Proximity to a high traffic road: Glucocorticoid and life history consequences for nestling white-crowned sparrows

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ABSTRACT

Roads have been associated with decreased reproductive success and biodiversity in avian communities and increased physiological stress in adult birds. Alternatively, roads may also increase food availability and reduce predator pressure. Previous studies have focused on adult birds, but nestlings may also be susceptible to the detrimental impacts of roads. We examined the effects of proximity to a road on nestling glucocorticoid activity and growth in the mountain white-crowned sparrow (Zonotrichia leucomystax oriaitha). Additionally, we examined several possible indirect factors that may influence nestling corticosterone (CORT) activity secretion in relation to roads. These indirect effects include parental CORT activity, nest-site characteristics, and paternal provisioning. And finally, we assessed possible fitness consequences of roads through measures of fledging success. Nestlings near roads had increased CORT activity, elevated at both baseline and stress-induced levels. Surprisingly, these nestlings were also bigger. Generally, greater corticosterone activity is associated with reduced growth. However, the hypothalamic–pituitary–adrenal axis matures through the nestling period (as nestlings get larger, HPA-activation is greater). Although much of the variance in CORT responses was explained by body size, nestling CORT responses were higher close to roads after controlling for developmental differences. Indirect effects of roads may be mediated through paternal care. Nesting CORT responses were correlated with paternal CORT responses and paternal provisioning increased near roads. Hence, nestlings near roads may be larger due to increased paternal attentiveness. And finally, nest predation was higher for nests close to the road. Roads have apparent costs for white-crowned sparrow nestlings – increased predation, and apparent benefits – increased size. The elevation in CORT activity seems to reflect both increased size (benefit) and elevation due to road proximity (cost). Whether or not roads are good or bad for nestlings remains equivocal. However, it is clear that roads affect nestlings; how or if these effects influence adult survival or reproduction remains to be elucidated.

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1. Introduction

A growing body of evidence indicates that roads have important effects on biological communities. Roads impact ecosystems by fragmenting habitat, increasing land use by people, causing road mortality of wildlife, and altering the composition of native plant and animal communities [19,20,52]. Consequently, areas with high road density are associated with decreased population densities, genetic diversity, and biodiversity in many taxa including plants, mammals, reptiles, amphibians, and birds [6,18,28]. Although roads have detrimental effects on some species, other species appear unaffected or even benefit from their presence (e.g. [38,42,46]). Roads can increase the availability of some food resources such as seeds, insects, and carrion, facilitate foraging by clumping resources along edge habitat, facilitate predator vigilance behavior allowing birds to feed more, and create corridors that facilitate wildlife dispersal [38,51,52,56]. Although the direction and degree of road effects appears to be highly species- and context-specific, roads clearly alter biological communities. The continual increase in both roads and human population make understanding these effects increasingly important for management and conservation.

One way to assess the impacts of roads on wildlife is to examine the effects roads have on physiological stress. The vertebrate stress response includes the release of cytokines and catecholamines, and the release of glucocorticoids via activation of the hypothalamic–pituitary–adrenal (HPA) axis. The acute response promotes survival, but chronic activation leads to suppression of growth, digestion, reproduction, and immune function [47,66]. Glucocorticoids become elevated in response to human disturbance in wildlife including spotted hyenas (Crocuta crocuta), European pine martens (Martes martes), yellow-eyed penguins (Megadyptes antipodes), gray wolves (Canus lupus), and elk (Cervus canadensis).
elaphus) [14,17,32,37,55], but see Romero and Wilkelski [45]). In birds, proximity to roads increased glucocorticoids in the northern spotted owl (Strix occidentalis caurina) and the mountain white-crowned sparrow (Zonotrichia leucophrys oriantana) [15,26,64]. Additionally, traffic noise has been shown to increase fecal corticosterone (CORT; the dominant avian glucocorticoid) in sage grouse (Centrocercus urophasianus) and increase behavioral stress and decrease immune function in domesticated chickens [Blickley et al. in prep [11]].

