EFFECTS OF EXPERIMENTAL NOISE EXPOSURE ON SONGBIRD NESTING
BEHAVIORS AND NEST SUCCESS

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ABSTRACT

Effects of Experimental Noise Exposure on Songbird Nesting Behaviors and Nest Success

Tracy Irene Mulholland

Anthropogenic noise is an increasingly prevalent global disturbance. Animals that rely on the acoustical environment, such as songbirds, are especially vulnerable to these sounds. Traffic noise, in particular, overlaps with the frequency range of songbirds, creating masking effects. We investigated the effects of chronic traffic noise on provisioning behaviors and breeding success of nesting western bluebirds (*Sialia mexicana*) and ash-throated flycatchers (*Myiarchus cinerascens*). Because anthropogenic noise exposure has the potential to interrupt parent-offspring communication and alter vigilance behaviors, we predicted that traffic noise would lead to changes in provisioning behaviors, such as fewer visits to the nest box, for each species. We also predicted the noise to negatively influence one or more metrics reflective of reproductive success, such as nest success, clutch size, number of nestlings or number of fledglings. Importantly, we were able to eliminate self-sorting among individuals with respect to noise and other possible effects of traffic, such as collisions and pollution, by experimentally introducing traffic noise into nest boxes after clutch initiation using playback systems. Our results indicate no effect of traffic noise on *S. mexicana* reproductive measures, despite seeing changes in provisioning behaviors suggestive of an increased stress response. However, *M. cinerascens* experienced fitness consequences from chronic anthropogenic noise exposure when combined with the effect of year. Despite equal clutch sizes to flycatchers in boxes with no noise exposure, noise-treated flycatcher nests experienced a reduction in

hatching success and subsequent metrics, such as number of nestlings or fledglings relative to control boxes, during the first study year. The year in which we witnessed the decline in nest success for ash-throated treatment individuals coincided with a significant drought year, suggesting that combinations of multiple stressors lead to nest abandonment. In recording provisioning behaviors during the fledgling stage, no difference in provisioning was found between treatment and control ash-throated flycatcher nests. We contrast these species-specific responses to recent observational work on both species in New Mexico and other studies that have examined fitness consequences of noise. Lastly, we stress the importance of these findings in addressing current conservation practices of nest box placement with respect to roads.

Keywords: anthropogenic noise, avian, fitness, conservation, provisioning behavior

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General Introduction

Wild organisms depend on sounds for numerous, critical, activities. Sound is used for prey detection in passive gleaners (Neuweiler 1989) and a variety of functions in numerous bird species (i.e., Rice 1982, Konishi 1973). Alarm calls to warn of predators have been demonstrated in primates (Seyfarth et al. 1990), birds (i.e., Templeton et al. 2005), and rodents (i.e., Blumstein and Armitage 1997, Randall and Rogovin 2002). Additionally, species such as songbirds rely on vocalizations for mate attraction and pair bonding (e.g., Swaddle and Page 2007). Given the importance of vocal communication across a variety of contexts for numerous species, it is no wonder that changes in acoustic environments, largely those brought on by human development, have become of increasing concern among conservationists and resource managers.

Sources of anthropogenic noise include air and ground transportation, resource extraction, and increased urban infrastructure (Barber et al. 2010). Increases in background sound levels brought on by the aforementioned sources can inhibit animals' ability to detect sounds, a process known as masking (Barber et al. 2010, Francis and Barber 2013). To cope with effects of masking, songbirds have been shown to exhibit vocal plasticity, and alter their songs in order to increase their detection (e.g., Francis et al. 2011a, Gross et al. 2010). Other behavioral adjustments in response to noise pollution include avoidance of the noise source area, as seen in mammals (Sawyer et al. 2006). In addition to potential signal interferences, continuous noise exposure has been shown to affect human physiology, such as increased blood pressure (Lang et al. 1982) and raised cortisol levels (Brandenberger et al. 1980).

In this study, we focus on one source of noise pollution in particular: traffic noise. Traffic from roads has increased dramatically in recent decades due to increases in both population size and transportation networks (reviewed in Barber et al. 2010). It is especially problematic for birds because it overlaps the frequency range where birds hear best and tend to vocalize (reviewed in Dooling and Popper 2007). In Chapter 1, we investigated the impact of experimentally introduced traffic noise on the reproductive fitness of two secondary-cavity nesting, songbird species. Fitness was measured in terms of nest success (0 or 1), clutch size, brood size, and number of fledglings. Nestling measurements, including tarsus length, wing chord, and weight, also served as fitness parameters. To further investigate responses to the traffic noise exposure, we monitored the provisioning behaviors of a subset of boxes for each species in Chapter 2. We expected chronic noise exposure to lead to changes in provisioning rates and behaviors in both species, measured by number of visits, length of the visits, and time upon first provisioning event (latency time).

