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CORRELATIONS OF DAILY ACTIVITY WITH AVIAN CHOLERA MORTALITY AMONG WILDFOWL

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ABSTRACT: We tested the hypothesis that wildfowl activities can influence the risk of avian cholera (*Pasteurella multocida* infection) for susceptible birds at Centerville, Humboldt County, California (USA). Avian cholera mortality characteristics from past epizootics were correlated with variations in flock size, habitat use and 11 feeding and nonfeeding behaviors among six empirically defined groups of wildfowl: American coots (*Fulica americana*), tundra swans (*Cygnus columbianus*), American wigeon (*Anas americana*), northern pintails (*A. acuta*), northern shovelers (*A. clypeata*)/ mallards (*A. platyrhynchos*), and teal (*A. discors, A. crecca, A. cyanoptera*). The position of these wildfowl groups in past mortality sequences was directly correlated with mean flock size, time spent on land, and time spent grazing on land or in shallow water. We propose that variations in bird density, habitat use and frequency of grazing may serve as predisposing factors to avian cholera among wildfowl.

Key words: American coots, *Anas* spp., avian cholera, behavioral ecology, *Cygnus columbianus*, epizootiology, *Fulica americana*, tundra swans.

INTRODUCTION

Avian cholera, caused by the bacterium *Pasteurella multocida*, annually kills thousands of wildfowl throughout North America (Rosen, 1971). While annual losses among affected species are well documented (Titche, 1979; Friend, 1987), little is known about the factors initiating the disease or facilitating its transmission in wildfowl.

Since 1945, seven avian cholera epizootics were confirmed and three more suspected at Centerville, Humboldt County, California (USA) (Titche, 1979; R. G. Botzler, unpubl. data). None have been reported since 1979. Based on evaluations of the January 1977 and January 1978 epizootics, two distinctive features were documented among affected wildfowl. A sequence in species mortality was observed. American coot (*Fulica americana*) mortality started and reached a peak early in the epizootics, followed by swans and American wigeon (*Anas americana*), northern pintails (*A. acuta*), northern shovelers (*A. clypeata*), mallards (*A. platyrhynchos*), and teal (*A. discors, A. crecca, A. cyanoptera*), respectively (Oddo et al., 1978; Mensik and Botzler, 1989). Secondly, coots suffered disproportionately high mortality. Coots composed 80 to 85% of the mortality, but only 45 to 55% of the wildfowl use on this site; in contrast, other wildfowl generally died at lower frequencies than predicted from their use of the area (Oddo et al., 1978; Mensik and Botzler, 1989).

Rosen (1969) observed that the extent of avian cholera mortality among tundra swans (*Cygnus columbianus*) had no statistical relation to their live populations over a 13-yr period, and hypothesized that avian cholera functioned in a density-independent fashion. We predicted that if Rosen (1969) was correct, there would be no relation between wildfowl densities and (a) their position in the mortality sequence or (b) the occurrence of disproportionate mortality.

While there are many studies on wildlife habitat use and behavior (Delacour and Mayr, 1945; Johnsgard, 1965, 1975; Bellrose, 1980), no one has assessed variation in behavior and habitat use of several species of wildfowl at a single site, in relation to their susceptibility to avian cholera. Rosen (1969) proposed that variation in susceptibility to avian cholera among wildfowl could be due to differences in habitat use or behavior. If Rosen (1969) was correct, we predicted there would be consistent behavioral differences among species that died early in avian cholera epizootics or had disproportionately high mortality, compared with other wildfowl. Because water is a likely medium for transmitting pasteurellae, we expect that birds dying early or which suffered disproportionate mortality would have different feeding behaviors than other wildfowl.

During past avian cholera epizootics at Centerville, we observed the greatest concentrations of carcasses in shallow water along mudflats and shorelines, partly in response to prevailing winds. Thus, we expected that wildfowl spending the most time in shallow water would receive the greatest exposure to *P. multocida* during epizootics. If this hypothesis was correct, we predicted the groups that died early and suffered disproportionately high mortality would be the ones spending the most time in shallow water.