Previous studies have focused on the effects of roads on adult birds; however nestlings are also susceptible to anthropogenic disturbances. Nestling Magellanic penguins (Spheniscus magellanicus) living in tourist-exposed sites had elevated stress responses compared to nestlings from undisturbed populations [62]. Similarly, juvenile Hoatzins (Opisthocomus hoazin) living in areas with tourists secreted more CORT in response to a stressor and had lower body weights than individuals in areas without tourists [40]. Nestlings may be particularly susceptible to stressors associated with roads because they are confined to nests during early development and are unable to move away from stressful stimuli [53]. Additionally, adult animals can habituate to stressors over time by reducing HPA activity, thus reducing the negative effects of elevated CORT [22,45,63]. In contrast, nestlings may not habituate to novel stressors over the short nestling period and thus anthropogenic disturbances may elevate stress responses in developing animals, but not in adults [9,63], but see [41].

In addition to being more susceptible to anthropogenic disturbances, nestlings may also suffer greater consequences from their exposure. Elevated CORT during development has immediate effects, such as inhibition of growth and immune function [54,59]. However, this brief elevation during development can have lifelong consequences for physiology, morphology, and behavior [12,24,57]. Stressed neonates can be hypersensitive to stress as adults [9,63, but see [41]].

Nestlings may be particularly susceptible to stressors associated with roads because they are confined to nests during early development and are unable to move away from stressful stimuli [53]. Additionally, adult animals can habituate to stressors over time by reducing HPA activity, thus reducing the negative effects of elevated CORT [22,45,63]. In contrast, nestlings may not habituate to novel stressors over the short nestling period and thus anthropogenic disturbances may elevate stress responses in developing animals, but not in adults [9,63], but see [41].

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2. Methods

2.1. Study area and birds

Our study was conducted on the population of white-crowned sparrows located in Tioga Pass Meadow, directly outside the eastern entrance to Yosemite National Park, CA (37°54'N, 119°15'W). This population of sparrows has been studied extensively since 1967, and a substantial proportion of adults in this population are marked with a unique combination of colored bands for identification. Mountain white-crowned sparrows are migratory songbirds that arrive at Tioga Pass in May and breed from late May to early August [39]. The principal nest predator on white-crowned sparrow nests in this area are Belding’s ground squirrels (Spermophilus beldingi) although long-tailed weasels (Mustela frenata), coyotes (Canis latrans), Clark’s nutcrackers (Nucifraga columbiana), and common ravens (Corvus corax) are also important predators [39]. Over a 22-year period, an average of 47% of nests at this site successfully fledged nestlings. Nest predation was the primary cause of nest failure (57%). The remaining nest failures were due to nest abandonment (22.3%), inclement weather (16.2%), and other factors (4.5%) including death of attending parents and nests falling apart due to poor construction [39].

Highway 120 runs through this study site to the entrance of Yosemite National Park (Fig. 1). Once the entrance into Yosemite opens (late May), traffic on HWY 120 is heavy during daylight hours. The California Department of Transportation recorded an average traffic rate of 2971 cars/day along this section of Highway 120 from June to August in 2009 [10]. Although this traffic load is low compared to larger highways and interstates, traffic-induced increases in adult bird stress responses have been demonstrated on smaller roads [15]. This traffic load exists throughout the white-crowned sparrow nesting and fledgling periods. The closest nests to Highway 120 were 5 m from it and the farthest over 300 m away (Fig. 1).

Nestling provisioning data was collected from 5 to 21 July of 2010. All other data were collected between 28 May and 18 July of 2009.

