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Where Has All the Road Kill Gone?

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An estimated 80 million birds are killed by colliding with vehicles on U. S. roads each year [1], and millions more die annually in Europe [2] and elsewhere. Losses to vehicles are a serious problem for which various changes in roadway design and maintenance have been proposed [3]. Yet, given the magnitude of the mortality reported for some species [4], we might expect natural selection to favor individuals that either learn to avoid cars or that have other traits making them less likely to collide with vehicles. If so, the frequency of road kill should decline over time. No information is available for any species on whether the extent of road-associated mortality has changed [2]. During a 30-year study on social behavior and coloniality of cliff swallows (*Petrochelidon pyrrhonota*) in southwestern Nebraska, we found that the frequency of road-killed swallows declined sharply over the 30 years following the birds' occupancy of roadside nesting sites and that birds killed on roads had longer wings than the population at large.

We have worked on cliff swallows since 1982 in southwestern Nebraska, centered in Keith County at the Cedar Point Biological Station (41°12.591′ N, 101°38.969′ W), where colonially nesting cliff swallows attach their gourd-shaped mud nests in clusters on a vertical wall underneath a horizontal overhang. The birds use primarily highway bridges, overpasses, and box-shaped concrete culverts underneath roads or railroad tracks as colony sites [5].

As we traveled among colonies daily in the course of our research, we stopped for each road-killed cliff swallow. We made the same effort to search for road kills and drove the same roads each year. We based our count of road kill retrospectively on the number of

specimens prepared as skins and assume that the number salvageable provides a relative measure of mortality among years. We compared road kills to a sample of cliff swallows accidentally killed during mist-netting in the same years. The net fatalities (hereafter considered "the population at large") did not differ from living birds caught at the same time (supplemental information).

The number of salvageable specimens each year declined significantly from 1983 to 2012 (fig. 1A). This result could not be explained by concurrent decreases in the cliff swallow population size around roads because the population increased over the 30-year period (fig. 1A). The decline in road kills also could not be related to increases in the number of avian scavengers over time, as none showed significant increases in our study area (supplemental information). Direct information is not available for mammalian scavengers within the study area, although populations of those species associated with humans probably have not changed, given that the resident human population of Keith County varied little during the study. Also, scavengers such as skunks have declined for the state of Nebraska as a whole [6]. Road-kill trends did not result from reduced vehicle traffic volume over time, which either did not change significantly or increased, depending on the metric used (supplemental information). Sport-utility vehicles, which have probably increased during our study and offer a greater surface area for collision (relative to sedans that were more common in the 1980s), might contribute to changing bird mortality. However, road kill decreased as the larger vehicles became more common. Differences in detection likelihood did not affect our results, as the total kilometers traveled by us annually did not change significantly (supplemental information). Thus, none of the obvious factors that confound most road-kill surveys applied to our study.

Wing length of road-killed cliff swallows was significantly longer than in the population at large (fig. 1B). Over time, wing lengths of cliff swallows killed on roads increasingly diverged from that of the population at large (fig. 1C). Average wing length of the population as a whole exhibited a significant long-term decline during the years of the study, whereas the opposite pattern held for the birds killed on roads (fig. 1C).

Cliff swallows now commonly nest on highway bridges, overpasses, and road culverts [5]. The Breeding Bird Survey that began in our study area in 1967 (fig. 1D) showed that these birds likely began commonly encountering vehicles when they started frequently using roadside nesting sites in the early to mid-1980s at about the time our research commenced, probably in response to construction of more bridges and culverts. Our results indicate that these birds since then have become increasingly less likely to collide with cars and that road mortality is not indiscriminate. One possible explanation is that selection has favored individuals whose wing morphology allows for better escape. Longer wings have lower wing loading and do not allow as vertical a take-off as shorter, more rounded wings [7]. Thus, individuals sitting on a road, as cliff swallows often do, who are able to fly upward more vertically may be better able to avoid or more effectively pivot away from an oncoming vehicle [8].

