Life and Death in the Fast Lane: Demographic Consequences of Road Mortality in the Florida Scrub-Jay

RONALD L. MUMME,* STEPHAN J. SCHOECH,† GLEN E. WOOLFENDEN,‡ AND JOHN W. FITZPATRICK§

*Department of Biology, Allegheny College, Meadville, PA 16335, U.S.A., email rmumme@alleg.edu
†Department of Biology and Center for the Integrative Study of Animal Behavior, Indiana University, Bloomington, IN 47405, U.S.A.
‡Archbold Biological Station, Venus, FL 33960, U.S.A.
§Cornell Laboratory of Ornithology, 159 Sapsucker Woods Road, Ithaca, NY 14850, U.S.A.

Abstract: We examined the demographic consequences of road mortality in the cooperatively breeding Florida Scrub-Jay (Aphelocoma coerulescens), a threatened species restricted to the oak scrub of peninsular Florida. Between May 1986 and July 1995 we monitored the survival and reproductive success of a color-banded population of jays along a two-lane highway at Archbold Biological Station. Annual mortality of breeding adults was 0.38 on road territories, significantly higher than the rate of 0.23 for breeders on nonroad territories. High mortality on road territories appeared to be a direct result of automobile traffic per se and not a consequence of road-induced changes in habitat characteristics. Mortality was especially high for immigrants without previous experience living along the road: in their first two years as breeders on road territories, naive immigrants experienced annual mortality of 0.50 and 0.45. From year 3 onward, however, annual mortality dropped to 0.29, not significantly different from the rate for birds on nonroad territories. This experience-dependent decline in road mortality could be caused either by surviving jays learning to avoid automobiles or by selective mortality operating through time (demographic heterogeneity). Proximity to the road had no effect on nesting success beyond its indirect effects on breeder experience and group size. Because the mortality of 30- to 90-day-old fledglings was significantly higher on road territories than on nonroad territories, however, breeder mortality greatly exceeded production of yearlings on road territories. Roadside territories therefore are sinks that can maintain populations of Florida Scrub-Jays only via immigration. Because Florida Scrub-Jays do not avoid roadside habitats and may even be attracted to them, road mortality presents a difficult challenge for the management and conservation of this threatened and declining species.

Vida y Muerte en la Carretera: Consecuencias Demográficas de Mortalidad Asociada a la Carretera en la Urraca Azuleja de florida

Resumen: Examinamos las consecuencias demográficas de la mortalidad causada por el tráfico automovilístico en la urraca azuleja de la florida (Aphelocoma coerulescens). A. coerulescens es una especie en peligro de extinción que exhibe cuidado cooperativo y cuya distribución está restringida al matorral de roble de la península de florida. Una población de urracas localizada a lo largo de una autopista en la Estación Biológica Archbold fue marcada y monitoreada para determinar su supervivencia y éxito reproductivo desde mayo 1986 hasta julio 1995. La tasa de mortalidad anual de adultos reproductivos con territorios en la carretera fue de 0.30 y significativamente mayor que el valor de 0.23 para aquellos adultos con territorios en zonas sin carreteras. La alta mortalidad en los territorios con carreteras parece ser un resultado directo del tráfico automovilístico y no una consecuencia de los cambios en el hábitat causados por la presencia de la carretera. La mortalidad fue especialmente alta en inmigrantes sin experiencia previa con territorios a lo largo de carreteras; estos exhibieron una tasa de mortalidad de 0.5 y 0.45 durante sus primeros dos años re-

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productivos. Del tercer año en adelante la tasa de mortalidad se redujo a 0.29, lo cual no fue significa-
mente diferente de la tasa de mortalidad de aves en territorios sin carreteras. Esta reducción en la mortal-
idad es dependiente de la experiencia y puede ser causada por el aprendizaje de la evasión del tráfico por las
urracas sobrevivientes o por una mortalidad selectiva a través del tiempo (heterogeneidad demográfica). La
proximidad de la carretera no tuvo efecto en el éxito de anidación más allá de los efectos indirectos relacio-
nados con la experiencia del reproductor y el tamaño del grupo. Sin embargo, debido a que las tasas de mor-
talidad para las crías de 30-90 días fueron significativamente más altas en los territorios con carreteras en
comparación con los territorios sin ellas, la mortalidad de individuos reproductivos excedió en gran medida
el reclutamiento de crías de un año en territorios en la carretera. Por ende, los territorios en carreteras son
sumideros que pueden mantener poblaciones de urracas azulejas en florida solamente debido a la inmi-
gración. Considerando que las urracas azules de la florida no evitan los hábitats a lo largo de las carreteras
y más aún parecen ser atraídas por éstas, la mortalidad causada por el tráfico automovilístico constituye un
reto difícil en el manejo y la conservación de esta especie reducida y en peligro de extinción.