2.2. Nest searching and GIS analyses

Nests were located by direct search as well as observation of adult behaviors. If nests were found prior to clutch completion, we checked them daily until the clutch was complete (number of nest checks did not influence predation rates, data not shown). Females begin to incubate the day before the last egg is laid and nestlings hatch an average of 123.3 days after incubation commences [39]. Using this information, we estimated hatch date for clutches and checked nests daily starting 1–4 days before hatching to determine hatch date. If nests were found with a complete clutch, we monitored them daily until hatch date. We did not check nests after nestlings hatched to ensure that our presence would not influence nestling glucocorticoid physiology.

Nests were considered successful if at least one nestling fledged. We confirmed fledging success by observing or trapping fledglings, or by watching parents carry food or feed fledglings. Nests were considered predated if eggs or nestlings vanished before fledging and were considered abandoned if parents stopped building nests, feeding nestlings, or laying eggs.
Fig. 1. GIS map of white-crowned sparrow nests in Tioga Meadow, CA.
We took GPS coordinates of each nest using a Garmin eTrexGPS device in WGS 84 datum. The distance between each nest and Highway 120 was calculated using the Nearest Features 3.8 extension in ArcView Geographic Information System (GIS).

2.3. Stress protocol and morphological measurements – nestlings

White-crowned sparrow nestlings respond to stressors with increased CORT secretion in as few as 5 days after hatching and reach peak levels of CORT by 30 min of stress exposure [60]. Seven days after hatching, the largest nestling in each nest was exposed to a standardized capture and handling protocol as described by Wingfield [65]. Although plasma CORT typically increases within 3 min of stress exposure [44], Nuttall’s white-crowned sparrows (Zonotrichia leucophrys nuttalli) do not show an increase in CORT until 4 min following stress exposure [60]. For this reason, we used blood samples obtained within 4 min of disturbing a nest as baseline samples. Samples obtained within 4 min show no significant increase in corticosterone (CORT; the dominant avian glucocorticoid; \( P < 0.56; \ r = 0.14; df = 1,19 \)). After initial blood samples were obtained, we placed nestlings in cloth bags and collected two more samples 15 and 30 min after initial disturbance. To collect blood, we punctured the alar vein with a 26-gauge needle and collected 25 \( \mu \)l of blood with heparinized microcapillary tubes. Immediately after collection, blood was kept on ice (<2 h) until it could be centrifuged to separate the plasma from red blood cells (3000 rpm for 7 min). After separation, the plasma was isolated and stored at -20 °C.

After blood sample collection, we weighed nestlings to the nearest 0.1 g and measured tarsus length (posterior to anterior tarsus) to the 0.1 mm. All nestlings were measured once by one person (O.C.). Each nestling was banded with a USGS service band on the right leg prior to release back into the nest.

2.4. Stress protocol – parents

To examine correlations between parental and nestling stress responses, we captured parents after fledging and exposed them to a standard capture and handling protocol. Parents were captured using Potter traps baited with millet seed between 1 and 9 days after at least one nestling had fledged. We determined parentage by noting which sparrows reacted defensively (chipping, swooping flights, etc.) when we disturbed nestlings for our study. Maternity could also be verified by noting the band combination of females if they flushed from their nests.

We collected 100 \( \mu \)l of blood from adults for a baseline sample within 3 min of approaching a trap (there is no significant increase in CORT within 3 min in this population, C. Breuner, unpublished data). Following the initial sample, birds were placed in cloth bags and two additional 50 \( \mu \)l blood samples were obtained after 15 and 30 min of restraint. Blood was collected as per described for nestlings (see above). We sampled 16 males for baseline CORT, but were unable to obtain post-disturbance samples for three males. Therefore, \( n = 16 \) for paternal baseline and \( n = 13 \) for stress induced levels of CORT.

