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Are Roadkills Density-Dependent? Case Study of the Barn Owl (*Tyto alba*)

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Abstract: Even though birds are some of the most common road-killed animals, it remains to be determined whether avian roadkills are related to breeding numbers and breeding success, mainly due to a lack of study areas that monitor breeding populations and roadkills. We studied whether barn owl breeding numbers and breeding success are related to roadkills. We monitored yearly barn owl breeding numbers (2174 breeding attempts and 1682 adults ringed) and breeding success (9380 nestlings ringed) and monitored 95 km of roads weekly for roadkills from 2009 to 2017 in the Beit Shean and Emek Yizreel Valleys, Israel. During the study period, we documented 1073 road-killed barn owls, of which 328 were ring recoveries. The highest mortality occurred between July to September, coinciding with the barn owl post-fledging period. The number of breeding pairs and the number of nestlings ringed were positively related to the total number of barn owl roadkill, the proportion of roadkill ring recoveries, and the proportion of ring recovered roadkills in the first year of their life. First-year owls represent the majority of ringed owls, accounting for 64.6%, while adult owls compose 35.4%. Notably, a substantial fraction of adult ring recoveries, encompassing 67.2%, may pertain to floaters since we did not observe these individuals as breeding adults. Even though more females were found as roadkill ring recoveries, the proportion of male/female ring recoveries from roadkills was similar to that of adults ringed at the nest boxes. This study is the first that shows that barn owl roadkills are density-dependent and demonstrate the importance of monitoring breeding and population numbers in roadkill studies.

Keywords: roadkill; barn owl; breeding; density; animal–vehicle collisions

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1. Introduction

The increasing human population and the accompanying infrastructure growth, such as roads, can significantly impact wildlife populations—for example, by habitat destruction and fragmentation [1,2]. In addition, roads can create dangerous barriers for animals trying to cross from one habitat area to another. The result is a significant increase in roadkill incidents (animal–vehicle collisions) as wildlife are struck by vehicles attempting to cross the road [3].

Roads are the largest source of anthropogenic mortality for many vertebrates [4]. As a result, scientific papers on road ecology have increased annually [5] since it was first described in 1998 [6]. Among the various dangers posed to avian species, vehicular collisions present a grave threat [7]. For example, in the USA alone, 9 to 340 million birds are killed yearly by vehicles [8], millions per year in European countries [9], and 13.8 million in Canada [10].

Various efforts have been made to reduce roadkill, including wildlife crossings, speed limits in sensitive areas, and road design modifications. However, the effectiveness of these measures can vary greatly depending on the location and specific species involved. Numerous studies have tried to explain roadkills by traffic factors, road infrastructure, habitat-related factors, and weather [11]. For example, roadkills were positively related to traffic volumes [12] and landscape connectivity [13,14]. In addition to those factors, it is of high importance to monitor wildlife populations while collecting data on wildlife–vehicle collisions [5] to understand and quantify roadkills' effects on wildlife. However, the relationship between roadkills and wildlife populations may be complex and needs to be fully understood. Therefore, roadkill may lead to changes in population structure and behavior, affecting the persistence of wildlife populations.

Most studies on the effect of population size on roadkills have been conducted in high-income countries, primarily focusing on animal species other than birds [15]. For example, red fox (*Vulpes vulpes*) population densities were related to the number of roadkills [16], as were raccoons [17] (*Procyon lotor*) and rabbits (*Oryctolagus cuniculus*) [18]. In addition, the number of fire salamanders (*Salamandra infraimmaculata*) killed in specific areas was related to the number of roads [19]. Despite the growing recognition of the importance of preserving bird populations, the available research suggests that much more attention is needed to understand the impact of roads on these species and to develop effective conservation strategies.

It is crucial to comprehend the relationship between the number of roadkills, population sizes, and yearly breeding numbers of the species affected. This understanding is crucial to gain insights into the mechanism behind roadkills. Although monitoring roadkills is relatively straightforward compared with monitoring the population demographics of the target species, it is still essential to have baseline data on population numbers. These data provide a foundation to understand the impact of roads on wildlife and allow us to evaluate the evolutionary responses of the species [20] in question to this artificial phenomenon. With these data, it can be easier to fully comprehend the complex interactions between wildlife, roads, and human activity.

Due to several factors, the barn owl (*Tyto alba*) is a common species frequently found as roadkill [21–23]. First, their low-flying flight patterns make them vulnerable to being hit by vehicles. Second, they have a slow reaction time to vehicles [24], contributing to their risk of becoming roadkill. Additionally, their large hunting home ranges [25,26] often overlap with roadsides, where they may prefer hunting [27], increasing their vehicle exposure. These characteristics make barn owls an excellent species for studying roadkill. However, while there have been attempts to investigate the relationship between the occurrence of barn owl populations using broadcast surveys and roadkills [28], these studies have been limited as they lacked data on the actual number of barn owls. This information is crucial as it would clarify the relationship between barn owl populations and the likelihood of roadkills.

