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Where has all the road kill gone?

Charles R. Brown[1,*] and Mary Bomberger Brown[2]

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 1983–2012 (Figure 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 (Figure 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 (Figure 1B). Over time, wing lengths of cliff swallows killed on roads increasingly diverged from that of the population at large (Figure 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 (Figure 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

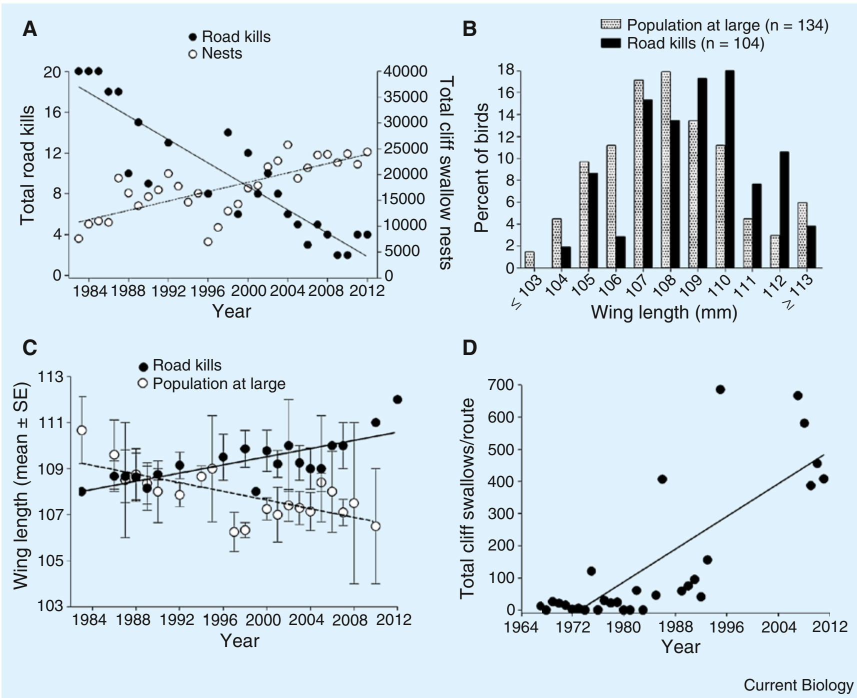

Figure 1. Changes in number and wing length of road-killed cliff swallows.
Road-killed cliff swallows in southwestern Nebraska have declined with time and constitute a disproportionately greater fraction of longer-winged birds in the years following the birds' occupancy of roadside colony sites. (A) 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.

(Figure 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].

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.

Supplemental Information

Supplemental Information including experimental procedures, supplemental results and one figure can be found with this article online at http://dx.doi.org/10.1016/j.cub.2013.02.023.

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