Introduction

Road mortality is recognized as a major conservation prob-
lem that affects amphibians (Fahrig et al. 1995; Ashley &
Robinson 1996), reptiles (Bernardino & Dalrymple 1992;
Rosen & Lowe 1994), birds (Loos & Kerlinger 1993; Melvin
et al. 1994), and mammals, including some primates
(Harris & Scheck 1991; Drews 1995; Romin & Bissonette
1996). Although the number of animals killed by vehicles
worldwide each year is staggering (Bennett 1991;
Forman & Alexander 1998), little is known about how this
mortality affects the demography and population dynamics
of particular species. We provide such data for the Florida
Scrub-Jay (Aphelocoma coerulescens).

The Florida Scrub-Jay is restricted to the oak scrub of
peninsular Florida, a fire-maintained community that
grows only on well-drained, sandy soil. Because of exten-
sive loss and degradation of its habitat, total population
size in 1993 was estimated to be about 4000 pairs, 10%
or less of presettlement numbers. In 1987 the U.S. Fish
and Wildlife Service listed the Florida Scrub-Jay as threat-
ened (Stith et al. 1996; Woolfenden & Fitzpatrick 1996).

Florida Scrub-Jays live in permanently territorial family
groups that are almost always based around a single monog-
amous breeding pair. About half of all groups also contain
one to six nonbreeders that are typically prebreeding off-
spring of one or both breeders. Most nonbreeders act as
helpers by feeding dependent young produced within their
social unit. Breeding vacancies created by the disappear-
ance of the male or female breeder in a group are nearly al-
ways filled by immigrants, usually by prebreeders that had
been living on a neighboring territory (Woolfenden & Fitz-

Three characteristics make Florida Scrub-Jays ideal sub-
jects for a study of the demographic consequences of
road mortality. First, because Florida Scrub-Jays are easily
tamed, nonmigratory, and defend territories year-round,
field workers can reliably detect 100% of individuals
present in a color-banded study population. An accurate
and complete census therefore can be conducted rou-
tinely (Woolfenden & Fitzpatrick 1984). Second, breeders
and juveniles <1 year old are extremely sedentary. Flor-
ida Scrub-Jays in these two categories that permanently
disappear from the study area can safely be assumed dead
(Woolfenden & Fitzpatrick 1984, 1996; McDonald et al.
1996). Thus, techniques to estimate mortality from mark-
recapture data or from census data from surveys in which
only a fraction of the total population was detected (e.g.,
Pollock et al. 1990; Gobert & Lebreton 1991) are unnec-
essary. Instead, survival and mortality for breeders and ju-
veniles can be determined directly with standard actua-
rial methods (e.g., McDonald et al. 1996). Third, because Flor-
da Scrub-Jays often forage in roadsides and other open ar-
cas (Cox 1987; Breiinger et al. 1996; Woolfenden & Fitz-
patrick 1996), they are sometimes killed by automobiles
(Dreschel et al. 1990; Fitzpatrick et al. 1991).

We focus on the effects of proximity to a paved road on
three major demographic parameters and components of
fitness in Florida Scrub-Jays: (1) survival of breeders, (2)
nesting success, as measured by the production of fledged
young, and (3) post-fledging survival of juveniles. We did
not include survival of adult prebreeders because pre-
breeders are less sedentary and occasionally disperse over
long distances (Stith et al. 1996; Woolfenden & Fitzpatrick
1996), which makes estimating survival for these birds
problematical (Woolfenden & Fitzpatrick 1984).

Methods

Study Area

Our study was conducted between May 1986 and July
1995 at Archbold Biological Station in Highlands
County, Florida, where a color-marked population of
Florida Scrub-Jays residing in the “demography tract” has
been under continuous study since 1969 (Woolfenden & Fitzpatrick 1984, 1990, 1996). We focused, however, on a second population of color-banded jays residing in the adjacent "experimental tract" (Mumme 1992; Schoech et al. 1996). The experimental tract is partially bounded by a two-lane paved county highway, Old State Road 8. Thus, some of the jays in the experimental tract were exposed to vehicle traffic but most were not (Fig. 1). Although the size of the experimental tract population varied annually and seasonally (approximately 35–55 territories and 100–200 color-banded birds), the proportion of birds and territories exposed to the road remained fairly constant. Throughout the 9 years of study, Old SR8 had a posted speed limit of 55 miles (89 km) per hour, although many vehicles traveled considerably faster. Old SR8 was relatively lightly traveled; in 58 hours of observation during daylight hours in June and July 1991, use averaged 21 vehicles per hour.

In all 9 years of study the population was thoroughly censused in summer (July to August) and winter (December to early February) by methods described elsewhere (Woolfenden & Fitzpatrick 1984). The study population also was monitored continuously throughout the nesting season (late February to late June) for 7 years (1987–1990 and 1992–1994). In 1991 and 1995, field work during the breeding season was limited to a single complete census. Although the total research effort varied from year to year, within any given year road and nonroad territories received equal attention. All young produced in the study area were color-banded either as nestlings (1987–1990 and 1992–1994) or as fledglings (1991 and 1995). Unbanded immigrants were captured and color-banded in almost all cases within a few weeks of first appearing in the study area.