Our objectives were to determine whether differences in flock size, habitat use and behavior among wildfowl at Centerville were correlated with their position in the sequence of mortality, or were related to the high disproportionate mortality from avian cholera among coots. An absence of correlations would conflict with the hypothesis that wildfowl activities influence the risk of avian cholera for susceptible birds.

STUDY AREA

The study was conducted at Centerville, 26 km southwest of Eureka, Humboldt County, California 40°30′N, 124°10′W). Two seasonal ponds (Ponds One and Two), approximately 3.9 and 5.5 ha, respectively, were separated from the Pacific Ocean by a 700-m strip of pasturelands and coastal dunes. Dominant vegetation included *Juncus* sp., *Rumex* sp., *Rubus* sp., *Scirpus* sp., *Potamogeton* sp., *Ruppia* sp., *Lemna* sp., and assorted Gramineae (Combs, 1988). Maximum water depths ranged up to 0.5 m in Pond One and 1.2 m in Pond Two. The area was grazed by cattle and sheep from February to October each year. From October through January, hunting rights were leased to a local hunting club. Additional information about this site is provided by Combs (1988).

Wildfowl generally begin to arrive at Centerville from late October to mid-November each year, and have departed by early March (Combs, 1988; R. G. Botzler, unpubl. data). Specific population characteristics for the years of this study are summarized by Combs (1988). The wildfowl evaluated in this study are present each year and have regularly died from avian cholera at Centerville.

MATERIALS AND METHODS

The ponds and adjacent land area were divided into 76 observation units to facilitate locating birds on the study site (Combs, 1988). Sizes and shapes of these units were determined by natural boundaries of shoreline, and water depth (≤ 0.15 m, >0.15 m). Mean area of units was 1855 m^2 (SE = 215); median size was 1,470 m^2.

Based on their positions in the mortality sequence, six wildfowl groups were empirically defined: coots, wigeon, swans, pintails, shoveler/mallards, and teal. Observations were limited to daylight hours (0600–1800) on non-hunting days, October through March, 1982–83 and 1983–84. Four scans (Altmann, 1974) were made every hour each day. A scan to determine the flock size of each wildfowl group within each of the 76 observation units of the site was made 15 min before the hour. At Pond Two, bird locations also were categorized as deep water (pond locations >0.15 m deep), shallow water (pond locations ≤ 0.15 m), and land (land surface adjacent to the pond). The location and behavior of individual coots were recorded on scans every half hour. Scans of all other wildfowl were made 15 min past each hour. All behavioral surveys were done with a 36× spotting scope mounted on a 1.5-m ladder located 75 m north of the ponds.

Eleven behaviors were defined: (a) grazing or ripping off tops of vegetation on land area or in shallow water; (b) dipping or feeding with the head and neck underwater but with the body horizontal on the water surface; (c) tipping or feeding with the body perpendicular to the water surface, and only the feet and tail visible; (d) gleaning or skimming the water surface with the bill; (e) preening or cleaning feathers with the bill, (f) bathing; (g) swimming; (h) walking; (i) taking-off; (j) landing; and (k) inactive such as roosting, loafing, or motionless on water or land.

The Statistical Package for the Social Sciences (SPSS) software (Nie et al., 1975; Hull and Nie, 1981) was used for statistical analyses. Standard nonparametric analyses (Zar, 1974) were used to test differences in wildfowl habitat use and behaviors between wildlife groups, and com-

TABLE 1. Average flock size maintained by six wildfowl groups on the Centerville Ponds, Humboldt County, California, October to March 1982–83, 1983–84.