In Israel, the use of barn owls as biological pest control agents in agriculture fields is widespread [29,30]. Favorable conditions for hunting and nesting in agricultural areas have led to one of the highest bird population densities in the world. Despite this, the number of breeding pairs and nestlings fledged each year can vary [31], with fluctuations primarily attributed to changes in the rodent population [32] and potentially influenced by weather conditions [33]. Unfortunately, barn owls in Israel also face a significant threat from vehicular-related roadkills as they often live in and around agriculture fields intersected by numerous small roads and highways. Since roadkills are often seasonal, increasing during and after breeding seasons [12,34,35], we expect there will be more barn owl roadkills after breeding, when nestlings fledge and the population is highest. These factors highlight the importance of considering both the benefits and challenges of using barn owls for pest control in agricultural areas.

The present study aimed to investigate the potential relationship between barn owl roadkill incidents, the breeding success of barn owl pairs, the number of breeding pairs, and traffic intensity in Israel. This objective was fulfilled by monitoring barn owl roadkills, breeding pairs, and the number of nestlings. We hypothesize that in years when more barn owl pairs fledged more nestlings, we would expect more barn owls as roadkills. We also studied whether the ringed recoveries from roadkills were related to the breeding numbers and the number of recaptures. We also hypothesized that in years when the barn owls were more productive, there would be more first-year ring recoveries from roadkills.

2. Materials and Methods

The study was conducted (300 km^2) in the adjoining Beit Shean [31] and Emek Yizreel Valleys (32°33′ N, 35°23′ E; Figure 1) and was mainly made up of crop fields comprising cattle fodder (wheat, sweet corn, alfalfa, clover, vetch, and oats), grain crops and seeds (wheat and sweet corn), spices and herbs (oregano, hyssop, basil, and dill), and vegetables (cucumber, pea, etc.) and small villages. In addition, farmers added 606 barn owl nest boxes in and around their fields to increase barn owl populations to be used as biological pest control agents to reduce rodent damage and rodenticide use in their fields [29,30].