Paired birds (potential breeders) were readily identified by their year-round joint defense of territory and by courtship feeding. Sex also was determined from behavior; only breeding females incubate eggs and brood young, and only females produce a characteristic "hic" call during territorial encounters (Woolfenden & Fitzpatrick 1996).

**Survival of Breeders and Juveniles**

We defined "breeders" as conspicuous male-female pairs that defended an exclusive territory and that potentially or actually nested. Because many birds that pair and establish a territory die before producing their first clutch of eggs, limiting our analysis of breeder survival to birds known to have nested would have excluded large numbers of potential breeders that died before actually reproducing. With the possible exception of rare cases of polygyny, only jays that are part of a conspicuous male-female pair produce offspring (Quinn et al. 1999; Woolfenden & Fitzpatrick 1996).

For breeders, survival time was calculated as the time elapsed from the date a bird acquired status as a potential breeder on a particular territory to the date of either its presumed death or censoring. The survival time of fledged juveniles was recorded in days of absolute age, with hatching day defined as day 0 and age of fledging approximately day 18. For both breeders and juveniles, date of presumed death was estimated as the midpoint between the date the bird was last seen and the date it was first determined to be missing and presumed dead.

Although mortality of breeding Florida Scrub-Jays typically increases slightly with age (McDonald et al. 1996), we analyzed breeder survival not as a function of absolute age but as a function of the number of years on a particular territory as a breeder. We used this approach for two reasons. First, because birds can become breeders at different ages (Woolfenden & Fitzpatrick 1984) and because unbanded immigrants that move into a study area are typically of unknown age, using years as a breeder rather than years of absolute age greatly simplifies analysis (McDonald et al. 1996). Second, established breeders occasionally abandon their original breeding territory and move to a neighboring territory. Such short-distance movements usually result from death of a
mate, rare cases of pair-bond breakage, or degradation of local territory quality caused by either an intense recent fire or long-term fire exclusion (McDonald et al. 1996; Woolfenden & Fitzpatrick 1996). Because a change in territory often resulted in a change in road exposure and risk of roadside mortality, survival records of breeders that moved to new territories were no longer kept after the territory change, and a new survival record was started on the new territory.

For some analyses of breeding survival, we distinguished between road-naive and road-experienced breeders. A road-naive breeder was an individual with <1 year of previous experience living along the road at the time it acquired breeding status on a particular territory. In contrast, a breeder was road-experienced if at the time it acquired breeding status on a particular territory it either (1) had been raised on a road territory from hatching until its first spring or (2) had spent at least 1 year on a road territory as an adult breeder or prebreeder.

For analysis of breeder survival, the total data set comprised 434 records of banded breeders on a particular territory. Of these, 244 records included the permanent disappearance (presumed death) of the breeder and were uncensored. We censored 190 records: 85 for breeders that moved to a neighboring territory, 83 for breeders still alive at the end of the study (July 1995), 15 for breeders on territories that were dropped from the study area, and 7 for birds captured and permanently removed from the population as part of two separate studies. We computed most analyses of breeder survival using individuals for which we knew complete histories on a particular territory. For the analysis of mean annual mortality, however, we included a few additional individuals that already were established as breeders at the time the study began (or at the time the study area was expanded to include their territories).

For analyses of juvenile survival, the total data set comprised 527 known-age young that were banded as nestlings and fledged (1987–1990 and 1992–1994). To simplify data analyses, we assumed age at fledging to be 18 days for all juveniles in the data set (Woolfenden & Fitzpatrick 1996). Because the probability of long-distance dispersal by juveniles increases as they approach their first spring (Woolfenden & Fitzpatrick 1984, 1996), we examined juvenile survival through only the first 180 days of life. Of the 527 fledglings in the data set, 328 disappeared permanently and were presumed to have died before day 180. The remaining 199 juveniles were alive after 180 days and were therefore surveyed in the survival analyses.

Survival data were analyzed with SurvivalTools of StatView 4.1 (Abacus Concepts 1994). Following McDonald et al. (1996), we made statistical comparisons of cumulative survival curves using the Breslow-Gehan-Wilcoxon rank test, a nonparametric chi-square test that gives greater weight to differences in survival early in life and less weight to differences later in life when sample sizes are typically smaller. We made statistical comparisons of age- or interval-specific mortality rates using standard chi-square contingency tests. Unless otherwise noted, df = 1 for all reported chi-square values.

**Nesting Success**

Complete data on nesting success were obtained in 7 of the 9 years of the study, 1987–1990 and 1992–1994. A total of 351 nests that received at least one egg were produced by 299 territorial pairs during these years. Of these 351 nests, 344 (98.0%) were found before the eggs hatched. We excluded from consideration a few nests produced by joint-nesting females or females nesting separately as part of a polygynous trio; such departures from monogamy and singular breeding are rare in Florida Scrub-Jays (Woolfenden & Fitzpatrick 1996; Quinn et al. 1999). During the nesting season, nests were checked every 3–6 days from discovery until failure or successful fledging. Success per nest was calculated as the total number of young fledged for nests that received at least one egg. Success per season was calculated as the total number of young fledged per pair throughout the breeding season.