We found no significant effect of experimentally introduced traffic noise on any measured fitness parameters for western bluebirds. The traffic noise did, however, result in significantly fewer ash-throated flycatcher chicks and fledglings when combined with the effect of year. Changes in provisioning behaviors were also species-specific, as noise-treated western bluebird individuals approached the nest box more cautiously upon first provisioning event than control individuals. No changes in provisioning behaviors were observed for ash-throated flycatchers. Our results indicate that responses to noise pollution are species-specific, and that the effect of traffic noise may be strengthened when coupled with environmental stressors such as drought and low food abundance.

Thus, we urge conservation management of secondary-cavity nesters to consider traffic noise when determining appropriate nest box placement.

Chapter 1: Effects of Experimental Anthropogenic Noise Exposure on the Reproductive Success of Secondary Cavity Nesting Birds

1.1 Introduction

Secondary-cavity nesting birds have experienced a decline in natural cavities due to habitat loss, forestry practices that target snags for removal and interspecific competition with non-native species (Willner et al. 1983). This loss in nesting sites, which are a critical limiting resource, is correlated with, and thought to contribute to, ongoing declines in breeding populations (Sauer and Hines 2013, Zeleny 1976). Recent conservation efforts have attempted to increase their breeding success and densities by supplementing natural cavities with nest boxes (Briskie et al. 2014, Libois et al. 2012, Purcel et al. 1997). The addition of nest boxes on the landscape should, ostensibly, support larger populations of secondary-cavity nesting species; however, they are often placed along public roadways, in recreational areas or urban or suburban backyards or other areas characterized by high levels of human disturbance (Miller et al. 1998, Jackson et al. 2013). Although providing an increased abundance of limited nest sites, and providing opportunities to enhance citizens' experiences with wildlife and knowledge about bird biology and behavior (Evans et al. 2005), it is less clear whether nest boxes represent a means to conservation aims of increasing nest success and bolstering populations. For example, nest boxes placed adjacent to roads or in urban and suburban settings are exposed to considerable traffic noise and other human made sounds, which could negatively affect the likelihood of a breeding pair to use the box or negatively influence the outcome of any nesting attempt. Thus, it is important to know whether pairs

breeding in boxes in noisy areas have similar reproductive success to those in less noisy areas and have the potential to bolster populations. In other words, the question is whether current practices of nest box placement near or along areas of human activity is a benefit or hindrance to reproductive success and, ultimately, population persistence for secondary-cavity nesting species.

Because nest boxes are often placed near roadways (e.g., Halfwerk et al. 2011), many boxes may experience considerable sound exposure from traffic, which is a low frequency, chronic stimulus that has increased dramatically in recent decades (Barber et al. 2010). Songbirds, including secondary-cavity nesting birds, are considered especially vulnerable to anthropogenic noise because of their reliance on vocal communication (Patricelli and Blickley 2006). Indeed, mounting evidence suggests that avian communities in areas exposed to anthropogenic noise are structured non-randomly based on vocal characteristics (e.g., Francis et al. 2011b, Proppe et al. 2013, Francis 2015). Additionally, recent evidence suggests that placing nest boxes in noise-polluted areas could decrease nest success rather than promote nest success. For instance, associations between anthropogenic noise and reduced reproductive success have been observed in eastern bluebirds (*Sialia sialis*; Kight et al. 2012), great tits (*Parus major*; Halfwerk et al. 2011) and house sparrows (*Passer domesticus*; Schroeder et al 2012). However, in these studies, effects from noise were not explicitly disentangled from effects of other disturbances that co-occur with noise levels (e.g. traffic, habitat modifications, presence of people and pets, etc.). Additionally, studies that report declines in reproduction in noisy environments (e.g., Kight et al. 2012, Halfwerk et al. 2011) were not able to identify the mechanisms responsible for declines in reproduction and two non-mutually

exclusive alternatives are especially possible. In one, noise may *cause* declines in reproduction directly by reducing parent investment in their brood. Alternatively, birds may settle non-randomly across the landscape such that individuals in good condition settle in quiet environments and those in poor condition are forced to occupy territories in noisy areas. Under either scenario, birds breeding in noisy areas may have lower reproductive success than those in quiet areas, but the mechanism producing the decline is different.