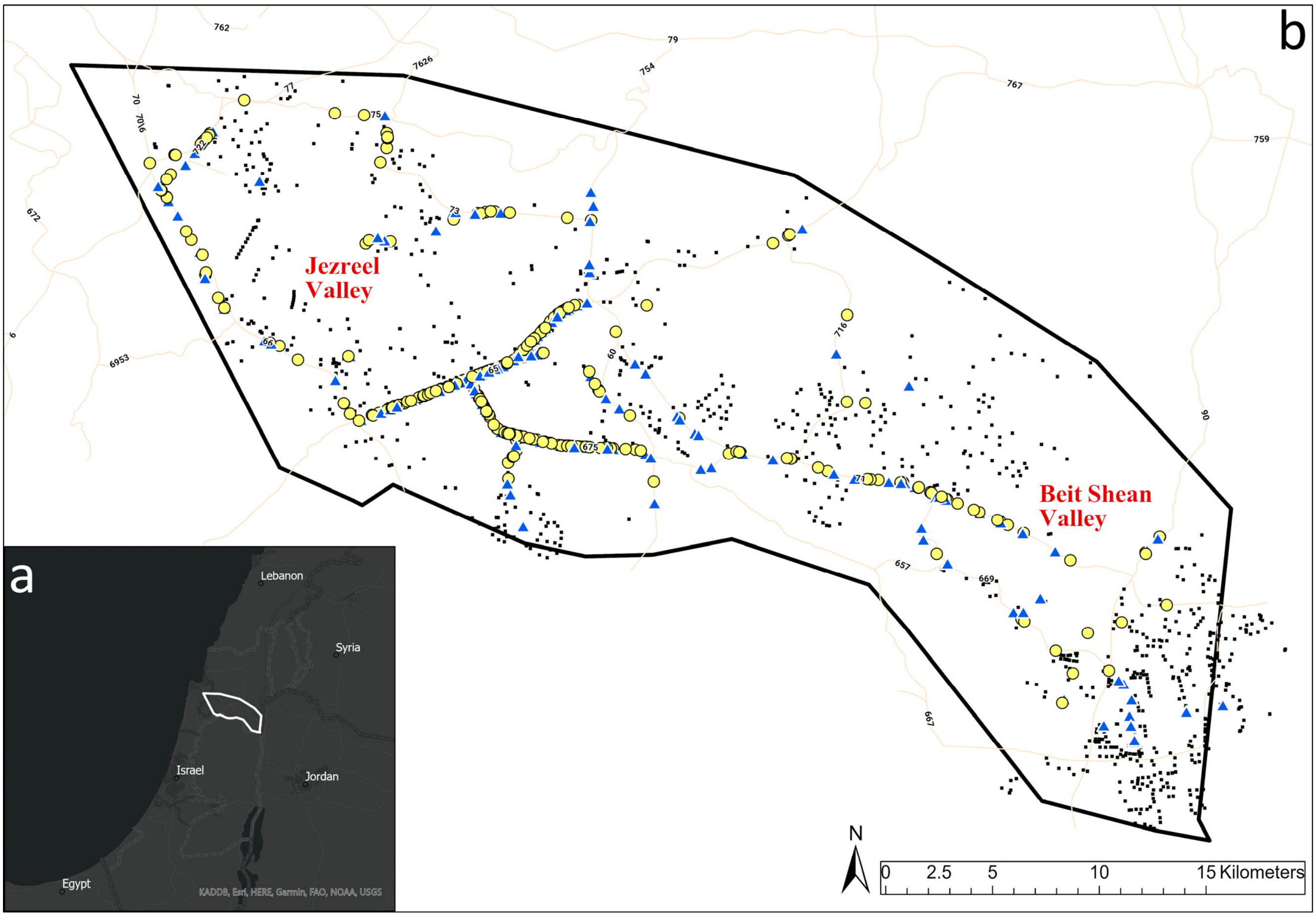

Figure 1. The map on the **bottom left** (**a**) shows the location of the study site in the Beit Shean and Jezreel Valleys in northern Israel and the neighboring countries. The study site is outlined in white on a black background. The larger zoomed-in map (**b**) of the study site with the white background shows the locations of barn owl nest boxes as black dots and the locations of barn owl roadkills collected from 2009 to 2017 as yellow circles (without rings) and blue triangles (with ring recoveries).

2.1. Breeding Data

We monitored, on average, 572 (SE = 19.0) barn owl nest boxes per year. Each nest box was visited two to five times between April 15 and July 30 from 2009 to 2017 to determine the occupied nest boxes. We also calculated the number of fledglings per each laying pair (pairs that laid clutches) by subtracting the number of nestlings when the oldest nestlings were 53 days old, minus any dead nestlings found a week after the fledgling. Based on years of experience researching barn owls in this study system, we assumed a 100% detection probability of breeding pairs, or very close to it, as we have never found any owls breeding outside this period [31,36,37].

All nestlings were ringed yearly [38]. In addition, adult barn owls inside the nest box were also ringed. Males frequently roosted outside the nest box when the nestlings were young, and females sometimes roosted outside the nest boxes when they started to hunt when the oldest nestling was around 25 days [25]. We therefore captured more females than males, and in some cases, neither of the adults were captured. To ensure that we did not harm or disrupt the breeding success of the owls, we took caution when approaching the nest box to avoid flushing them and also when returning the owls after our visit.

2.2. Road Survey

A total of 95 km of roads (road identifying numbers 60, 65, 66, 71, 75, 77, 90, 669, and 6678; Figure 1) were surveyed from two to five times per week by driving slowly to identify roadkills from 2009 to 2017 (n = 9). We only surveyed the roads during the day due to visibility and safety. We used car surveys because compared with foot surveys, car surveys could cover more extensive areas faster and were just as efficient in detecting carcasses on the pavement [39]. During the road survey, we documented each owl's location using the ARC GIS collector mobile data collection app for the ArcGIS platform. The app allowed us to collect, edit, and update geographic data in the field, offline or online, and synchronize changes with a central GIS database. We collected fresh carcasses of owls used in studies on pheomelanin-based coloration and flying strategies [40] and the anatomy of bristles on the nares and rictus of barn owls [41]. In addition to the owls we found during the survey, people would frequently alert us of dead owls in a large WhatsApp group of birders, and we were also alerted by other people, including local rangers. We cleared all other carcasses from the roads to minimize the danger to scavengers and avoid pseudoreplication (counting the same carcass more than once). We defined first-year owls as those in their first calendar year since hatching and adults as those at least one year old. A ring recovery was a ringed dead owl.

2.3. Traffic Intensity

We calculated the traffic intensity from the annual daily traffic collected by the Israel Center Bureau of Statistics (https://teunot.cbs.gov.il/niturtnuaenterprise/ (accessed on 1 January 2023). We presented the traffic data as the mean daily average traffic volume per road (95 km of roads 60, 65, 66, 71, 75, 77, 90, 669, and 6678) during 2009–2017.

2.4. Statistics

The study aimed to investigate the relationships between barn owl roadkills, breeding, ringing data, and traffic intensity over nine years. We used Pearson's correlation to identify correlations between roadkill, breeding, traffic data, and ringing data because the number of observations in our analysis was limited to 9 years, which falls short of the recommended minimum number to carry out a multiple regression analysis. In ecological studies, it is generally advised to have a minimum of 10 to 20 observations per predictor, which can provide a robust estimation of the relationships between variables [42]. In addition, we employed a t-test to determine whether the sex ratio differed between the recovered and recaptured barn owls. For our results, all tests were two-tailed, and p values <0.05 were considered significant. All tests were analyzed using SPSS version 22 software.