2.5. Corticosterone assays

Corticosterone was quantified with Enzyme Immunoassay (ELA) kits (Cat No. 901-097, Assay Designs), previously optimized for white-crowned sparrow nestlings [60]. Following the protocol used by Wada et al. (2007) [60], we used a raw plasma dilution of 1:40 to determine CORT levels. Briefly, we added 10 \( \mu \)l of 1:100 steroid displacement buffer (SDB) to 10 \( \mu \)l of plasma. After 15 min, we added 380 \( \mu \)l of assay buffer for a total dilution of 1:40. Samples were vortexed and 100 \( \mu \)l of a sample was added to individual wells in triplicate. These samples were compared to a standard curve with six samples run in triplicate ranging from 20,000 to 15.53 pg/ml (100 \( \mu \)l/well). An external standard of 500 pg/ml was run on every plate in triplicate and used to calculate inter-plate variation. Plates were read on a Multispec Ascent microplate reader at 405 nm corrected at 595 nm. Intra- and inter-plate variation was 6.04% and 11.77%, respectively.

From the plasma samples, we were able to calculate baseline CORT (the amount of endogenous CORT prior to disturbance) and total integrated CORT (the total amount of CORT secreted over the 30-min period of restraint).

2.6. Nest-site vegetation analysis

To examine the effects of nest site habitat on nestling stress responses, we quantified the composition of the dominant vegetation in a 12-m² area around each nest using a qualitative ranking system adapted from [25]. Briefly, a 1 m² divided into four equal quadrats was placed at each compass direction surrounding a nest (e.g. west, north, etc.) covering a total of 4 m². Two additional 1-m² plots were placed on each side of the 4-m² block creating a cross of plots that covered a total of 12 m². Within each 1-m² plot, the density of two dominant willow species diadem leaf willow (Salix planifolia) and Sierra willow (S. orestera), lodgepole pine (Pinus contorta), herbaceous plants (grasses and forbs), and dirt/rock cover was rated on a scale from 0 to 5 using estimates of percent cover as follows: 0 = 0%, 1 = 0–20%, 2 = 20–40%, 3 = 40–60%, 60–80%, and S = 80–100%. We also measured the height of each vegetation type for each quadrat. The values for the quadrats were averaged for each 1-m² plots and then all 12 plots were averaged for mean total density and mean height scores for each type of vegetation at each nest site.

2.7. Parental provisioning rates

We measured nestling provisioning by recording nests for \( \approx 1.5 \) h for three consecutive days starting 4 days after hatching. We recorded nests using VehoMuv mimcDV camcorders that were zip-tied to vegetation surrounding nests or attached to stakes planted in the ground. Parental feeding rates were recorded starting on average between 9 and 10 AM. Video footage was downloaded and analyzed by one single observer (E.J.) using VideoLAN VLC media player. Videos were scored for male and female behaviors including number of feeding trips, time spent feeding nestlings, nest attendance, and, for females, incubation bouts and time spent incubating. We defined nest attendance as the total time spent provision nestlings, removing fecal sacs, and maintaining the nest. We divided the amount and duration of behaviors observed by the total length of video footage which varied slightly between cameras depending on battery life. We used the subsequent behaviors/hour in all statistical analyses. We were able to distinguish between individuals because parents were color banded with a unique combination of color bands. We excluded one nest from analyses because we were unable to obtain videos for three consecutive days so \( n = 11 \) for analyses of provisioning and incubation. Additionally, we were unable to obtain a blood sample from one nestling so \( n = 10 \) for analyses involving parental provisioning and nestling stress physiology. The nests used in these analyses were located 17–279 m from the road.

2.8. Statistical analyses

Tarsus length and mass were highly associated (\( P < 0.01; r^2 = 0.79 \)). For this reason, we used a principal component analysis (PCA) to reduce morphological traits to one component score for size. Both traits loaded highly and positively on component one.
3. Results

3.1. Nest searching and GIS analyses

Between 28 May and 7 July, we located 50 nests. Of these, 27 were predated or abandoned. We obtained stress series on nestlings from the remaining 23 nests. Three nests were later excluded from analyses because either the nestlings died before fledging \(n = 1\) or we were uncertain about hatching date \(n = 2\). We did not obtain wing measurements for two nestlings therefore \(n = 18\) for analyses with body measurements. Nests ranged between 5 and 300 m from the road.