In this study, we sought to determine whether noise causes a decline in reproductive success by experimentally manipulating the acoustic environment with playbacks after nest-site selection and nest initiation. Importantly, this approach controls for the possible effects of self-sorting with respect to noise and isolates the influence of noise alone on reproductive success. We hypothesized that chronic noise exposure induces critical behavioral changes during both the incubation and nestling provisioning stage. Noise exposure has the potential to increase visual vigilance at the cost of fitness enhancing behaviors. Increases in vigilance coupled with declines in foraging have been observed in laboratory studies in birds (*Fringilla coelebs* & *Zonotrichia leucophrys*; Quinn et al. 2006 & Ware et al. 2015 respectively) and mammals (*Cynomys leucurus*; Shannon et al. 2014) and similar trade-offs could exist for nesting birds, such as maintaining visual vigilance off the nest at the expense of incubation. Additionally, during the nestling provisioning stage, noise interferes with parent-offspring communication at the nest (Leonard and Horn 2012), although it is unknown whether this results in any changes in reproductive success. Because of these potential changes, we predicted that individuals using nest boxes experimentally exposed to noise (treatment

nests) would experience lower reproductive success, reflected by fewer eggs, chicks or fledglings or smaller nestlings, compared to individuals using nest boxes without noise exposure (control nests). We also expected that a smaller proportion of nest attempts by individuals exposed to experimental noise exposure would result in a successful outcome, defined as at least one fledgling leaving the nest, relative to individuals in control nests. By highlighting the reproductive consequences induced by anthropogenic noise, we hope this study can be used to assess current practices of nest site placement and improve conservation efforts.

1.2 Materials and Methods

Study Area & Species- We studied wild populations of western bluebirds (*Sialia mexicana*) during the 2015 breeding season and ash-throated flycatchers (*Myiarchus cinerascens*) during the 2015 and 2016 breeding seasons. Our nest box study system was established on California Polytechnic State University Lands and situated adjacent to campus in San Luis Obispo County on the central coast of California. The study area is situated far from major roadways and experiences low levels of anthropogenic activities, including occasional university vehicles, recreational hikers, runners and mountain bikers. The system consisted of 217 nest boxes placed roughly 60 meters apart (mean = 61.66 ± 1.58 SE) across 4.8 km² of habitat consisting of open grassland, chaparral, and oak woodland (Figure 1). Nest boxes were constructed using redwood and placed approximately 1 m above the ground on pre-existing fence lines (n = 200) or posted on coast live oak (*Quercus agrifolia*) or California bay (*Umbellularia californica*) trees (n=17).

Data Collection and Field Monitoring- In each year nest box monitoring began in early March and continued until mid-July. We monitored nest boxes for nesting material or nesting activity about every 3 days and always at least twice a week. Complete nests were checked daily for clutch initiation. After the first egg was laid, active nests were monitored every 2-3 days, with the exception of one critical period: Nearing the end of incubation stage (day of hatch), in which cases the nests were monitored daily. Nestlings were banded and measured on day 12 of the nestling stage to diminish the possibility of force-fledging and to standardize measurements across all nests. We continued to monitor nests throughout the nestling provisioning stages at least every 3 days. Nests were considered successful if one or more chicks successfully fledged, or were missing from the box after day 12 (Morton 2002, Crino et al. 2013) and there were no obvious signs of depredation or abandonment.

Nest box manipulation- Nest treatments were assigned such that the first nest with an egg was randomly assigned to either a treatment or control, but then alternated with assignment in an attempt to control for differences in clutch initiation dates among the treatment and control nests. This was completed due to known declines in clutch size with clutch initiation dates (Siikamäki 1998). For occasions in which active nests were discovered on the second egg-laying day (n=8, western bluebird only), they were assigned control boxes. All second nesting attempts (n=8, western bluebird only), were given the opposite treatment received from the first nesting attempt. Nests were assumed to be second nesting attempts (same parent ID) if the same nest box was utilized twice within the breeding season in rapid succession (n=3). For those that had visible fledglings

at or near the nest box (n=5), we used two criteria to deduce the parent ID: 1) Location/proximity to previously utilized nest box and 2) Timing, as second-attempt nest building often started near the end of the fledgling stage.

Treatment boxes contained one of two kinds of playback systems: one with a Satechi SD mini portable pocket speaker mp3 player attached via a USB cord to an external battery pack (IntoCircuit Power Bank), and the other with an mp3 speaker (STORMp3). Both systems were fixed to the nest box roof with zip-ties attached to cable holders (Figure 2b,c). Despite several successful earlier lab trials with the Satechi system, several units failed to remain playing continuously in the field when the internal battery lost power (~5 hrs) or external battery pack turned off (~5-24 hrs), and had to be manually reset daily. The initial nests (western bluebird nests only, n=8) that were exposed to this intermittent treatment were switched to the continual playback system (STORMp3) by the time the incubation stage began (i.e., before the final egg was laid). In control boxes we installed wooden blocks (5.08 x 10.16 x 15.24 cm³) containing electrical wire and tape drilled into the roof of the nest box to account for the potential influence of a novel object in the nest box (Figure 2a).