3. Results

During the 9-year study, our observations yielded 1073 barn owl roadkills (mean of 119.2 per year, SE = 3.8), among which 328 (30.6%, SE = 7.8) were ring recoveries (Figure 1). The highest mortality occurred during the months of July–September (Figure 2). We monitored 2174 breeding pairs (241.6 adults/year, SE = 23.7) during the study period and ringed 1682 adults (71.6/year, SE = 23.9) and 9380 nestlings (186.9/year, SE = 23.9). The number of breeding pairs and the number of nestlings were positively related (r = 0.93,

$p < 0.001$; Figure 3). The number of breeding pairs (r = −0.10, $p = 0.795$; Figure 3) and the number of nestlings (r = −3.01, $p = 0.432$; Figure 3) were not related to the year.

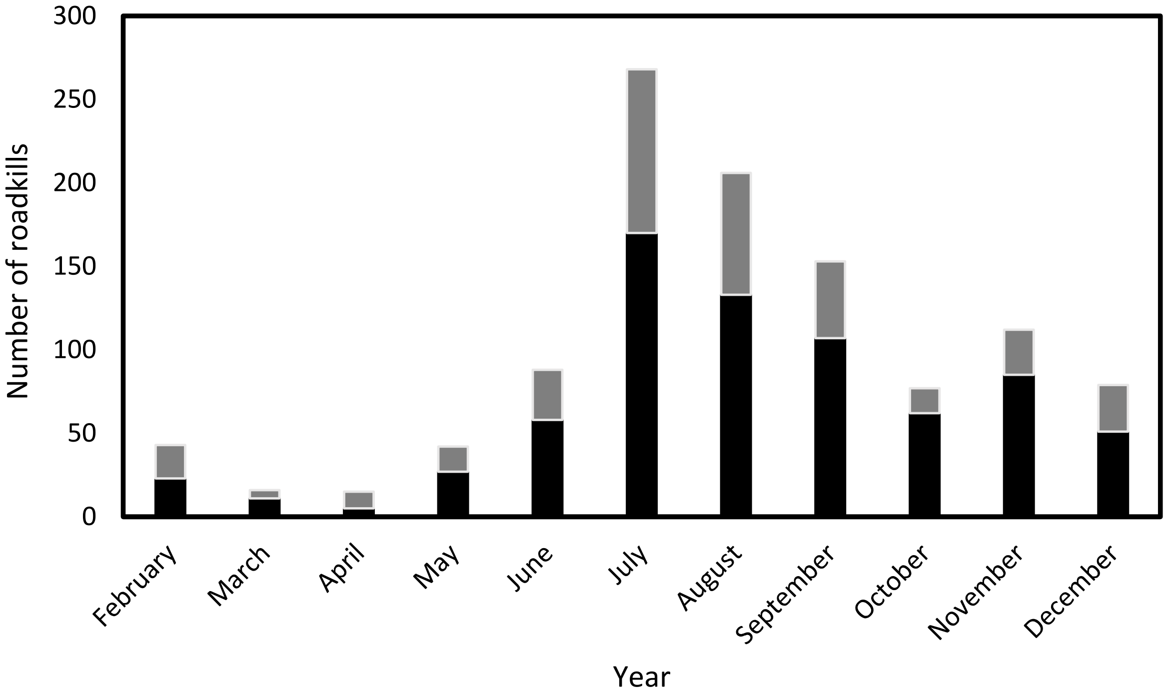

Figure 2. The monthly number of barn owl roadkills that were not ringed (black) and ringed recoveries (gray) from 2009 to 2017 (n = 1073).