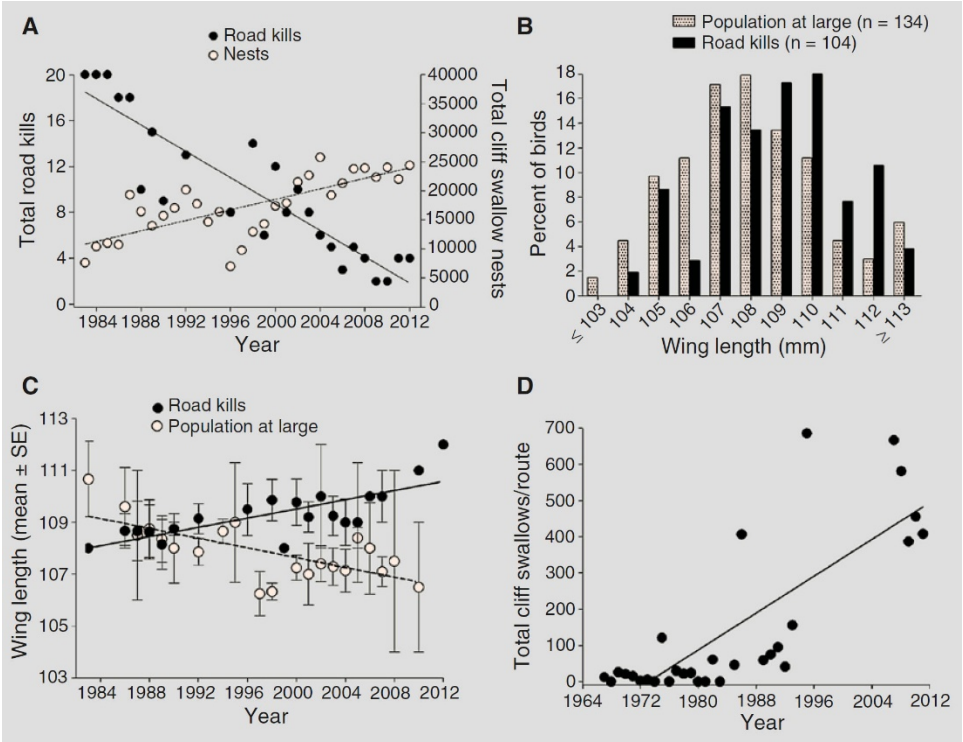

Figure 1. Changes in number and wing length of road-killed cliff swallows. Road-killed cliff swallows in southwestern Nebraska have declined with time and constitute a disproportionately greater fraction of longer-winged birds in the years following the birds' occupancy of roadside colony sites. (A) The number of salvageable road kills (closed circles, solid line) declined significantly with time ($r_s = 0.93$, $p < 0.0001$, $n = 25$ years) despite the population size around roads (open circles, dotted line) increasing over the study period ($r_s = 0.76$, $p < 0.0001$, $n = 30$ years), with year being a significant predictor of the number of road kills found ($F_{1,22} = 38.8$, $p < 0.0001$, GLM) but not population size ($F_{1,22} = 0.01$, $p = 0.93$); (B) wing lengths for birds killed on roads (dark bars) versus the population at large (as represented by mist-net fatalities; shaded bars) were significantly different ($F_{1,229} = 7.06$, $p = 0.007$, ANCOVA); (C) mean wing length (± SE) for cliff swallows killed on roads (closed circles, solid line) increased significantly over time ($r_s = 0.78$, $p < 0.0001$, $n = 20$ years), while that of the population at large (open circles, dotted line) decreased significantly over time ($r_s = 0.63$, $p = 0.002$, $n = 21$); (D) total cliff swallows reported on a Breeding Bird Survey in Keith County, Nebraska, per year 1967–2011 indicate that the species began commonly encountering vehicles at about the time this study commenced. Lines indicate best-fit least-squares regression.

Vehicle mortality is likely to be not the only factor contributing to the decline in wing length in this population over time; severe weather events that cause selection on body morphology and changes in insect prey may also be responsible [9]. Other explanations for the reduction in road kill are that swallows may learn to avoid collisions as they encounter a vehicle themselves or observe other birds flying away from vehicles or getting hit, or that risk-taking individuals have been selectively removed [10]. We cannot directly

evaluate these hypotheses, although if individuals are likely to avoid cars after a close encounter, we would expect younger birds to be overrepresented among the road kills, which they were not (supplemental information). Cliff swallows do exhibit social learning in other contexts, such as by observing the foraging success of neighbors [5]. Regardless of mechanism, the drop in traffic-related mortality over 30 years suggests that researchers should consider the possibility that road mortality in other species may change temporally and exert selection.