For each species, treatment nests received a randomly assigned unique playback file to provide a range of acoustic conditions that characterize busy highways. There may be relatively small changes in sound levels across a 24-hr period for many busy roads (see Fig. 3 in Halfwerk et al. 2011). This occurs because the average vehicle is slower when vehicle density is high and, thus, produces less noise than at night when vehicle density is lower. To simulate exposure to relatively constant traffic noise levels we recorded traffic noise on local highways between October 2014 and May 2015 using Roland R05

recorders at a distance of 10 m from the roadway, which is often the shortest distance of many fence lines bordering roadways on which nest boxes are placed (TIM, personal observation). Additional recordings were made at 20 m at many of these locations for comparison to recordings made at 10 m and playback recordings (see results). Recordings made at 10 m averaged 200 ± 16 SE seconds and were looped continuously. Recording amplitudes were standardized to the same peak power in Raven Pro 1.5 to control for the influence of especially high amplitude acoustic events. Prior to standardization, a 5 second fade in and fade out was added to each recording to control for rapid onset and falloff of noise levels, which have the potential to elicit startle responses in animals (*reviewed in* Francis and Barber 2013). These standardizations streamlined calibrating playback files during field playbacks to approximately 65 dB(A), an amplitude known to result in behavioral changes in other studies (*reviewed in* Shannon et al. 2015) and lasted throughout the entire nesting period. Batteries were changed every 2-3 days during monitoring visits to assure continuous exposure to the noise. Time-weighted sound levels (A-weighted $L_{eq, fast response}$, re. 20 μ Pa) were taken for 5 minutes after initial treatment instillation and following each battery change to calibrate experimental playback sound level using either a Larson-Davis 824 or 831 Sound Level Meter, or, on rare occasions, a MicWi436 measurement kit paired with an iPhone using the SLMnFFT application, which has been shown to be equivalent to a type two sound level meter (Kardous and Shaw 2014). We also monitored control nests every 2-3 days and measured ambient noise levels using the same devices. Immediately after each nest fledged or failed, we recorded sound levels in the box for approximately 1 hour so that we could qualitatively compare spectral profiles of the received experimental noise to the original

recordings of traffic noise.

Morphological Measurements and Banding- Because we predicted that experimental traffic noise would negatively affect nestling development, we measured three standard morphological measurements on day 12 of the nestling stage. Tarsus length (mm) and unflattened wing chord (mm) were measured to 0.1 mm precision using a standard wing ruler or caliper. Weight (g) was measured using a spring scale (Avinet, Pesola 50 g) to the 0.1 g precision. Prior to taking these measurements, we banded all nestlings with standard United States Geological Survey aluminum bands. Morphological measurements were standardized to day 12 of the nestling stage except for three western bluebird nests (6.25%), which were measured on day 11 or day 14 due to logistical constraints.

Data Analysis- To determine the effects of treatment on nest success, we used linear and generalized linear mixed effect models (LMM and GLMM). All statistical analyses were performed using either the lme4 package (Bates et al. 2012) or nlme package (Pinheiro et al. 2016) in R v. 3.2.2. Models were performed independently for each species and for each response variable: nest success, clutch size, number of hatchlings, number of fledglings, nestling weight, nestling wing chord, and nestling tarsus measurement. Treatment and clutch initiation date (CID) were included as fixed effects for all models. System type was swapped with treatment in all models to determine whether the type of playback system used could better explain response variables. For nestling measurements, Box ID was included as a random effect to account for the non-

independence among nestlings in the same nest and Parent ID was used to link double broods from the same pair. Random effects were removed if the estimated variance equaled zero. Final, best-fit models were selected using backward elimination of uninformative variables, such that we sequentially removed variables with the highest p -value (or lowest t) until the model only included variables where $P < 0.1$, a threshold previously found to produce valid models (Murtaugh 2009). After final model selection, we used $\alpha = 0.05$ to determine variable significance. For linear mixed effect models with significant fixed effects, we performed likelihood-ratio tests to gauge final model fit against intercept only models that included the same random effects as the best-fit model. Additionally, because the impairment of parent-offspring communication (Leonard and Horn 2012) could potentially lead to an uneven allocation of food among nestlings, we also used linear regression to determine whether variance in nestling measurements (i.e., mass, tarsus or wing cord length) for each nesting attempt was influenced by noise exposure. For ash-throated flycatcher analyses, we also included a treatment by year interaction in our generalized linear models (number of eggs, number of chicks, and number of fledglings), and our linear mixed effect models (nestling weight, nestling tarsus length, and nestling wing chord). This inclusion was to account for the variation (i.e. weather, food availability) between breeding seasons, a factor previously shown to influence breeding success and patterns, including second brood attempts in western bluebirds (Jacobs et al. 2013) and great tits (Husby et al. 2009). The 2015 breeding season was characterized by extreme drought (total rainfall in San Luis Obispo, January 2015-March 2015: 6.1 cm, U.S. Climate Data), which may pose as an additive stressor on breeding, insectivorous birds due to low food abundance (e.g., Cody 1981, Smith 1982).