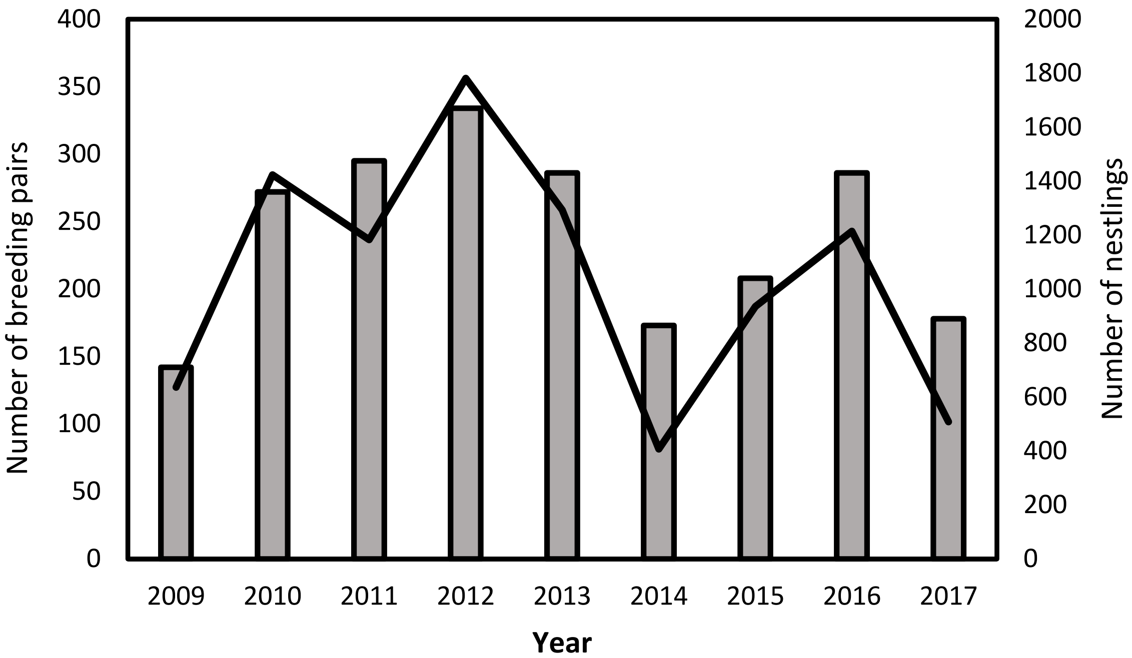

Figure 3. The number of breeding pairs (columns) and the yearly number of nestlings ringed (line) from 2009 to 2017.

The number of barn owl roadkills was positively related to the number of breeding pairs (r = 0.67, p = 0.047; Figure 4a) and the number of nestlings ringed (r = 0.77, p = 0.015; Figure 4b) through the nine years of the study period, whereas it was not related to the traffic intensity (r = −0.32, n = 9, p = 0.398). The proportion of roadkill ring recoveries was positively related to the number of breeding pairs (r = 0.69, n = 9, p = 0.042; Figure 5a) and the number of nestlings ringed (r = 0.69, n = 9, p = 0.038; Figure 5b), whereas it was not related to traffic intensity (r = −0.009, n = 9, p = 0.982). Of the roadkill ring recoveries, adults composed 35.4% (SE = 40.8) and first-year owls 64.6% (SE = 38.5). Of the roadkill adult ring recoveries, 67.2% (SE = 56.6) were owls we ringed as nestlings but never recaptured as breeding adults in active nests. The proportion of roadkill ring recoveries in the first year of their life was related to both the number of breeding pairs (r = 0.80, n = 9, p = 0.010; Figure 6a) and the number of nestlings (r = 0.88, n = 9, p = 0.002; Figure 6b) ringed in the area, whereas it was not related to traffic intensity (r = −0.47, n = 9, p = 0.203). We knew the sex of 89 ring recoveries that we previously captured as breeding adults. The proportion of male/female ring roadkill ring recoveries (29.2% male and 70.8% females) was similar to the proportion of the adults ringed alive at the nest boxes (31.9% male and 68.1% females) (t_{16} = 0.34, p = 0.34).