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Supplemental Information

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Supplemental Results

Factors Potentially Affecting Road Kills

Based on data from the BBS route within the study area from 1983–2011, populations of neither turkey vultures (r_s = 0.31, P = 0.27, n = 14 years), Swainson's hawks (r_s = 0.05, P = 0.85, n = 14 years), nor the two corvid species combined (r_s = 0.32, P = 0.26, n = 14 years) changed significantly over the years of the study. American crows are uncommon and seldom breed in the study area, and both Swainson's hawks and black-billed magpies have been declining in southwestern Nebraska since the 1990's [S1]. Turkey vultures are abundant in the study area but seldom feed on small bird carcasses [S2]. The human population of Keith County varied little during this study (1980 population; 9364; 1990, 8584; 2000, 8875; 2010, 8368; U.S. Census Bureau), suggesting that dogs, cats, and other mammalian scavengers associated with humans likely did not change during the 1983–2011 period.

Human visitation to Lake McConaughy did not change significantly for Memorial Day weekends (Figure S1a) and increased over the period of the study for July 4th weekends (Figure S1a) and for total annual visitation (Figure S1b). The type of vehicle commonly found on roads in the study area may have changed with time. Sport-utility vehicles first entered the North American automobile market in force in about 1983 (when our study began), with sharp annual increases in the numbers of these vehicles sold beginning in about 1991 and continuing each year [S3]; no specific information on vehicle type is available for the study area *per se*. Total kilometers traveled by us annually (and thus our opportunity to

detect road kill) did not change significantly with time (Figure S1c), with a trend for our travel to be lower in the earlier years of the study when the most road kill was found.

Phenotypic Characteristics of Road Kills

In comparing road-killed adult cliff swallows (n = 104) with a sample of the population at large (accidental mist-netting fatalities) in the same years (n = 134), only method of collection influenced wing length; sex ($F_{1,229}$ = 0.00, p = 0.99, ANCOVA) and relative age ($F_{1,229}$ = 2.56, p = 0.11) had no effect on wing length for the specimens used in this analysis, nor were there any significant interactions among these variables. The percentage of males among adult road kills (52%) did not differ from the percentage in the population at large (56%; χ^2_1 = 0.33, p = 0.57), and mean (± SE) age of adult road kills (1.63 ± 0.13 years) did not differ from that of the population at large (1.69 ± 0.11 years, Wilcoxon test, p = 0.94).

Supplemental Methods

Study area

Cliff swallow colonies in our study area range from 1 to 6000 nests (mean ± SE, 404 ± 13, n = 2318 colonies). The birds are migratory, arriving in our study area in late April through mid-May, and most have departed for their South American wintering grounds by late July. The overall cliff swallow habitat within the study area remained essentially unchanged throughout this study. With no increase in the human population during this time, there was no change in landscape urbanization over the 30 years of our study. Additional cliff swallow nesting sites (bridges, culverts) were constructed during the study, and the birds' occupancy of these sites is reflected in the increases in breeding population size estimated for each year. Most of the new colony sites were created through replacement of existing wooden structures.

Collection of Road Kill

Virtually all of our cliff swallow research over the 30 years involved frequent visits to different colony sites in the study area, usually visiting multiple ones each day. In addition, we frequently passed by sites

at which we were not working that day. As we traveled among these colonies daily, we continually searched for road kills. Specimens came from roads in our main study area from roughly Paxton to Oshkosh, Nebraska, and primarily during the months of May, June, and July (the period when cliff swallows are present in the study area). Roads surveyed were two-lane U.S. or state highways, paved county roads, dirt county roads, or dirt roads maintained by the Nebraska Public Power District. No roads changed status during the 30 years (e.g., 2 lanes to 4 lanes, dirt to paved), nor were any new roads built or roads closed. Interstate 80 in the study area did not allow stopping for road kill and was not surveyed. The same observers (C.R.B., M.B.B.) were responsible for collecting road kill each year. The number of salvageable specimens varied from 2 to 20 per year. Those salvaged represented 15-20% of the total carcasses found, based on data from 2009-2011 only (information not available for other years). All salvageable road kills were prepared as museum skins and are housed in the University of Tulsa bird collection and, for 1984 and 1985, at the American Museum of Natural History and Yale University's Peabody Museum of Natural History, respectively. Some years lacked data because specimens were donated elsewhere or destroyed in the process of testing the carcasses for arboviruses.

To determine whether the extent of our travel in the study area might have changed over time and thus accounted for differences in observed road kill, we compiled mileage totals each year by accessing annual financial accounting as required by our institutions and/or funding agencies. We used only mileage accumulated in the actual study area. Financial records for some years were missing.