In contrast, the 2016 breeding season was characterized by strong El Niño-Southern Oscillation (ENSO) pattern, where heavy rains increased primary productivity and thus food availability within the study site (total rainfall in San Luis Obispo, January 2016-March 2016: 24.9 cm, U.S. Climate Data). Therefore, we also examined whether effects of noise could be more severe under stressful drought conditions than when resources are abundant.

1.3 Results

Experimental noise exposure- Sound levels for western bluebird and ash-throated flycatcher treatment nest boxes were significantly louder than control boxes (bluebirds: $t = -21.26$, $df = 19.92$, $P < 0.001$; flycatchers: $t = -13.11$, $df = 5.04$, $P < 0.001$, Figure 3). Power spectra of the original recordings versus the playback within the box show that our playback systems elevated sound levels across the spectral range most audible to birds (i.e., 0.5-10 kHz; Dooling and Popper 2007) (Figure 4). In general, playbacks had less energy at these frequencies than the original recordings that were 10m from roadways and were more typical of noise spectral profiles at twice that distance (i.e., 20m, Figure 4) and well within the range of values documented to influence breeding success previously (i.e., > 100m, Halfwerk et al. 2011).

Western Bluebirds- We exposed 16 western bluebird nests to experimental traffic noise and included 20 nests as controls. We found no significant effect of treatment on nest success, clutch size, number of chicks, or number of fledglings (all models, $P > 0.78$). Playback system type (i.e., Satechi during laying and switched to STORMp3 for

remainder or nesting period versus STORMp3 throughout) was uninformative for all models (for all models, $P > 0.55$), and no significant effect of clutch initiation date was found (all models, $P > 0.28$). Similarly, treatment did not affect nestling tarsus length, unflattened wing chord length, or weight (all models, $P > 0.22$). However, clutch initiation date had a significant negative effect on nestling tarsus length, with nestlings experiencing reduced tarsus length later in the breeding season ($\beta = -0.04 \pm 0.01$ SE, $\chi^2 = 24.13$, $P < 0.001$)(Figure 5).

Ash-throated Flycatchers- We exposed six ash-throated flycatcher nests to experimental traffic noise and included six nests as controls. Number of eggs did not significantly differ between treatment or control groups in either breeding season ($P > 0.79$). However, the playback of traffic noise in the first breeding season resulted in 1.18 fewer hatched chicks per nest ($\beta = 1.18 \pm 0.57$ SE, $z = -2.06$, $df=11$, $P = 0.04$) relative to control nests, but there was no significant difference in number of hatched chicks between individuals nesting in control boxes across breeding seasons ($z = 0.00$, $df=11$, $P = 1.00$) and control and treatment boxes in year two ($\beta = 1.18 \pm 0.69$ SE, $z = 1.70$, $P = 0.09$, Figure 6a). We also found a significant negative effect of treatment on number of fledglings ($\beta = -1.87 \pm 0.76$ SE, $z = -2.46$, $P = 0.01$) relative to control boxes in the first year, but no difference in number of fledglings was detected between years for control boxes ($\beta = -0.62 \pm 0.47$ SE, $z = -1.32$, $P = 0.19$). As with number of chicks, we found an interaction between treatment and year ($\beta = 2.49 \pm 0.89$ SE, $z = 2.79$, $P = 0.01$), suggesting a difference in number of fledglings among treatment boxes in year one and two, but not between years for control nests (Figure 6b). Finally, there was no significant effect of clutch initiation date on any response measures (all, $P > 0.67$).

For analyses of ash-throated flycatcher nestling measurements, we found a significant positive influence of the noise treatment on nestling weight ($\beta = 5.73 \pm 1.18$ SE, $t = 4.84$, $P = 0.01$). There was no overall difference in nestling weight between year one and two ($\beta = -0.98 \pm 0.73$ SE, $t = -1.35$, $P = 0.24$); however, there was strong evidence for an interaction between treatment and year ($\beta = -4.13 \pm 1.39$ SE, $t = -2.97$, $P = 0.03$, Figure 6c), indicating no difference in weights among nestlings in control boxes between years, but significantly smaller nestlings in treatment boxes in year two relative to year one. We found no influence of treatment, year or their interaction on nestling tarsus or wing chord length (all $P > 0.10$). There was a trend of decreased tarsus length with increasing clutch initiation date ($\beta = -0.06 \pm 0.02$ SE, $t = -2.57$, $P = 0.06$).

1.4 Discussion

The expanding human population, and our accompanying network of transportation, poses several threats to wildlife. Noise pollution has recently been associated with changes in animal behavior (Quinn et al 2006, Leonard and Horn. 2012), physiology (Crino et al. 2013) and reproductive success (Halfwerk et al 2011, Kight et al. 2012). However, the mechanisms responsible for a reduction in fitness are still largely unknown (Halfwerk et al. 2011), including the possibility of self-sorting of individuals across the landscape with respect to noise. Here, we were able to control for any inherent fitness differences among breeding individuals by assigning treatments after clutch initiation. Additionally, our study system provided breeding habitat far from major roadways, removing possible confounding variables associated with traffic apart from noise.