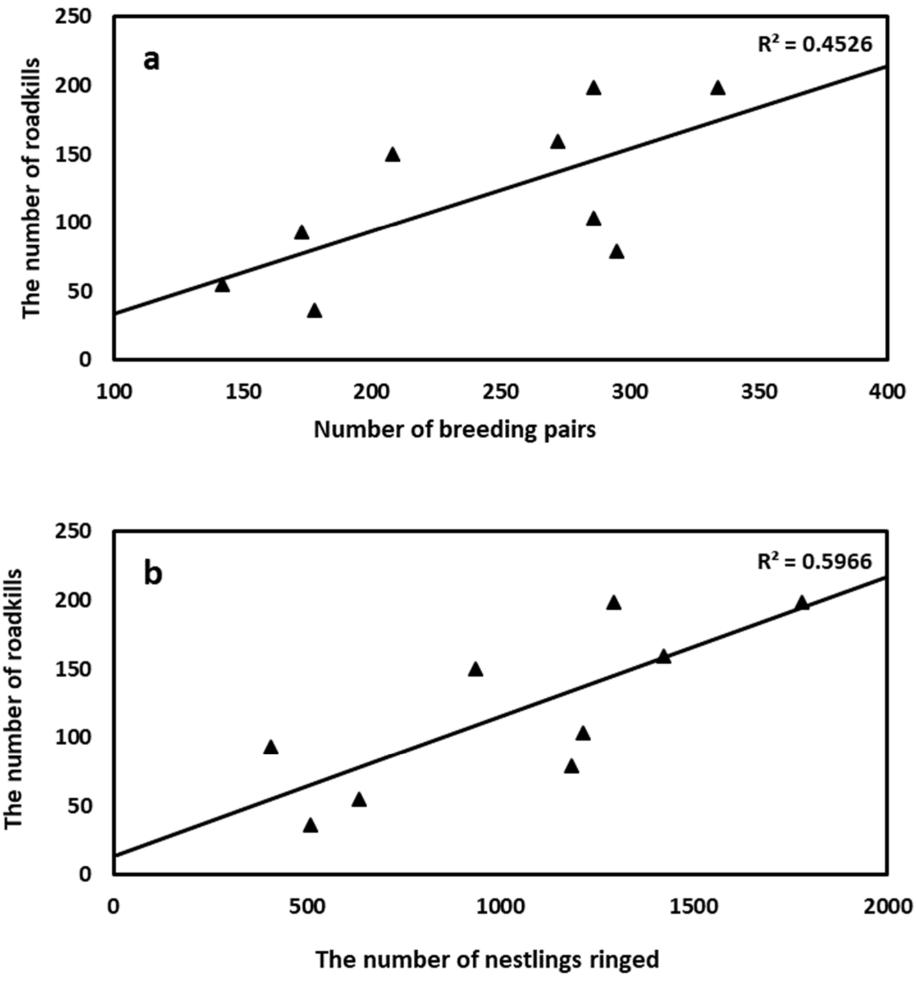

Figure 4. (**a**,**b**) The number of barn owl roadkills from 2009 to 2017 was positively related to the number of barn owl breeding pairs (**a**) and the number of nestlings ringed (**b**).

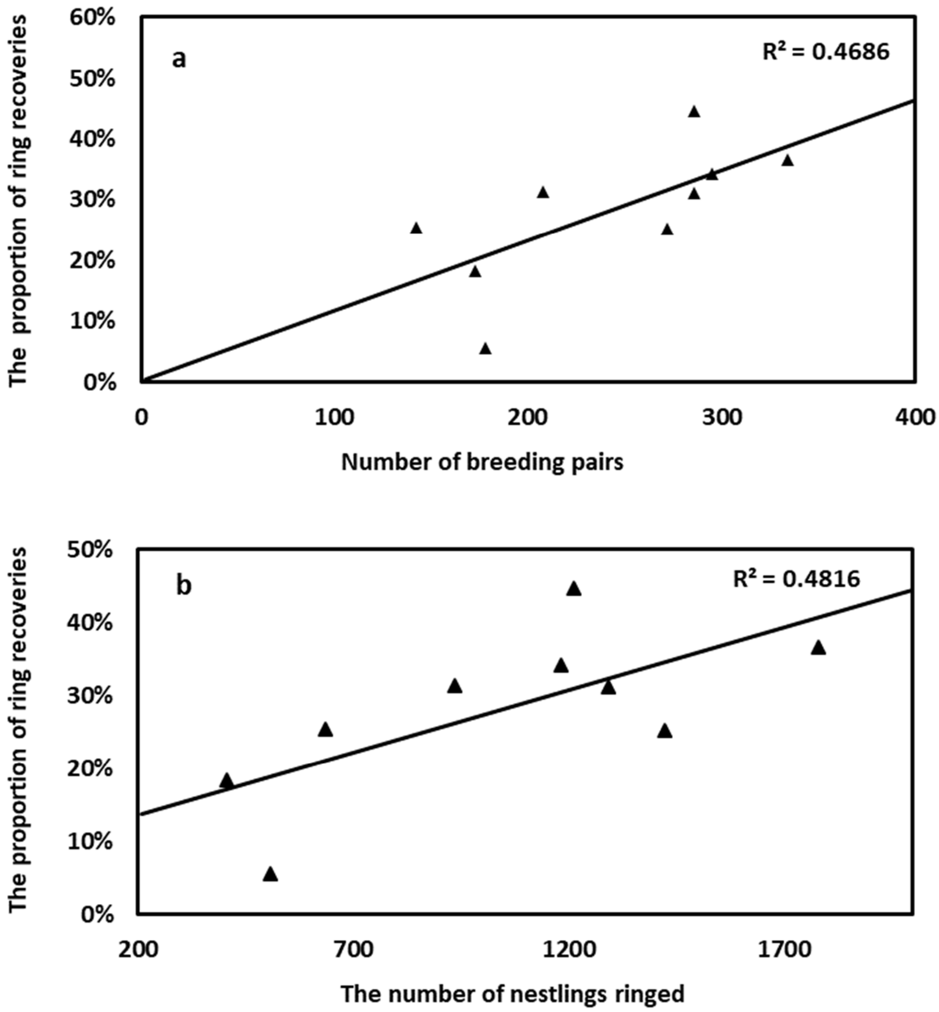

Figure 5. (**a**,**b**) The proportion of barn owl roadkills from 2009 to 2017 that were ring recoveries was positively related to the number of breeding pairs (**a**) and the number of nestlings ringed (**b**).