Vehicle Traffic Estimation

Given the low and temporally unchanging human population size of Keith County, annual variation in traffic within the study area is primarily associated with visitation to Lake McConaughy, the premier recreational destination of western Nebraska and situated in the center of our study area. To track general vehicular traffic across time, we used two measures: reported number of visitors during the Memorial Day and July 4th holidays each year, and total annual visitation, to the Lake McConaughy State Recreation Area. Holiday visitor totals were extracted from information provided by the Nebraska Game and Parks

Commission (the agency that administers the state recreation area) as reported in issues of the local newspaper, the *Keith County News* (data for some years were missing). The Memorial Day and July 4th holidays occur during the cliff swallow's breeding season in our study area, and thus are appropriate times for traffic estimation and the only specific dates for which long-term visitation data could be reconstructed. Total annual visitation came from information available on the Nebraska Department of Economic Development's web site (www.neded.org/business/data-a-research/tourism-recreation) but was not available prior to 1993. Annual differences in visitation reflect weather conditions, lake levels, and prohibition (in about 1989) of alcohol on the lake's beaches.

Population Size and Breeding Bird Survey

We summed the annual colony sizes (number of nests) for each colony site in our main study area each year, and used this sum as our measure of cliff swallow population size. We excluded from this tabulation any colonies not near roads (e.g., colonies on natural cliff faces along Lake McConaughy) and ones not visited by us at least twice in a season. Field methods for determining colony sizes [S4] were the same each year, and a single observer (C.R.B.) used the same methods each year of the study.

For information on avian scavenger numbers and historical presence of cliff swallows in the study area, we relied on the U. S. Geological Survey's Breeding Bird Survey (BBS) route 54020 that ran through the center of the study area. This route passed near currently occupied cliff swallow colony sites. Surveys on this route began in 1967 and continued to the present (by different observers) using standard BBS methodology [S5], with gaps for some years. The route was the same, and observers stopped at the same points, each year. We tabulated the total turkey vultures (*Cathartes aura*), Swainson's hawks (*Buteo swainsonii*), American crows (*Corvus brachyrhyncos*), and black-billed magpies (*Pica hudsonia*) reported each year as an annual index of avian scavengers. A single Swainson's hawk (probably the same individual) was observed scavenging cliff swallow road kill [S6], while vultures and the two corvids were potential scavengers of swallow-sized carcasses (although never seen to take a dead cliff swallow on a road in our study). The total cliff swallows recorded on the route each year was used as an index of the

species' historical occurrence in the study area. BBS data are available online (www.pwrc.usgs.gov/bbs/results/).

Wing Measurements, Determining Sex and Age, Designating Population at Large

Wing length was measured on museum specimens with a stoppered wing ruler, expressed as the distance from the wrist joint to the longest (un-flattened) primary. Only the right wing was measured, and the same person (C.R.B.) measured all specimens. Only adult specimens were included in wing-length analyses, because wing length in juveniles continues to grow for an undetermined time after fledging [S7]. Sex was based on dissection at the time of skin preparation. Age for those measured was a relative index, expressed as years since first banded, and was appropriate for comparing relative age of road kills versus the population at large. Relative age was denoted as "1" for unbanded birds or ones first banded that year, "2" for birds banded the previous year, etc. All adult specimens used for wing measurements and sex and age determinations were those from the University of Tulsa; those donated to other institutions (from 1984 and 1985) were not measured.

Specimens noted as having died during mist-netting were considered a sample of the population at large. Usually net fatalities occurred when a bird accidentally choked when the mesh around it was pulled tight by the presence of other birds in the net, when a net pole inadvertently fell over, or a bird died in a holding bag for unknown reasons. There was no evidence that these accidental netting deaths were more likely to occur among birds with certain phenotypic characteristics. For example, the sample of net fatalities (n =134) did not differ significantly from all other birds (n =4104) caught at the same time at the same sites in body mass (Z = 1.16, P = 0.25, Wilcoxon test), relative age (also a measure of whether they had been previously banded; see above; Z = 0.98, P = 0.33), or sex ratio (χ^2_1 = 1.05, p = 0.30). In addition, in the years 1997–2006 when wing lengths of live birds caught in nets were measured, a decline in wing length among those individuals [S8] matched that of the net fatalities reported here (Figure 1c).

Thus, net fatalities were representative of the population at large, at least as measured by characteristics of mist-netted birds.