Our results show that ash-throated flycatchers exposed to chronic traffic noise produced significantly fewer chicks and fledglings during year one compared to year two, despite equal clutch sizes. Control boxes experienced no difference in number of chicks or fledglings between years. The difference could be the result of a combination of environmental conditions (i.e. the effects of drought) and chronic noise disturbance that drive nest abandonment during the incubation stage (see below). In contrast, western bluebirds experienced no apparent fitness consequences from chronic anthropogenic noise exposure. Contrary to similar studies on the great tit (Halfwerk et al. 2011) and eastern bluebird (Kight et al. 2012), which showed reduced fitness in areas of increased noise levels, we controlled for the possibility of self-sorting among individuals. It remains possible that non-random distributions of individuals across landscape, such that lower quality individuals breed in areas of greater noise pollution, explain previous declines in reproduction (i.e., Halfwerk et al 2011, Kight et al. 2012). Habitat-filtering, whereby some species are included in the habitat and others are not, by noise among species has been documented on several occasions (i.e., Francis et al. 2011b, Proppe et al. 2013, Francis 2015) and filtering within species is also possible. For example, Habib et al. (2007) reported that a larger proportion of young ovenbird (*Seiurus aurocapilla*) males defend territories in noisy areas relative to comparable quiet locations. Whether this is due to inexperience or lower quality is unknown, but warrants additional investigation.

Alternatively, it is possible that our experimental playback did not accurately mimic real road sounds at frequencies relevant to birds in the nest box (i.e., 0.5-10 kHz; Dooling and Popper 2007). However, power spectra of the actual traffic recordings

versus those made in the box from the playback systems reveal that our playbacks produced sound levels at most frequencies that are well within the range experienced near real roads, albeit at farther distances than the distances at which original recordings were made (i.e., 20 m rather than 10 m, Figure 4). Still, the systems only exposed parents to noise while in the nest box (i.e. incubating, provisioning). It may be that sound levels across the territory, where acoustic cues are used in many other facets of birds' daily lives, such as to passively survey for predators or aide in hunting prey, are equally or more important than sound levels at the box during nesting. In support of this possibility, Kleist et al. (in review) found evidence that the presence or absence of energy-sector noise across the landscape had a strong influence on the number of active nests for mountain bluebirds (*Sialia currucoides*) and ash-throated flycatchers in NW New Mexico, but that sound levels at individual nest boxes had a minor influence on occupancy patterns for ash-throated flycatchers and no influence on occupancy patterns in mountain bluebirds. Kleist et al. also found no influence of noise on nest site selection in western bluebirds. That the effect of experimental noise treatment on reproductive success in western bluebirds and ash-throated flycatchers in this study match the effect of noise on nest site selection in both species reported by Kleist et al. (in review) suggests consistent differences in sensitivities between these species, even among populations that are separated by approximately 1200 km (i.e., central coast of California and NW New Mexico).

Species-specific responses to noise could also be the result of behavioral differences, such as differences in tolerance to human disturbance (Kight and Swaddle 2007) and different abilities to adjust vocalization frequencies through behavioral

plasticity (Gross et al. 2010), or differences in life histories. Western bluebirds produce slightly larger clutch sizes than ash-throated flycatchers, and a significant proportion of western bluebirds double brood (Fair and Myers 2002). High investments in first and only brood among breeding for ash-throated flycatchers may present a possible reason for early abandonment in response to noise exposure or other disturbances, causing individuals to choose self-preservation over nesting attempts. Despite this sensitivity to noise while breeding, previous studies have found ash-throated flycatchers to be equally common on noisy and quiet sites and that singing at a higher pitch might explain their ability to persist in noisy areas (Francis et al. 2011a). However, changes in vocalizations may come at a cost to fitness. For example, a study on male reed buntings (*Emberiza schoeniclus*) found more unpaired males in noisy sites compared to quiet areas, and these unpaired males sung at a higher minimum frequency than paired males at quiet locations (Gross et al. 2010). Changes in critical breeding behaviors, such as song performance, may be responsible for a decline in nesting success, regardless of an equal occupation of noisy areas.