	Ranking of sequential avian cholera mortality[a]					
	1 Coots	2.5 Swans	2.5 Wigeon	4 Pintails	5 Shoveler/mallards	6 Teal
Mean flock Size per observation Unit[b]	20.7	28.7	19.1	9.4	6.2	6.3

[a] Ranking based on Oddo et al. (1978) and Mensik and (Botzler (1989). Those dying first in the epizootics have a rank of "1"; those with a rank of "6" died last. Since the peak mortality of swans has occurred both before and after wigeon mortality, both species received a rank of "2.5."

[b] Means based on observation units with at least one bird, for each respective wildfowl group.

pare species mortality from past epizootics to variation in flock size, habitat use, and behavior. Behaviors and locations were ranked and compared using Mann-Whitney U-tests for two independent samples, and Kruskal-Wallis tests for three or more independent samples. For both species and behavior, the unit of replication was days, with a pooling of grid units and time of day. Both tests were weighted for unequal sample sizes and corrected for ties within SPSS. Due to large sample sizes, the Mann-Whitney U-statistic was transformed into a normally distributed Z statistic. When Kruskal-Wallis test results indicated significant differences between samples, nonparametric multiple comparisons similar to Newman-Keuls, but which use rank sums instead of rank means, were used to determine which samples were significantly different from each other (Zar, 1974). The significance level for these tests was set at $\alpha = 0.05$.

Hypotheses of correlations between position in the mortality sequence of past epizootics and differences in flock size and behavior were tested using Spearman's rank correlation test (Zar, 1974). Mortality rankings varied from 1 (coots) to 6 (teal). Because peak wigeon mortality occurred both before (Oddo et al., 1978) and after (Mensik and Botzler, 1989) that of swans, both species were assigned a rank of 2.5. Exact probabilities were calculated for all correlations.

RESULTS

Swans had the highest mean flock size, followed by coots, wigeon, pintails, teal, and shoveler/mallards, respectively (Table 1). Ranking of mean flock size was directly correlated ($r = 0.84$, $P = 0.036$) to the position of these species in the mortality sequence of past epizootics (Oddo et al., 1978; Mensik and Botzler, 1989). The relationship between flock size and the high disproportionate mortality among coots in past epizootics was less clear. Coots had the second highest mean flock size. But swans had the highest mean flock size, despite not having had disproportionately high mortality at Centerville.

Coots, wigeon and swans used land significantly more than did pintails, shoveler/mallards and teal (Table 2). The position of wildfowl in the mortality sequence was

TABLE 2. Percentage of total time birds were observed on three habitats of Pond Two, Centerville, Humboldt County, California, October to March 1982–83 and 1983–84.

	Coots $n = 32,108$[a]	Wigeon $n = 4,231$	Swans $n = 1,040$	Pintails $n = 3,149$	Shoveler/Mallards $n = 2,659$	Teal $n = 979$
Land area	21.9	28.8	39.6	3.8	2.0	6.4
Shallow water (≤0.15 m)	39.0	40.7	11.4	57.6	31.0	48.9
Deep water (>0.15 m)	39.1	30.5	49.0	38.6	67.0	44.7

[a] Number of observations made for each group.

weakly correlated with their ranking of time spent on land ($r = 0.75$, $P = 0.084$). There was no evident relationship between high disproportionate mortality among coots during past epizootics, and differences in time spent on land between coots and the other wildfowl groups in this study.

We recorded 62,460 behavioral acts among wildfowl (Table 3). Coots spent significantly more time grazing (73.0%) than all other activities combined (Table 3), and grazed more frequently than other waterfowl (Tables 3, 4). Swimming (11.5%) was the next most frequent behavior for coots. The remaining nine behaviors accounted for only 15.5% of coot sightings (Table 3). Coots exhibited significantly less inactivity than any other wildfowl group (Tables 3, 4).

Overall, coots and wigeon had some similarities in behaviors (Table 3). Like coots, wigeon spent significantly more time grazing (62.3%) than all other behaviors combined (Tables 3), and swimming also was the second most common behavior observed. The position of wildfowl in the mortality sequence of past epizootics was directly correlated ($r = 0.93$, $P = 0.008$) to the rank order of their grazing frequency (Table 4).