3.2. Nestling morphological measurements and CORT responses

Nestlings were larger near roads (Fig. 3, \(N = 18\), \(F_{1,18} = 7.12, P = 0.02\)). Nestling HPA activity increased with proximity to road (Fig. 4). This was observed for baseline CORT \((N = 20, F_{1,19} = 5.343, P = 0.033)\) and total integrated CORT \((N = 20, F_{1,19} = 6.99, P = 0.017)\). As they age, nestlings mount stronger stress responses during standardized handling \[58\]. Because of the positive correlation between proximity to road and body size, it is possible that slight differences in age or size explain the positive correlation between stress response and proximity to road. However, (1) nestling body size was not correlated with nestling baseline or total integrated CORT \((P > 0.25\) for all); (2) when corrected for body size, total

### Table 1

<table>
<thead>
<tr>
<th>Nest characteristics</th>
<th>Lodgepole pine cover</th>
<th>Diamondleaf willow cover</th>
<th>Sierra willow cover</th>
<th>Ground cover</th>
</tr>
</thead>
<tbody>
<tr>
<td>Nest height (m)</td>
<td>0.77</td>
<td>0.26</td>
<td>-0.15</td>
<td>0.06</td>
</tr>
<tr>
<td>Mean diamondleaf willow height (m)</td>
<td>0.17</td>
<td>0.96</td>
<td>-0.12</td>
<td>-0.01</td>
</tr>
<tr>
<td>Mean diamondleaf willow density</td>
<td>-0.41</td>
<td>0.93</td>
<td>-0.28</td>
<td>0.15</td>
</tr>
<tr>
<td>Mean Sierra willow height (m)</td>
<td>0.14</td>
<td>-0.11</td>
<td>0.96</td>
<td>-0.10</td>
</tr>
<tr>
<td>Mean Sierra willow density</td>
<td>-0.08</td>
<td>-0.21</td>
<td>0.96</td>
<td>-0.03</td>
</tr>
<tr>
<td>Mean lodgepole pine height (m)</td>
<td>0.96</td>
<td>-0.02</td>
<td>0.12</td>
<td>0.05</td>
</tr>
<tr>
<td>Mean lodgepole pine density</td>
<td>0.97</td>
<td>-0.06</td>
<td>0.07</td>
<td>0.07</td>
</tr>
<tr>
<td>Mean herbaceous pine density</td>
<td>-0.13</td>
<td>-0.42</td>
<td>-0.06</td>
<td>-0.86</td>
</tr>
<tr>
<td>Mean bare ground density</td>
<td>0.06</td>
<td>-0.49</td>
<td>-0.35</td>
<td>0.74</td>
</tr>
</tbody>
</table>

Bold values indicate nest site variables that load highly on component scores.

CORT data for nestlings were normally distributed (Shapiro–Wilk test of normality, \(P > 0.05\) for all). For this reason, raw data were used in all analyses for nestlings. Hormonal data for adults were not normally distributed (Shapiro–Wilk, \(P < 0.05\) for all). However, because rank-order statistics were used to analyze parental stress responses, we did not transform CORT data (see below).

Baseline and total integrated CORT for nestlings were highly associated \(P < 0.01, r^2 > 0.58\). For this reason, we used simple linear regressions to examine relations between proximity to road and both nestling adrenocortical activity and body size. To analyze nest site characteristics, we used principal components analysis (PCA) with varimax rotation to reduce nine nest-site variables to four component scores that explained 92% of cumulative variation (Table 1). We examined associations between each PCA score and nestling adrenocorticoid activity and body size using a general linear model (GLM). We also used GLM analysis to examine changes in nest-site vegetation in relation to proximity to the road.