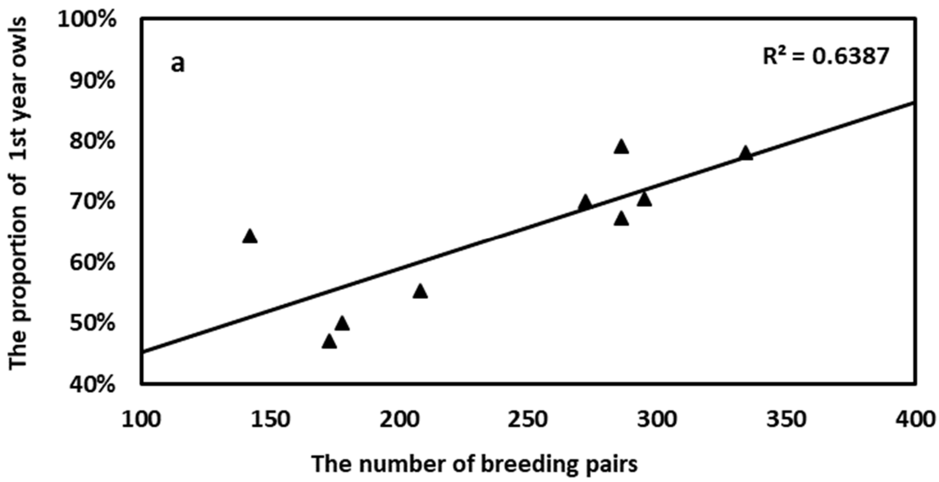

Figure 6. *Cont.*

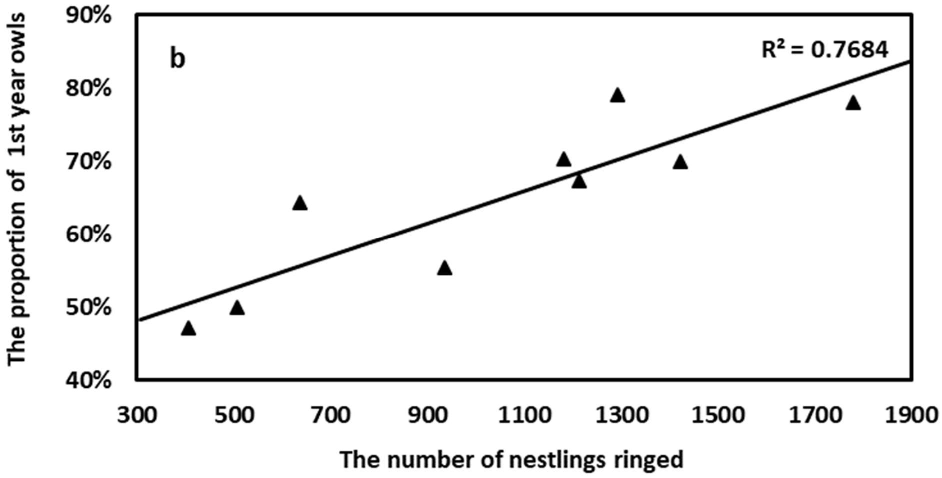

Figure 6. (**a**,**b**) The proportion of barn owl roadkills from 2009 to 2017 that were less than one year old was positively related to the number of breeding pairs (**a**) and the number of nestlings ringed (**b**).

4. Discussion

Understanding population densities and animal behaviors are essential to determine whether mitigation can reduce roadkill [43]. We found that roadkill barn owls were density-dependent. Specifically, the yearly number of barn owl roadkills was directly related to the number of barn owl pairs and the number of nestlings fledged. Furthermore, we found more ring recoveries, and the proportion of first-year owls increased in years with more breeding pairs and more nestling fledge. Therefore, when there are more owls, more are exposed to roads, most likely higher due to intraspecific competition for hunting sites forcing young owls to less attractive habitats [36] and simply because more young owls are dispersing.

Interestingly, compared with the number of owl pairs and nestling, roadkill rates did not fluctuate in response to yearly traffic volume changes, likely because traffic volume remained consistent yearly. Furthermore, in contrast to our investigation, the quantity of roadkill incidents did not correlate with the number of fledged nestlings in 25 km^2 plots in the Netherlands [21]. As barn owl young are capable of fledging far from their nests, a comprehensive evaluation of larger areas, as conducted in our research, may be imperative.

Roadkill monitoring can be used indirectly to monitor wildlife population changes, especially in areas where direct monitoring is impossible. Since roadkills were related to population size, monitoring yearly roadkills can be used to monitor population changes in conservation projects in areas where researchers cannot monitor wildlife demographics. For example, researchers have used roadkill monitoring schemes to determine when species are in decline, as found in the U.K.'s hedgehog (*Erinaceus europaeus*) numbers [44,45]. However, it is essential to validate the relationship between roadkill numbers and population size for each species in each region as different species and regions may have different relationships. In addition, roadkill monitoring should be one of many methods used to monitor wildlife populations because it may vary between populations and is an indirect method that may not always accurately reflect the actual population size. Therefore, it should be used with other methods, such as direct population surveys, to provide a more comprehensive understanding of population changes.

The seasonal peaks in road mortality occurred during the breeding season, especially in the post-fledging period. The temporal mortality of the barn owls, which peaked in July to September, is indicative of both the breeding season and the fledging of the young. When the young barn owls start flying, they will fly far and are at a higher risk of crossing roads. In contrast, adult barn owls are less likely to disperse far from the nest sites after the breeding season, and they also tend to fly less frequently (Charter unpubl. data) after feeding the fledglings. Hence, adult barn owls are primarily at risk while feeding the nestlings.