We found a significant interaction between year and treatment type whereby ash-throated flycatcher nests exposed to noise in year one produced fewer chicks and fledglings, despite initially laying equal clutch sizes to control individuals. Unlike year two (2016), year one (2015) was a drought year. Importantly, severe drought has been previously associated with fewer breeding attempts and reproductive failure in passerine birds (Bolger et al. 2005, Christman 2002). These declines in fitness are often attributed to a decrease in food (i.e. arthropod) abundance during drought years. Christman (2002) found that nearly half of the breeding pairs of bridled titmouse (*Baeolophus wollweberi*)

of the study population in Southeast Arizona made no attempt to breed during the drought year, whereas all breeding pairs attempted nesting the previous ENSO year. In our study, however, we found no indication that drought alone caused declines in reproductive success: there were no differences between years among control nests. Additionally, individuals in treatment boxes attempted to breed during the drought year and laid equal clutch sizes to those of control individuals. It is possible that an additional stressor, other than the environmental conditions, may be responsible for the differences among treatment boxes between years. The addition of the chronic stressor of traffic noise to the already stressful conditions of a drought year could be responsible for failed nesting attempts, although results for ash-throated flycatcher nesting attempts should be viewed with caution because the difference among years could be caused by other unmeasured environmental variables that differed between years interacting with noise or due to relatively low power of our sample. Nevertheless, because most organisms experience myriad of stressors when breeding, future research should attempt to characterize the many factors that could influence reproductive success in additive, antagonistic or synergistic ways.

Despite no immediate fitness consequences in western bluebirds, it is unclear whether there may be future costs to chronic noise exposure. Changes in energy allocation, such as a reduction in self-maintenance behaviors (Kight and Swaddle 2007), may impact the success of future breeding attempts. Another potential hidden cost may be a decrease in longevity, as a reduction in telomere length was found in house sparrow (*Passer domesticus*) nestlings exposed to traffic noise during development (Meillère et al. 2015). Thus, we believe future studies should examine survival rates and lifetime

reproductive success to gain a more rounded understanding of the potential long-term costs of noise exposure and attempt to link observed responses of vigilance in response to noise (i.e., Quinn et al. 2006, Ware et al. 2015) to reproductive consequences. This may provide further evidence of actual fitness costs associated with increased vigilance at the cost of feeding behaviors (Gavin and Komers 2006) and/or a heightened stress response (Horton and Holberton 2009).

Lastly, we note that our study focused on only one of the potential effects of traffic and roadways. It may be that noise, taken by itself, is negligible in its influence on fitness for some species, but combined with other factors associated with traffic, such as collisions, light pollution, etc., may lead to reduced breeding success. For example, Kuitunen et al. (2003) found that pied flycatchers (*Ficedula hypoleuca*) breeding near the road produced fewer fledglings but not fewer eggs or chicks, presumably because parents died via collision with traffic during the nesting period. Because of its co-occurrence with other disturbances, and varying sensitivities among species, soundscapes should be taken into account when assessing habitat quality for secondary-cavity nesters along with landscape features that are typically managed, such as the type and arrangement of land cover. Future efforts intended to bolster populations of secondary-cavity nesters should consider the species that will be occupying the boxes and their sensitivity to anthropogenic noise in order to determine if placement near roads is beneficial to their breeding success.

Chapter 2: Changes in Provisioning Behaviors of Two Songbird Species in Response to Chronic Anthropogenic Noise

2.1 Introduction

Traffic from roads has increased dramatically in recent decades (reviewed in Barber et al. 2010) and has gained the attention of researchers due to its ability to affect wild organisms (i.e., Crino et al. 2011, 2013, Slabbekoorn and Peet 2003). Behavioral changes as a result of this chronic disturbance include changes in temporal patterns, movement or distributions, mate attraction, and foraging efficiency (reviewed in Francis and Barber 2013). Songbirds, in particular, rely on vocal communication to carry out a variety of functions and thus may be especially vulnerable to chronic noise pollution (Patricelli and Blickley 2006). Because of this reliance, traffic from roads has the potential to impact songbird breeding success during various stages of the breeding process through a process known as masking. Masking occurs when a sound interferes with or inhibits the discrimination or detection of another sound (Barber et al. 2012). Indeed, several studies have documented declines in reproductive success due to noise (e.g., Halfwerk et al. 2011, Kight et al. 2012). However, the mechanisms responsible for the decline are not fully known. To date, existing evidence suggest that noise can negatively affect breeding success by influencing settlement patterns (Kleist et al. *in review*), decreasing pairing success (Gross et al. 2010) and possibly by disrupting parent-offspring communication (Leonard and Horn 2012), but noise may also disrupt incubation rates and rhythms and nestling provisioning behaviors critical for reproductive success.

Here, we focus on how chronic anthropogenic noise (i.e., traffic) alters changes in provisioning rates and behavior in two secondary-cavity nesting songbirds, western bluebirds (*Sialia mexicana*) and ash-throated flycatchers (*Myiarchus cinerascens*). We placed traffic noise playback systems into nest boxes after clutch initiation (first egg laid) to eliminate the possibility of self-sorting among individuals (e.g., potential for lower quality individuals to breed in noisy habitats perceived as lower quality), which could influence provisioning patterns and could also explain previous findings of reduced reproductive success with high traffic noise levels near roadways and noisy urban areas (e.g., Halfwerk et al. 2011, Kight et al. 2012).