**Results**

**Survival of Breeders**

Of 116 individual Florida Scrub-Jays that acquired breeding status on a road territory at some point during the study, 11 (6 females, 5 males; 9.5%) were found dead on the road. This number, however, underestimates the number of breeders actually killed by motor vehicles for at least three reasons. First, we were unable to search the road regularly for evidence of road-killed jays. Second, our observations suggest that nocturnal and diurnal scavengers often quickly remove remains of road-killed vertebrates, greatly reducing the probability that a kill will be detected. Third, road-killed jays occasionally become lodged in fast-moving vehicles and transported far from the scene of the accident. We know of two such cases. One driver, for example, recovered a road-killed breeder from under the front end of her car about 15 km from where the jay had been struck and killed. That road-killed jays occasionally can be subjected to such incidences suggests that many breeding jays that disappear from road territories without a trace may have suffered a similar fate.

Because the number of road-killed jays recovered may not represent the extent of roadside mortality, we examined overall patterns of survival and mortality on road and nonroad territories. The mean (±SE) annual mortality of breeders was 0.375 ± 0.030 (n = 259 breeder-
years) on road territories but only 0.226 ± 0.016 (n = 649 breeder years) on nonroad territories, a statistically significant difference (χ² = 20.64, p < 0.0001). Similar results were obtained when the sexes were considered separately: Annual mortality was 0.378 ± 0.043 on road territories versus 0.218 ± 0.023 on nonroad territories (χ² = 11.61, p = 0.0007) for male breeders and 0.372 ± 0.042 versus 0.235 ± 0.023 (χ² = 9.15, p = 0.0025) for female breeders. Males and females did not differ significantly in their annual mortality rates either on road territories (χ² = 0.002, p = 0.96) or nonroad territories (χ² = 0.28, p = 0.60).

Similar patterns were evident in an analysis of long-term survivorship schedules (Fig. 2); pronounced differences between nonroad and road territories were evident for both males (Breslow-Gehan-Wilcoxon rank test (χ² = 11.00, p = 0.0009) and females (χ² = 8.94, p = 0.0028), but no differences between the sexes were evident within either nonroad territories (Breslow-Gehan-Wilcoxon rank test, (χ² = 1.90, p = 0.17) or road territories (χ² = 0.53, p = 0.47; Fig. 2). Therefore, we pooled data for males and females in subsequent analyses.

For breeders on nonroad territories, the observed survivorship schedules departed only modestly from the schedules expected under an assumption of constant annual mortality and was slightly concave downward (Fig. 2), suggesting that annual mortality increased gradually over time (McDonald et al. 1996). Surprisingly, however, for suggesting that annual mortality increased gradually over time (McDonald et al. 1996). Surprisingly, however, for

We further investigated the possibility of decreasing mortality over time on road territories by performing a more restrictive analysis limited to road-naive breeders (Fig. 3a & 3b). In their first year as potential breeders, road-naive birds living on road territories experienced extraordinarily high annual mortality, 0.50, compared to just 0.17 for naive birds on nonroad territories (χ² = 27.71, p < 0.0001). By year 2 the difference was smaller (0.45 vs. 0.26) but still statistically significant (χ² = 13.73, p = 0.0002). From year 3 onward, the annual mortality of breeders on road and nonroad territories did not differ significantly (Fig. 3b). Thus, the risk of road mortality appears to be greatest for naive birds in the first 2 years of living on the road. This result is further supported by an analysis of survival and annual mortality in road-experienced breeders. Survival and annual mortality of road-experienced birds breeding on road territories did not differ significantly from those of birds breeding on nonroad territories (Fig. 3c & 3d).

The conclusion that roadside mortality was especially pronounced in road-naive breeders also is supported by direct evidence of the time of death of the 11 breeders found dead on the road during the study. Only 1 of the 11 had previous experience living on the road, and only 2 (1 of which was the road-experienced breeder) lived more than 2 years on the road before being killed. Of the 9 remaining birds, 7 were killed <1 year after immigrating to a road territory.

One question that arises from the preceding analyses is the degree to which differences in breeder survival on road and nonroad territories are attributable to road-related differences in habitat quality. It is possible that some, or perhaps even most, of the reduced survival on road territories may have resulted from road-induced changes in habitat quality rather than directly from automobile traffic. This issue can be addressed by examining patterns of breeder survival on territories bordering the west and south boundaries of the study area (Fig. 1). Birds living on the west and south boundaries were exposed to many of the same set of anthropogenic habitat modifications—such as a broad firelane cleared of all vegetation with powerlines and fencing—as birds on roadside territories, but not to high-speed vehicle traffic. Survival of breeders living on the west and south boundary was significantly higher than that of breeders on road territories (Breslow-Gehan-Wilcoxon rank test, χ² = 10.74, p = 0.001, but was not significantly different from that of birds breeding on interior territories (χ² = 0.04, p = 0.85; Fig. 4). Therefore, we have no evidence that road-induced habitat modifications contributed to the differences in breeder survival on road and nonroad territories.