DISCUSSION

This was an exploratory study designed to test hypotheses about the possible roles of wildfowl density, habitat use and behavior, as predisposing factors to avian cholera. In themselves, correlations are not adequate to establish cause and effect relationships. Rather, correlation patterns were used to test these hypotheses.

The position of wildfowl in the mortality sequence of past epizootics at Centerville was directly correlated to their mean flock size, time spent on land, and frequency of grazing on land and shallow water.

The observation that species with large flock sizes died earlier in avian cholera epizootics conflicted with the hypothesis that avian cholera operates in a density-independent fashion. Finding evidence for a density-dependent relationship is not surprising, however, since high densities facilitate the transmission of avian cholera through domestic bird populations (Van Es and Olney, 1940).

Correlation of position in the mortality sequence with time spent on land was unexpected. Because most carcasses occur in shallow water, we assumed the greatest exposure to infection would occur there. Thus, we expected that time spent in shallow water would be better correlated with avian cholera mortality than time spent on land. Perhaps pasteurellae originating from carcasses on land are not subject to dilution, and are transmitted in a more concentrated dose to birds grazing or scavenging on land. Coots have been observed scavenging on carcasses during avian cholera epizootics (Paullin, 1987). It also is possible that the correlation to time spent on land was confounded by flock size; rank of flock size for each wildfowl group was directly correlated to rank of time spent on land ($r = 0.89$, $P = 0.019$).

Our behavioral observations (Tables 3, 4) were consistent with earlier reports on wildfowl behavior (Johnsgard, 1965, 1975; Bellrose, 1980). Because bacteria tend to concentrate near the surface of the water (Potter and Baker, 1961; Potter, 1964), birds grazing at the surface would be exposed regularly to *P. multocida* in water during an avian cholera epizootic. In contrast, birds ingesting food or water below the surface, such as dippers and tippers, would be expected to receive less exposure to bacteria on the water surface.

Several factors added uncertainty to these findings. One important factor is that avian cholera did not occur during this study; thus, mortality patterns from one set of years were compared to wildfowl activities observed during a second set of years. However, the major variation between years appears to be weather, and Combs (1988) noted that weather had a minimal impact on wildfowl activity. We assumed that the observations of these two

TABLE 3. Ranking of behaviors from highest to lowest frequencies, for wildfowl groups at Centerville, Humboldt County, California, October to March 1982–83, 1983–84. Frequencies for behaviors underlined with the same line were not significantly different, based on the Kruskal-Wallis and multiple rank comparison tests.

Species	Behaviors									
Coots	73.0[a]	11.5	5.6	3.6	2.9	1.6	0.6	0.6	0.3	0.3	0
(n = 47,499[b])	Graze	Swim	Dip	Preen	Tip	Inactive	Walk	Take-off	Land	Bathe	Glean
Wigeon	62.3	16.6	13.4	2.6	2.3	1.3	1.1	0.2	0.2	<0.1	0
(n = 4,975)	Graze	Swim	Inactive	Take-off	Preen	Dip	Land	Tip	Bathe	Walk	Glean
Swans	41.1	17.1	16.7	12.9	8.8	2.7	0.4	0.3	0	0	0
(n = 1,348)	Inactive	Graze	Preen	Swim	Walk	Dip	Take-off	Bathe	Glean	Tip	Land
Pintails	38.6	28.3	12.6	8.7	5.3	4.2	0.9	0.6	0.5	0.4	<0.1
(n = 4,319)	Dip	Inactive	Swim	Preen	Tip	Graze	Walk	Take-off	Land	Bathe	Glean
Shoveler/mallards	41.2	16.0	15.0	14.1	7.6	3.6	0.9	0.8	0.4	0.4	0
(n = 3,116)	Dip	Tip	Swim	Inactive	Preen	Take-off	Land	Glean	Graze	Bathe	Walk
Teal	42.1	33.2	10.8	4.8	3.3	3.1	1.2	0.6	0.5	0.2	0.1
(n = 4,319)	Swim	Inactive	Dip	Tip	Preen	Graze	Walk	Bathe	Land	Glean	Take-off

[a] Percent of this behavior among all behaviors recorded for a species.
[b] Number of observations made for each species.