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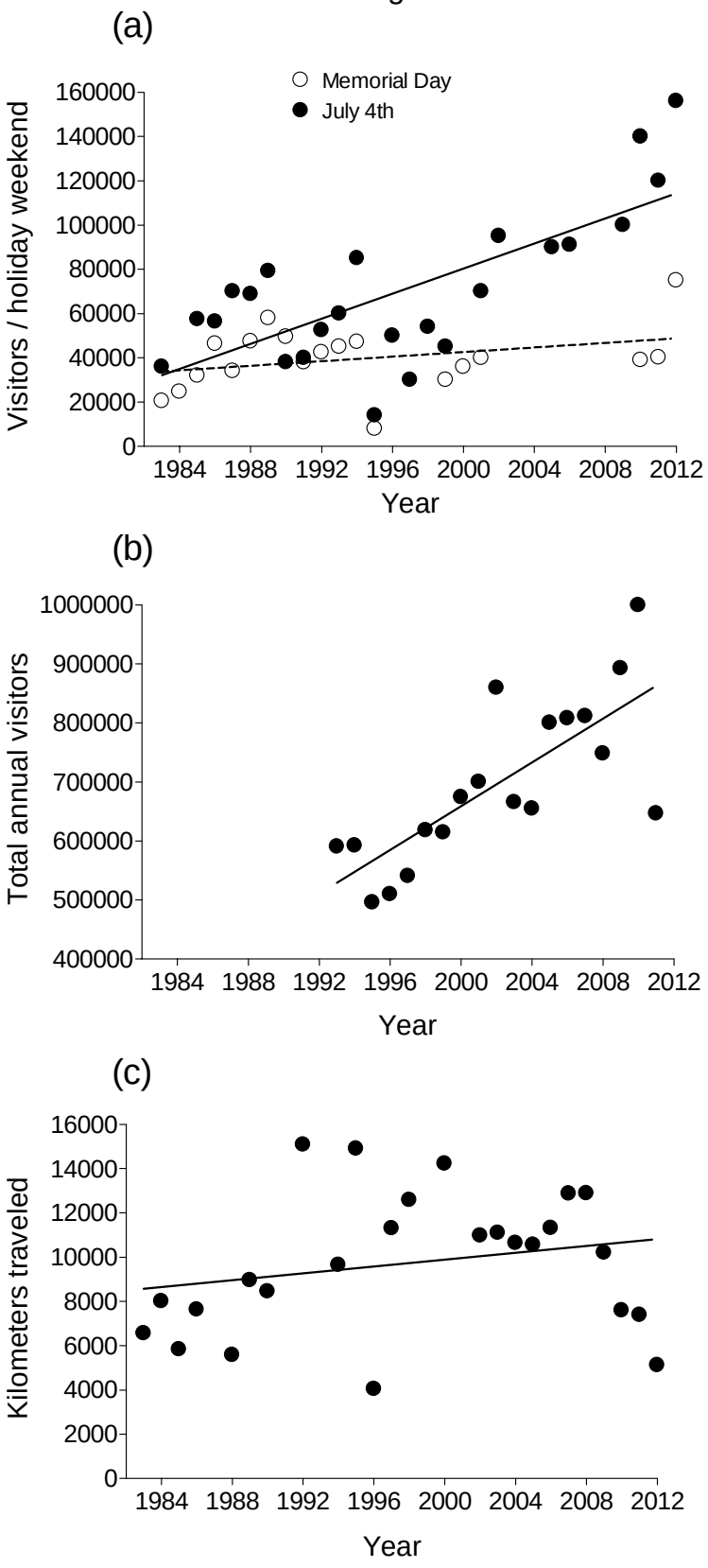
Figure S1

(a) Human visitors to Nebraska's Lake McConaughy per holiday weekend, as a measure of traffic volume, did not change significantly over time for Memorial Day (open circles, dotted line; $r_s = 0.22$, $p = 0.35$, $n = 19$ years) but increased significantly for July 4th (closed circles, solid line; $r_s = 0.59$, $p < 0.0001$, $n = 24$); (b) total annual human visitors to Lake McConaughy increased significantly over time ($r_s = 0.79$, $p < 0.0001$, $n = 19$); (c) kilometers traveled by researchers in the study area each year, as a measure of effort at detecting road killed cliff swallows, did not vary significantly over time ($r_s = 0.19$, $P = 0.35$, $n = 25$). Lines indicate best-fit least-squares regression.

Figure S1


(a)
Memorial Day
July 4th
Visitors / holiday weekend
160000
140000
120000
100000
80000
60000
40000
20000
0
1984 1988 1992 1996 2000 2004 2008 2012
Year
(b)
Total annual visitors
1000000
900000
800000
700000
600000
500000
400000
1984 1988 1992 1996 2000 2004 2008 2012
Year
(c)
Kilometers traveled
16000
14000
12000
10000
8000
6000
4000
2000
0
1984 1988 1992 1996 2000 2004 2008 2012
Year