3.3. Parental CORT response

Nestling CORT responses were positively correlated with paternal CORT responses (Fig. 6; paternal integrated CORT: \(N = 13, r_p = 0.516, P = 0.036\) one-tailed, \(P = 0.071\) two-tailed). There was no association between nestling CORT responses and maternal CORT responses \((N = 17, r_m = 0.027, P = 0.918)\). Likewise, there was no relationship between nestling baseline CORT and CORT level in either parent (paternal: \(N = 16, r_p = 0.091, P = 0.86\); maternal: \(N = 17, r_m = -0.076, P = 0.772\)).

3.4. Nest-site characteristics

PCA produced four factor scores that explained 92% of the variation in nest site characteristics (Table 1). Nest height and lodgepole pine height and density loaded highly and positively on factor 1. Nests in pine trees are higher from the ground than nests in other vegetation. That nests that were high from the ground were found at sites with high pine tree abundance. In this way, factor 1 seems to be a measure of pine cover. The mean height
and density of diamondleaf willow loaded highly and positively on factor 2 (hereafter: diamondleaf willow cover) and the mean height and density of Sierra willow loaded highly and positively on factor 3 (hereafter: Sierra willow cover). Factor 4 (hereafter: ground cover) captured variation in mean bare ground (positively) and mean herbaceous plant density (negatively).

Nestlings from nests with low ground cover (more open ground, less herbaceous plants) had elevated baseline CORT compared to nestlings from nests with low ground cover ($N = 17$, $F_{1,16} = 5.447$, $P = 0.04$). No other factor score explained variation in nestling baseline CORT ($P > 0.69$ for all). There were no association between nestling total integrated CORT and body size with any factor score ($P > 0.31$ for all). Analysis of variance (MANOVA) revealed no difference in nest-site characteristics between nests that fledged and those that failed ($N = 35$, $P > 0.53$ for all factors). Of nests that failed, there was no difference in nest-site characteristics between nests that were found by predators and those that were abandoned ($N = 13$, $P > 0.144$ for all factors).

Willow type tended to change with proximity to the road. Diamondleaf willow cover increased close to the road ($N = 17$, $F_{1,16} = 3.905$, $P = 0.07$), while Sierra willow cover decreased ($N = 17$, $F_{1,16} = 4.332$, $P = 0.06$). Examining the direct interactions between raw variables and road proximity, diamondleaf willow density increased significantly close to roads ($N = 17$, $F_{1,16} = 7.439$, $P = 0.015$) and diamondleaf willow height had a non-significant trend to increase close to road ($N = 17$, $F_{1,16} = 3.953$, $P = 0.064$). In contrast, Sierra willow density and height decreased significantly close to the road ($F = 5.132, 7.052, P = 0.038, 0.017$).

### 3.5. Parental feeding rate

Fathers with nests close to the road were more attentive (Fig. 7A; $N = 11$, $F_{1,10} = 8.334$, $P = 0.018$) and tended to engage in more feeding trips per hour than fathers with nests far from the road (Fig. 7B; $N = 11$, $F_{1,10} = 4.252$, $P = 0.069$). There was no association between road proximity and other measures of male provisioning behavior, female provisioning behavior, or incubation ($P > 0.233$ for all). A paired samples t-test revealed no difference between males and females in the number of feeding trips per hour ($N = 11$, $t_{11} = -0.243$, $P = 0.813$). Linear regression revealed no significant association between nestling adrenocorticoid activity and any measure of parental provisioning or incubation ($P > 0.120$ for all). Finally, there were no associations between average nestling mass, tarsus length, or wing length with adrenocorticoid activity.
or any measure of parental provisioning or incubation ($P > 0.587$ for all).

3.6. Nest success and distance from road

There was no relationship between nest success and distance from the road (Fig. 2A; $N = 50, F_{1,49} = 0.19, P = 0.67$). However, of the nests that failed, those near the road were more likely to be predated whereas those far away were more likely to be abandoned (Fig. 2B; $N = 27, F_{1,26} = 5.16, P = 0.03$).