**Nesting Success**

When analyzed on a per-nest basis, nesting success on road and nonroad territories was similar. For nests that
received at least one egg, the mean (±SE) of young fledged was 1.29 ± 0.15 (n = 86 nests) for nests on road territories versus 1.33 ± 0.15 (n = 265 nests) for nests on nonroad territories (t = 0.23, p = 0.82). On a per-season basis, the difference between road and nonroad territories was more pronounced but not statistically significant. Over the course of an entire nesting season, potential breeding pairs produced 1.35 ± 0.16 fledged young (n = 82 pair-seasons) on road territories versus 1.65 ± 0.11 fledged young (n = 217 pair-seasons) on nonroad territories (t = 1.39, p = 0.17).

Simple comparisons of nesting success on road and nonroad territories are confounded by two additional variables known to influence reproductive success in Florida Scrub-Jays: breeder experience and the presence of nest helpers (Woolfenden & Fitzpatrick 1984; Mumme 1992). Because of high mortality and rapid turnover of breeders on road territories, jays breeding there were less likely to have previous reproductive experience than birds breeding on nonroad territories. The percentage of groups in which neither member, one member, or both members of the breeding pair had nested previously was, respectively, 17.6%, 21.6%, and 60.8% for nonroad territories (n = 204 pair-seasons) versus 30.5%, 29.3%, and 40.2% for road territories (n = 82 pair-seasons) (χ² = 10.48, df = 2, p = 0.005). Pairs of which one or both members are novices often either fail to nest or initiate nesting late in the season when the probability of nest predation is high and the chance of re-nesting is low (Woolfenden & Fitzpatrick 1984; Schaub et al. 1992).

Similarly, because of the high proportion of novice breeders and poor post-fledging survival of young (Fig. 5), breeding pairs on road territories typically had fewer potential helpers than breeders on nonroad territories.
(0.48 ± 0.09 vs. 0.76 ± 0.07; \( t = 2.32, p = 0.02 \)). Previous research, both correlative and experimental, has shown that reproductive success in Florida Scrub-Jays is higher when potential helpers are present (Woolfenden & Fitzpatrick 1984, 1990; Mumme 1992).

To control for the confounding effects of breeder experience and the presence of helpers, we subjected our data on seasonal reproductive success to an analysis of variance (ANOVA). The three main factors in the ANOVA model were road exposure (road or nonroad), breeder experience (neither member of the the pair experienced, one member experienced, or both experienced), and the presence of potential helpers (absent or present). Year was included as an additional factor to control for annual variation. In this model, both prior breeding experience and the presence of potential helpers had significant effects on reproductive success (main effects \( F_{2,268} = 9.93, p < 0.001 \), and \( F_{1,268} = 9.04, p = 0.003 \), respectively). The effect of road exposure was not significant, however, either as a main effect (\( F_{1,268} = 0.27, p = 0.60 \)) or in interaction with other factors (all interaction terms \( p > 0.05 \)). Road exposure therefore had no effect on nesting success beyond its indirect effects on breeder experience and group size.

Post-Fledging Survival of Juveniles

Of 130 young jays that were banded as nestlings on road territories and fledged successfully, 8 (6.2%) were found dead on the road before they were 180 days old. Because this number underestimates the extent of road mortality, a comparison of overall patterns of juvenile survival on road and nonroad territories is appropriate. Survival of young from fledging (day 18) to day 180 was lower on road territories than on nonroad territories (Fig. 5a). This difference fell short of statistical significance (Breslow-Gehan-Wilcoxon rank test, \( \chi^2 = 3.48, p = 0.062 \)), apparently because of strongly varying patterns of age-specific mortality (Fig. 5b).

Fledgling mortality between day 18 and day 30 did not differ significantly between road and nonroad territories; in fact, it was slightly lower for fledglings on road territories (Fig. 5b). This result is consistent with the timing of behavioral development in Florida Scrub-Jays; fledglings <30 days old are largely immobile, are completely dependent on their parents and helpers, and do not forage on their own (McGowan & Woolfenden 1990; Woolfenden & Fitzpatrick 1996). Thus, fledglings at this early age are unlikely to be vulnerable to road mortality. Nevertheless, fledglings on road territories experienced
significantly higher mortality than did nonroad fledglings in the intervals of 30–60 days and 60–90 days ($\chi^2 = 12.15$ and $14.80$, $p = 0.0005$ and 0.0001, respectively; Fig. 5b). Juvenile jays in these age intervals are highly mobile and capable fliers. They forage extensively on their own by day 60 and achieve nutritional independence by day 85 (McGowan & Woolfenden 1990; Woolfenden & Fitzpatrick 1996). After day 90, however, juvenile mortality on road and nonroad territories did not differ significantly (Fig. 5b).