In comparison with this study, a study in Portugal found the number of barn owl roadkills peaked in November–January after the dispersal period and suggested it was due to the owls' need to fly farther due to a lack of food [46]. Like the barn owls in this study, more Eurasian badgers (*Meles meles*) were road-killed during dispersal [35]. A study in New Zealand found that the three most common mammal and bird species had increased road mortality during dispersal and breeding [12]. Red foxes' (*Vulpes vulpes*) and stone martens' (*Martes foina*) road mortality increased during the breeding season while provisioning young. In the U.K., 13 out of 19 of the most common species showed significant and consistent seasonal variations in road mortality, and many species were also more vulnerable to being road-killed around breeding and dispersal [34].

Juvenile-ringed barn owls in this study were overrepresented in roadkill statistics, with higher proportions of first-year owls (65%) making up more roadkill than adults (35%). This finding is consistent with studies on barn owls conducted in different regions, including the Netherlands (70% juveniles and 30% adults), Florida, USA (61% juveniles and 29% adults) [47], and Idaho, USA (79% juvenile and 21% adults) [22]. The high proportion of juvenile roadkills is likely due to their dispersal behavior as young owls leave their birth sites to establish territories. These movements increase the likelihood of encounters with roads, leading to higher rates of road mortality.

Of the adult recoveries ringed as nestlings, 67.2% we never captured as breeding adults. These adults could be floaters—mature owls that are not breeding. Floater owls are crucial in maintaining the population structure because floaters may also act as potential breeders in case of breeding failures in the population. The elevated count of floaters observed could be attributed to the fact that unlike breeding owls, these birds tend to cover greater distances while flying [48–50], making them more susceptible to road hazards. In addition, floaters may search for prey in less desirable regions farther from occupied nests, such as roads [36].

In this study, the proportion of female/male adults ringed was similar to the sex ratio of roadkills (29% male and 71% female). More females barn owls were also found in roadkills in Florida, USA (26% male and 74% females) [47], but differed from studies in Idaho, USA (42% males and 58 % female) [22], and the Netherlands (50% male and female) [21]. In Israel, females flew farther than males during the breeding season, most likely because males occupied territories first while females were incubating and brooding (Charter unpubl. data), which could increase their exposure to roads and increase the risk of roadkills. More studies using tracking devices are needed to determine whether the movement of males and females may explain exposure to roads and roadkills.

Despite the high frequency of roadkill incidents reported in this study, there were no annual trends or decreases in the size of the barn owl breeding population. It should be noted that roads are not a new phenomenon in the study region, as roadkill incidents were also observed both before and following the duration of this study (Charter pers. observ). It is still unclear whether roadkills limited the population numbers of owls in the study. Fluctuation in the number of breeding pairs and nestlings suggests that barn owl yearly population fluctuations are more likely to be linked to something other than roadkills, such as changes in prey abundance [32,51]. Barn owls in Israel can fledge up to 11 nestlings [31], and the r-selected reproductive strategies and many floater adults seem to offset mortality by roads. Studies on roadkills and breeding in other regions where barn owls raise less young and population density is lower [52], such as in natural habitats, are needed to determine whether less dense and less productive populations may be affected differently. For example, in small populations, the loss of even a few individuals can significantly affect the conservation status of a species. Even though roadkills frequently appear in clusters [53], this may only be the case in some areas, but further studies are needed.

Even though barn owls seem to cross roads/highways regardless of traffic volume [24], there are signs that barn owls prefer nest sites farther away from roads and highways.

For example, in Israel, barn owls preferred to occupy nest boxes farther away from the surrounding [36] roads, most likely due to some disturbance. Similarly, barn owls in Canada were most likely to occupy nest sites in areas with less traffic exposure [54]. Finally, it appears that barn owls are incapable of assessing the speed of vehicles from afar; however, they may try to evade them at the last second by abruptly veering away (Charter unpubl. data). This indicates that barn owls have some level of aversion toward roads and traffic and prefer to breed in quieter, less disturbed areas.

5. Conclusions

This study highlights the importance of monitoring wildlife and roadkills together. In this study, yearly breeding output but not traffic intensity explained the yearly fluctuation in roadkills. Even though many owls were roadkills, the number of pairs did not show a negative trend during the study, and fluctuating breeding numbers occurred before and after this study. The high prey abundance, abundance of nest sites, high breeding success, and a large floater population most likely offset any adverse effects of roadkills in Israel's large barn owl breeding population. There is a need to monitor roadkills and breeding numbers in other smaller populations to determine whether the populations are affected differently. Last, there is a need to ring barn owls to tag them using tracking devices to determine whether there is a difference in movement between breeding and nonbreeding (floaters) adults.

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