4. Discussion

4.1. Nestling HPA activity, growth, and road proximity

Nestling sparrows reared close to a road had elevated HPA activity and were larger than nestlings reared far from the road (Figs. 3 and 4). In developing birds, exposure to elevated levels of glucocorticoids decreases growth and development e.g. [27], reviewed in [58]. For this reason we expected HPA activity to be negatively associated with body size in nestling white-crowned sparrows. However, altricial nestlings (including white-crowned sparrows), can have dampened HPA responses during early development that increase over the nestling and fledgling periods [7,8,60,61]. A positive association between nestling body size and HPA activity could result from maturation of the HPA axis. Therefore, elevated HPA activity in nestlings in relation to road proximity may simply indicate that nestlings close to the road develop faster, not that they are more stressed. In this study, body size accounts for a significant amount of variation in CORT secretion. However, when body size was accounted for, nestling stress-induced CORT still increased with proximity to the road (Fig. 5). Additionally, proximity to the road did not shorten the nestling period suggesting that developmental rate was not influenced by the road. Hence, even though nestling body size explains some of the variation in nestling HPA activity, it appears that nestling HPA activity and growth are affected by independent mechanisms that are both associated with road proximity. To our knowledge, this is the first study to demonstrate that proximity to roads affects nestling body size/growth.

4.2. Indirect parental effects

Fathers closer to the road had greater nest attendance and tended to provision more than fathers further away from the road (Fig. 7A and B). Nest attendance combines several behaviors and could indicate the amount of food delivered to nestlings. Fathers closer to roads may provision nestlings more often and with greater amounts of food because road proximity increases food availability, facilitates foraging, or decreases vigilance behavior. The primary foods for nestling white-crowned sparrows are arthropods, adult insects, and larvae [39]. The amount of insects killed by cars on roadways...
increases with increased traffic load [49]. Male white-crowned sparrows provisioning nests close to the road may increase provisioning effort because insect prey is more abundant and easier to obtain. Morgan et al. [38] describe similar results with male Florida scrub-jays living close to roads increasing energy intake and nestling provisioning despite lower foraging rates, suggesting that food is more plentiful or easier to obtain close to the road.

Although male sparrows increase nest attendance and provisioning close to the road, there was no association between maternal provisioning and road proximity. In tree swallows (Tachycineta bicolor), males modulate feeding behavior more than females in response to artificial brood-size manipulations [3]. Additionally, male tree swallows provision nestlings more in areas with higher food abundance, while food availability has no effect on female provisioning [3]. In many passerines, females provision nestlings more than males suggesting that sexes differ in foraging costs and/or the benefits [3,29,31,39]. In our study system, female sparrows may already maximally provision nestlings, and therefore changes in food availability associated with the road have no effect on their provisioning rate.

We observed a correlation between paternal and nestling stress physiology. Such correlations between parents and offspring are not surprising because there is thought to be a strong genetic component to the stress response [48]. However, in our study, we assessed social and not genetic paternity. A high rate of extra-pair fertilizations (EPFs) occur in this population of white-crowned sparrows, so that 30–56% of nestlings are not genetically related to attending males [33]. Therefore, it is likely that correlations between paternal and nestling stress responses arise through paternal behavior or epigenetic effects and not from genetic relatedness. Elevated CORT levels increase foraging behavior in birds such as the Adélie penguin (Pygoscelis adeliae), red-eyed vireos (Vireo olivaceous), and black-legged kittiwakes (Rissa tridactyla) [1,2,30]. Dietz [15] describes elevated levels of CORT in male mountain white-crowned sparrows trapped close to a road. In our system, proximity to the road could elevate paternal CORT which elevates foraging and, thus, nestling provisioning (as per Angelier et al. [1]). Increased resources could accelerate nestling growth and HPA axis development. Therefore, the positive correlation between paternal and nestling CORT physiology would result from increased provisioning mediated by proximity to the road. Conversely, there was no association between maternal and nestling stress physiology. Assuming that provisioning rate is important for nestling growth and HPA axis development, this lack of association is not surprising because females did not provision nestlings more close to the road.