These results suggest that juvenile Florida Scrub-Jays on road territories were most vulnerable to road mortality between the ages of 30 and 90 days, a time when juveniles were reaching independence. Further support for this conclusion is provided by data on the time of death of the eight known-age juveniles found dead on the road during the study. All eight were between 42 and 78 days old when killed (mean $\pm$ SD = 65.0 $\pm$ 11.4).

Post-fledging survival of young on road territories appeared to be unrelated to parental experience with roads. Survival of fledglings with at least one road-experienced parent did not differ significantly from that of young with road-naive parents (Breslow-Gehan-Wilcoxon rank test, $\chi^2 = 0.92$, $p = 0.34$).

**Patterns of Dispersal and Immigration**

During 9 years of study, 127 breeding vacancies were filled on road territories. Of these, 42 (33%) were filled by road-experienced birds. Thus, most (67%) breeding vacancies on road territories were filled by road-naive immigrants.

Jays were just as likely to move from road territories to nonroad territories as vice versa. For example, of 57 jays that fledged on nonroad territories and eventually became breeders, 14 (24.6%) dispersed to and attempted breeding on road territories. Of 8 jays that fledged on road territories and eventually became breeders, 2 (25.0%) dispersed to and attempted breeding on nonroad territories (Fisher’s exact test, $p = 0.99$). Similar indifference to road and nonroad territories was evident from an analysis of the 12 jays that bred on both a road territory and a nonroad territory at some time during their lives: 7 bred initially on a road territory and subsequently moved to a nonroad territory, whereas 5 did the reverse (binomial test, $p = 0.77$). We therefore found no compelling evidence that road territories were avoided by the jays or perceived by them as inferior habitat.

**Demographic Consequences of Road Mortality**

We examined the effect of proximity to the road on overall mortality and reproduction of Florida Scrub-Jays by using demographic parameter estimates based both on long-term averages reported by Woolfenden and Fitzpatrick (1984, 1996) and on data we collected (Table 1).

For example, because we found that proximity to the road significantly affected both the mean annual mortality of breeders and the mortality of fledglings through day 90 (Fig. 5), we estimated these parameters for nonroad territories and road territories from our data. Because we found no effect of proximity to the road on either the production of fledged young or the survival of juveniles beyond day 90, we estimated these parameters using long-term averages reported in Woolfenden and Fitzpatrick (1984, 1996).

On road territories, breeder mortality exceeded production of yearlings by 0.30 birds per year (Table 1). The actual shortfall in demographic success on road territories was undoubtedly greater, given that most Florida Scrub-Jays do not begin breeding until they are 2–3 years old. Nonroad territories, in contrast, produced a surplus of yearlings relative to breeder mortality (Table 1).

**Discussion**

Proximity to a paved road had two major demographic consequences for Florida Scrub-Jays. First, road-naive immigrants that established roadside breeding territories suffered extremely high annual mortality during their first 2 years as breeders (Fig. 3b), in many cases not even surviving long enough to attempt nesting. Second, although nesting success and the production of fledged young were comparable on road and nonroad territories, mortality of fledglings 30–90 days old was significantly greater on road territories (Fig. 5). Our results also suggest that the cause of the high mortality of breeders and fledglings on road territories was motor ve-

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<th>Table 1. Estimation of the overall effects of proximity to road on the annual mortality of breeders and production of yearlings in the Florida Scrub-Jay.</th>
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<td><strong>Nonroad territories</strong></td>
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<tr>
<td>Number of young fledged per breeding pair per year</td>
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<td>Proportion of young surviving from fledging to day 90</td>
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<td>Proportion of young surviving from day 90 to year 1</td>
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<td>Annual mortality of breeders</td>
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<td>Annual breeder mortality per breeding pair</td>
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<td>Annual production of yearlings per breeding pair&lt;sup&gt;d&lt;/sup&gt;</td>
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<td>Demographic surplus (deficit)</td>
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<sup>a</sup>Long-term average derived from Woolfenden and Fitzpatrick (1996).
<sup>b</sup>This study.
<sup>c</sup>Long-term average derived from Woolfenden and Fitzpatrick (1996).
<sup>d</sup>Calculated as twice the annual mortality of breeders.
<sup>e</sup>Calculated as number of surviving 1-year-olds produced per breeding pair per year.
Vehicle traffic per se and not anthropogenic, road-induced habitat modifications.

**Decreasing Mortality with Increasing Experience**

One of the most striking results of our analysis is that the risk of road mortality in Florida Scrub-Jays declined in older, more road-experienced breeders and juveniles (Figs. 3b & 5b). For example, although juveniles were highly vulnerable to road mortality when 30–90 days old, thereafter juvenile mortality on road and nonroad territories was virtually identical (Fig. 5b). We never found a juvenile older than 78 days dead on the road, and no jay that fledged on a road territory and survived past 90 days was ever found road-killed later in life.