TABLE 4. Ranking of each wildfowl group by the frequency with which they exhibited a particular behavior (Table 3), October to March 1982–83, 1983–84, Centerville, Humboldt County, California. Species underlined with the same line were not significantly different in ranking, based on Kruskal-Wallis and multiple rank comparison tests.

Behavior	Wildfowl species (Highest frequency)					(Lowest frequency)
Graze	Coots	Wigeon	Swans	Pintails	Teal	Shoveler/mallards
Dip	Shoveler/mallards	Pintails	Teal	Coots	Swans	Wigeon
Tip	Shoveler/mallards	Pintails	Teal	Coots	Wigeon	Swans
Glean	Shoveler/mallards	Teal	Pintails	Coots	Wigeon	Swans
Preen	Swans	Pintails	Shoveler/mallards	Coots	Teal	Wigeon
Bathe	Teal	Pintails	Shoveler/mallards	Coots	Swans	Wigeon
Swim	Teal	Wigeon	Shoveler/mallards	Swans	Pintails	Coots
Walk	Swans	Teal	Pintails	Coots	Wigeon	Shoveler/mallards
Take-off	Shoveler/mallards	Wigeon	Coots	Pintails	Swans	Teal
Land	Wigeon	Shoveler/mallards	Pintails	Teal	Coots	Swans
Inactive	Swans	Teal	Pintails	Shoveler/mallards	Wigeon	Coots

years were representative of wildfowl activities both for years with and without avian cholera. Secondly, comparable nighttime observations were not made, and some activities could vary at night. We assumed that feeding strategies (e.g., grazing versus gleaning) did not vary between day and night, but our findings generally must be considered as day-time observations. Thirdly, it could be argued that species differences in physiological susceptibility to *P. multocida* account for the past mortality patterns. We do not dispute that physiology may play an important role in susceptibility to *P. multocida*; rather we suggest that wildfowl activities also may influence susceptibility. Determining the respective roles of physiology and behavior in susceptibility to *P. multocida* is an important problem that has yet to be adequately addressed. Finally, no distinction was made between the activities of various sex and age classes within each wildfowl group. Mensik and Botzler (1989) found no differential mortality from avian cholera by sex or age among coots. We assumed that the activities assessed did not vary significantly among sex and age classes within each wildfowl group, during the study period at Centerville.

The disproportionately high mortality reported among coots in past epizootics is not clearly related to any distinctive feature of coot behavior, habitat use of density. However, coots grazed more than any other species, and a high frequency of grazing in shallow water or land may expose them to large doses of pasteurellae originating from carcasses once an epizootic starts. Besides a high frequency of grazing, the take-off behavior of coots also may contribute to their high disproportionate mortality. Coots usually left the ponds en masse by running along the surface. In contrast, other species usually departed singly and lifted almost vertically into the air. The take-off of coot rafts caused substantial air and water displacement and could produce a bacteria-rich aerosol. Many wildfowl, including coots, are susceptible to *P. multocida* through aerosol inoculation (Titche, 1979). Coots also may be physiologically more susceptible to *P. multocida* than other wildfowl groups.

Overall, there is little information on the biological and environmental factors triggering avian cholera epizootics, or in accounting for differences in observed mortality among wildfowl. Variation in physiology undoubtedly affects the susceptibility of wildfowl to avian cholera. Based on our findings we propose that differences in wildfowl densities, land use, and frequency of grazing also may affect the risk of acquiring avian cholera among wildfowl. We believe that the possible role of daily activities as predisposing factors to avian cholera is a fruitful topic to explore more fully in developing a management model for avian cholera in wildfowl.

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