4.3. Nest-site vegetation and nestling stress

We observed a negative association between ground cover and nestling baseline CORT (PCA factor 4). Reduced ground cover could increase nestling exposure to wind and/or temperature changes. Nestling white-crowned sparrows are unable to thermoregulate until three to 4 days after hatching [39]. Therefore, until they transition to endothermy, nestlings are dependent on their mother to minimize fluctuations in temperature that can occur at night or during the day when the nest is exposed to direct sunlight [39]. Fluctuations in temperature increase CORT responses in some birds and nestlings are potentially susceptible to these effects [13,14,23]. Female sparrows could compensate for reduced ground cover (hence greater temperature fluctuations) by increasing incubation or shading. However, we found no association between incubation bouts/duration and proximity to the road. Alternatively, reduced ground cover could increase nestling CORT physiology by increasing exposure to predators. However, nests surrounded by low ground cover were equally likely to fail as to succeed and were no more likely to fail from predation compared to nest abandonment. The amount of ground cover surrounding a nest is predictive of nestling baseline CORT, but how or if this relates to road proximity is unclear.

Roads can affect the composition of plant communities which could affect food abundance for white-crowned sparrows. The height and density of diamondleaf willow increased close to the road while the height and density of Sierra willow increased far from the road. Parents feed nestlings bits of plants including leaves, buds, and arthropods including caterpillars [39]. Although, the specific components of nestling diet are unknown at this site, it is possible that changes in the abundance of willows affects food availability which could influence both nestling growth and CORT physiology. Even though there were no associations between diamondleaf willow and Sierra willow cover surrounding nests and any measure of nestling HPA physiology or growth, large-scale changes in this vegetation (i.e. along a gradient from the road) may be more important determinants of food availability than the vegetation closely surrounding nest sites.

4.4. Nest success and proximity to road

Nest success has previously been shown to decrease with proximity to road [5,15]. In contrast to these findings, we found no association between nest success and road proximity (Fig. 2A). However, of nests that failed, nests close to the road were more likely to fail from predation than abandonment (Fig. 2B). In Tioga Pass Meadow, Belding’s ground squirrels are thought to be the principal predator on white-crowned sparrow nests [39]. Other
nest predators in this area such as long-tailed weasels and coyotes may avoid areas close to the road because of traffic or human activity [43]. A decline in predators that prey on nests and small mammals could make roadside habitat safer for Belding’s ground squirrels and indirectly increase nest predation by increasing ground squirrel populations. Alternatively, nest predation may be higher close to roads because increased provisioning by males attracts predators to nests. In a study of ten open-nesting passerines, Martin et al. [34] showed that large increases in parental activity around the nest during the nestling period increase nest predation. In our system, we describe increases in both nest attendance and nestling provisioning by fathers in relation to road proximity. Potentially, increased paternal activity around nests explains increased nest predation close to the road.

5. Conclusions

Like adults, nestling passerines are affected by roads: road proximity increases nestling stress and body size. However, the majority of variance in nestling stress physiology was explained by differences in body size indicating elevated CORT levels result from HPA axis development and not necessarily from stressors. Nestlings may grow and develop faster close to the road because paternal provisioning rate increased with road proximity. Overall, it appears that roads have consequences for nestling white-crowned sparrow stress physiology and life-history. However, these effects do not appear to be directly influenced by the road, but rather appear to be indirectly mediated through interactions with social fathers. Whether or not roads are bad for nestlings remains unclear. Nestlings close to the roads were larger which could increase survival after fledging, but these nestlings have a greater chance of dying from predation while in the nest. While not explored in the current study, future work should examine whether these influences of road proximity during early development influence later life history stages and the population dynamics of avian communities. Finally, this study examined just one population; future studies should examine the influence of roads across populations of birds to assess whether the findings described here are representative of the impact of roads on avian communities.

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