Why did the risk of road mortality decline with age and experience in breeders and juveniles? We propose two hypotheses. First, jays living on road territories may have eventually learned to avoid vehicles, resulting in reduced vulnerability of these individuals over time. Learning could have been experiential (e.g., through nonfatal encounters with automobiles), observational (e.g., seeing other jays killed or nearly killed by vehicles), or a combination of the two. The second hypothesis is that declining rates of road mortality may reflect selection through time, or demographic heterogeneity (Carey et al. 1992; Rexstad & Anderson 1992; McDonald et al. 1996). Under this hypothesis, naive adults and juveniles living on road territories varied in their inherent degree of vulnerability to automobile traffic, and the most vulnerable individuals were rapidly eliminated by vehicular selection. Only those individuals inherently unlikely to be killed by vehicles survived long enough to join older age classes and to be classified as “road-experienced.”

Regardless of whether learning or selection through time was responsible for the experience-dependent decrease in road mortality, the period during which Florida Scrub-Jays suffered high road mortality was more compressed in juveniles than in adults. Although mortality rates for road-naive breeders were elevated for at least 2 years following dispersal to a road territory (Fig. 3b), the period of high mortality for juveniles was limited to a 2-month window when young were 30–90 days old (Fig. 5b). One possible explanation for this difference between breeders and juveniles is that a sensitive period exists early in life, during which time young jays are especially proficient at learning how to avoid fast-moving vehicles. Road-naive adults, on the other hand, may be less capable of learning these skills and therefore experience high rates of road mortality for a longer period of time. Sensitive periods early in development are known to be important in many learned behaviors of birds, such as species recognition and song (Alcock 1998). It is also possible, however, that the difference between juveniles and adults in the length of the period of high road mortality may simply indicate that vehicular selection on recently fledged young was especially intense and that the relatively few juveniles that survived to 90 days of age on road territories were the ones least likely to be killed by vehicles.

**Road Mortality and Source-Sink Dynamics**

During our 9-year study, Florida Scrub-Jay habitat adjacent to a highway was a demographic sink in which breeder mortality exceeded production of yearlings by a wide margin (Table 1) and jays persisted only because of immigration from nonroad territories. Our analysis (Table 1), is based on demographic averages for all road and nonroad territories, however, and the exact consequences of living on a road territory varied. For example, road territories in which both breeders were road-experienced were not subject to high breeder mortality (Fig. 3d). Nonetheless, because 67% of breeding vacancies on road territories were filled by road-naive immigrants, and because these naive birds suffered extraordinarily high mortality during their first 2 years on the road (Fig. 3b), mean annual mortality was considerably higher on road territories than on nonroad territories (Table 1). Furthermore, high post-fledging mortality occurred on all road territories, even on those with road-experienced breeders.

Our analysis of mortality and reproduction is conservative in that we assumed that road exposure had no effect on the production of fledged young (Table 1). In fact, nesting success was slightly but not significantly lower on road territories than on nonroad territories. In addition, pairs on road territories were significantly more likely to have no previous breeding experience and fewer potential helpers, both factors that are known to have significant effects on reproductive success in Florida Scrub-Jays (Woofenden & Fitzpatrick 1984; Mumme 1992). It is therefore likely that road exposure had weak indirect effects on the production of fledged young, and these were not considered in our analysis.

Although road territories in our study area clearly were demographic sinks for Florida Scrub-Jays, the jays did not behave as if roadsides were inferior habitat. All suitable scrub adjacent to the road was continuously occupied and defended throughout our 9-year study. Territory density was at least as high, if not higher, along the road as it was in interior habitats (e.g., Fig. 1). Jays were no more likely to move from road territories to nonroad territories, or vice versa. In short, we found no evidence that Florida Scrub-Jays regarded roadsides as suboptimal habitat. In fact, given the species’ well-known preference for clearings and open areas within a matrix of scrub (Cox 1987; Breininger et al. 1996; Fitzpatrick et al. 1991), it is quite possible that roadsides are perceived by Florida Scrub-Jays as being particularly attractive habitat.

The apparent inability of Florida Scrub-Jays to recognize roadsides as inferior and dangerous habitat is not
surprising given that automobile traffic has been a significant agent of animal mortality for less than a century (Stoner 1925), and locally for only a few decades. Thus, assuming that heritable genetic variation in the tendency to settle near roads even exists in Florida Scrub-Jays, opportunity for selection to produce an adaptive evolutionary response and innate avoidance of roadside habitat has been limited.

We also saw no indication that jays learned to avoid roadside habitat based on individual experience. This contrasts sharply to the situation in Willow Warblers (Phylloscopus trochilus) living along a heavily traveled highway in the Netherlands (Foppen & Reijnen 1994; Reijnen & Foppen 1994). Although survival of Willow Warblers was similar on road and nonroad territories, males that established territories near the highway produced about 40% fewer young, apparently because traffic noise interfered with male song and made it difficult for males to attract and retain mates. As a result, territory density was lower near the road, and road zones were occupied primarily by first-year males that often bred unsuccessfully and actively moved away from the highway in subsequent years. The behavior of male Willow Warblers toward roadsides therefore was modified by experience, and males treated roadsides as inferior habitat.

