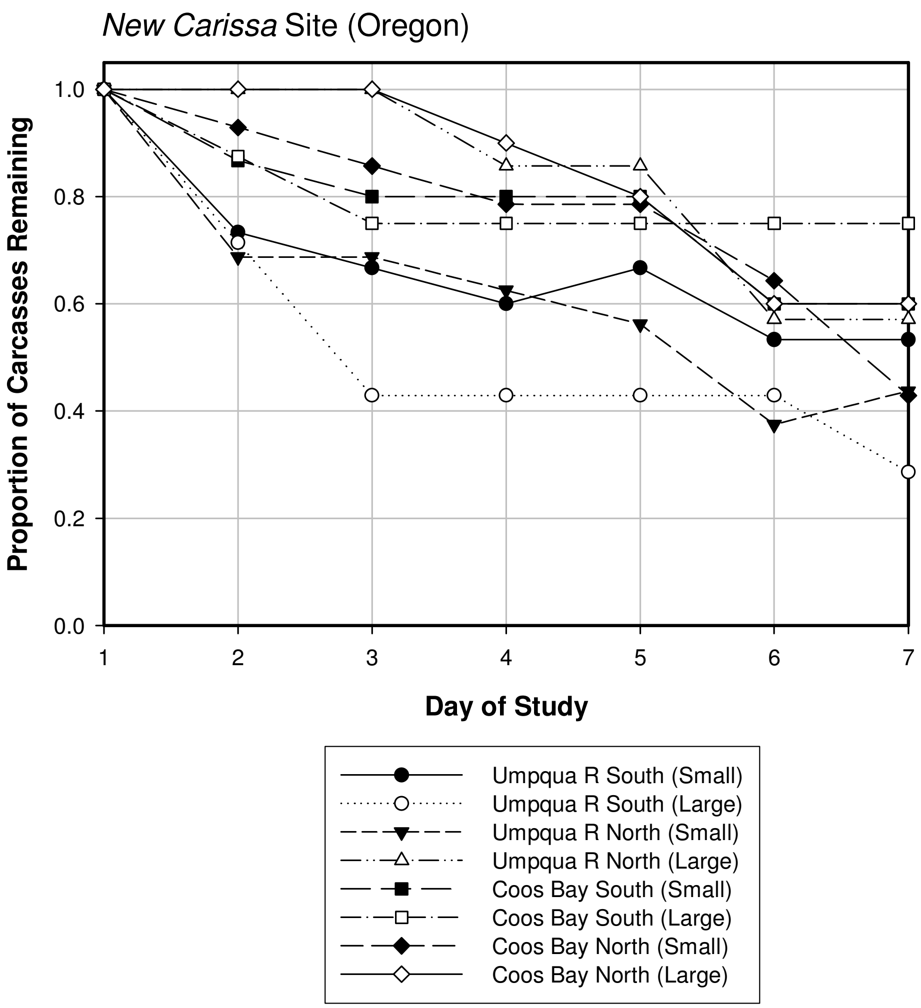
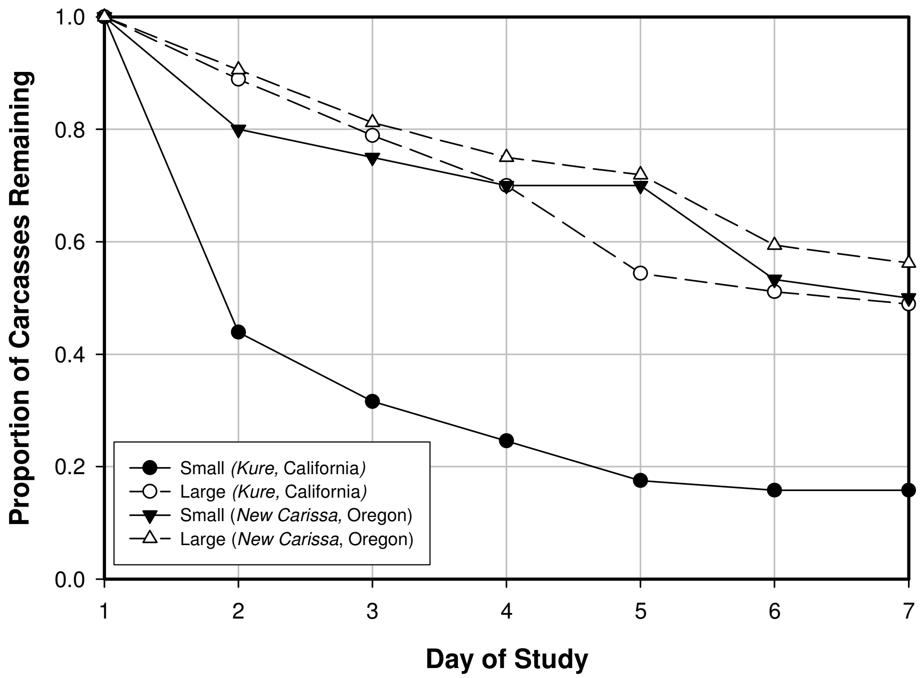

New Carissa Site (Oregon)
Proportion of Carcasses Remaining
1.0
0.8
0.6
0.4
0.2
0.0
1
2
3
4
5
6
7
Day of Study
Umpqua R South (Small)
Umpqua R South (Large)
Umpqua R North (Small)
Umpqua R North (Large)
Coos Bay South (Small)
Coos Bay South (Large)
Coos Bay North (Small)
Coos Bay North (Large)

Figure 3.


1.0
0.8
0.6
0.4
0.2
0.0
Proportion of Carcasses Remaining
Small (*Kure,* California)
Large (*Kure,* California)
Small (*New Carissa,* Oregon)
Large (*New Carissa*, Oregon)
1
2
3
4
5
6
7
Day of Study