Why do male Willow Warblers respond to roadsides as sinks, whereas Florida Scrub-Jays do not? One possible explanation is that, because roadsides are mate-attraction sinks for Willow Warblers, male warblers receive significant and ongoing feedback about the suitability of roadsides as breeding habitat. In Florida Scrub-Jays, however, roadsides are mortality sinks, and mortality is generated by an unnatural "predator" of recent anthropogenic origin. As a result, the feedback that Florida Scrub-Jays receive about the quality of road habitat may be limited, making it unlikely that jays will learn that roadsides are dangerous places and best avoided. The inability of Florida Scrub-Jays to learn to avoid roadsides also may reflect the extreme habitat limitation in which these birds exist, and their general sedentary nature (Woolfenden & Fitzpatrick 1984, 1996).

Conservation Implications

Regardless of why Florida Scrub-Jays do not recognize roadsides as sinks, the ultimate result is that jays inhabiting a landscape of both road and nonroad habitats have less-than-ideal rules of habitat selection (Pulliam & Danielson 1991). This has important conservation implications, because in species with limited abilities to select ideal (source) habitat and avoid suboptimal (sink) habitat, subtle changes in the amount and distribution of source and sink habitat can have significant and destabilizing effects on the dynamics of populations and metapopulations (Pulliam 1988; Pulliam & Danielson 1991; Holt 1994; Dias 1996). For example, Pulliam and Danielson (1991) have shown that for species with limited abilities to avoid inferior habitats, an increase in the amount of suboptimal sink habitat may lead to a decrease in global population size and an increased risk of extinction.

In the case of the Florida Scrub-Jay, it is therefore possible that preservation of oak scrub habitat along a highway could do this threatened species more harm than good. Although population viability modeling will be necessary to specify the conditions under which this theoretical possibility might be realized, the amount of roadside (sink) habitat relative to nonroad (source) habitat will clearly be important (Pulliam & Danielson 1991). More subtly, however, population viability may also depend on the extent and nature of dispersal between road and nonroad territories. In our study, for example, 67% of all breeding vacancies on road territories were filled by road-naive immigrants that were especially susceptible to road mortality (Fig. 3b). On the other hand, although relatively few yearlings were produced on road territories (Table 1), these road-experienced birds appeared to be largely immune to road mortality (Fig. 3d). Therefore, in populations where most or all jays raised on road territories become breeders on other road territories, immigration of road-naive birds would be reduced proportionally and the demographic consequences of road mortality would be less severe than if most birds raised on road territories dispersed to nonroad territories. Viability analysis for populations exposed to road mortality will need to incorporate explicit assumptions about dispersal and the frequency with which breeding vacancies on road territories are filled by road-naive and road-experienced immigrants.

We conclude that roadside habitat constitutes a population sink of a particularly insidious and destabilizing nature for Florida Scrub-Jays. First, because of high rates of breeder mortality on road territories, roadsides are death traps that continuously attract new immigrants, most of which are road-naive and likely to become road kills themselves. Second, because immigrants that fill breeding vacancies along roads typically are young adults at peak reproductive value (Woolfenden & Fitzpatrick 1984), the death of these immigrants is likely to have a disproportionate effect on the potential for population growth. Third, probably because roads are mortality sinks of recent anthropogenic origin, Florida Scrub-Jays show neither innate nor learned aversions to these inferior habitats.

Road mortality clearly presents a difficult challenge for the conservation and management of Florida Scrub-Jays because most remaining populations exist near major roads or in regions of rapid human population growth. Our data provide concrete backing for the recommendations of Fitzpatrick et al. (1991) that habitat preserves tended for long-term Florida Scrub-Jay protection be buffered from direct interaction with vehicular traffic. Placement of new roads through existing tracts of scrub

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habitat in Florida should be minimized. Finally, in areas either supporting or being restored to support Florida Scrub-Jays, traffic management should include diversions, stop signs, and speed bumps whose collective effects will slow vehicle speeds to levels below which they can affect the demography of this threatened and still rapidly declining species.

Although road mortality is a significant source of animal mortality and a major conservation problem (Bennett 1991; Forman & Alexander 1998), its effect may be widely underestimated. Because of difficulties in detection, the number of carcasses found along roads represents only a fraction of the total number of animals actually killed by vehicles (Melvin et al. 1994; Rosen & Lowe 1994; Ashley & Robinson 1996). Our study provides further support for this view. If the differences in mortality we observed between road and nonroad territories are entirely the result of road kill, we estimate that 65 Florida Scrub-Jays (39 breeders and 26 juveniles) were killed by vehicles during our study and that we found only about 30% of them (11 breeders and 8 juveniles). The demographic consequences of road mortality, and its effect on the dynamics of populations and metapopulations, deserve increased attention from conservation biologists.

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