Previous studies have demonstrated that noise can influence vigilance patterns in foraging birds (Quinn et al. 2006, Meillere et al. 2015, Ware et al. 2015), whereby animals increase visual vigilance in response to impaired acoustical surveillance brought on by masking. Because of these potential changes in vigilance behaviors and parent-offspring communication (Leonard and Horn 2012), we predicted that experimental chronic noise exposure within the nest would negatively impact nestling provisioning rates and rhythms by parents. Specifically, we expected parents nesting in noise-exposed boxes to make fewer provisioning visits (i.e., longer duration between visits), and spend less time within boxes. We also expected treatment individuals to take longer to visit the box after a perceived threat (i.e., longer latency of first approach) than parents in quiet control boxes, because of potential changes in stress responses brought on by exposure to a chronic stressor (Romero 2004). Additionally, we expected time spent in the box to be inversely related to the number of visits and brood size to be positively correlated to both the number of visits and average time spent in the nest box during visits.

2.2 Methods

Study Species and Study Site- We studied wild populations of western bluebirds and ash-throated flycatchers during the 2015 and 2016 (ash-throated flycatchers only) breeding seasons. The study site consisted of 217 nest boxes situated on California Polytechnic State University owned lands in San Luis Obispo, California. The location experiences relatively few disturbances from anthropogenic activity other than occasional hikers, recreational mountain bikers, and minimal road use by university-owned vehicles.

Treatment- Nest treatments were assigned semi-randomly, as the first nest with an egg was randomly assigned to either a treatment or control, and subsequent nests were assigned opposite treatment types to mitigate the influence of clutch initiation date on breeding success between treatment and control boxes. Treatment boxes contained an mp3 speaker (STORMp3) attached to the nest box roof with zip-ties secured to cable holders (Figure 2b). To account for the potential influence of a novel object in the nest box, we installed wooden blocks (5.08 x 10.16 x 15.24 cm³) with electrical wire and tape into the nest box roof to serve as control boxes (Figure 2a). Treatments lasted the entire reproductive attempt until the nest successfully fledged young or failed.

Treatment playback files were unique for each species to supply a variety of highway conditions. All playbacks were recorded from local highway traffic between October 2014 and May 2015 using Roland R05 recorders at a distance of 10 m from the roadway, as this distance is typical of fence lines, and thus nest boxes, bordering roads (personal observation). Recordings averaged 200 ± 16 SE seconds and were looped continuously, with a 5 second fade in and fade out added to each recording to reduce

potential startle responses caused by a drastic onset of noise (reviewed in Francis and Barber 2013). Recording amplitudes were standardized in Raven Pro 1.5 with peak power to control for the influence of especially high amplitude acoustic events. Power spectra of the original recordings versus the playback within the box show that the playback systems raised the sound levels across the spectral range most audible to birds (i.e., 0.5-10 kHz; Dooling and Popper 2007, Figure 4), and closely resemble the original recordings, although at a distance slightly farther than the original recordings were made (i.e., 20m versus 10m).

Playback amplitudes were standardized at approximately 65 dB(A) (mean $L_{eq} = 65.23 \pm 0.22$ SE dB(A) at 10 cm), which is within the range of amplitudes shown to result in behavioral changes in other studies (reviewed in Shannon et al. 2015). To ensure continuous noise exposure, we changed batteries every 2-3 days during monitoring visits. Time-weighted sound levels (L_{eq}) were taken for 5 minutes after first treatment instillation and after each battery change to measure experimental playback sound level using either a Larson-Davis 824 Sound Level Meter or 831 Sound Level Meter. On rare occasions, we used a MicWi436 omnidirectional microphone paired with an iPhone using the SLMnFFT application, which has been shown to be equivalent to a type two sound level meter (Kardous and Shaw 2014). Control nests were also monitored every 2-3 days and ambient noise levels measured using the same devices (mean $L_{eq} = 45.27 \pm 1.03$ SE dB(A) at 10 cm).

Monitoring of Provisioning- We recorded provisioning behaviors at 13 western bluebird nests and 7 ash-throated flycatcher nests using a video camera (Canon Vixia HF R50)

placed approximately 5 meters from the nest box. Recordings lasted approximately one hour (average length = $58.63 \text{ mins} \pm 2.79 \text{ SD}$). All recordings were made between days 10 and 14 of the provisioning stage (western bluebird mean = $11 \pm 1.19 \text{ SD days}$, ash-throated flycatcher mean = $11.6 \pm 1.13 \text{ SD days}$), as nestling age-class has been previously shown to influence feeding rates (Barba et al. 2009). While all recordings were made during daylight hours, time of day was not standardized across video recordings because provisioning rates were found to be largely uninfluenced by time of day during daylight hours in other songbirds (e.g., Goodbred et al. 1996, Barba et al. 2009). Because adults were not uniquely marked with bands or otherwise identifiable to individual, the number of total visits to the box by both adult male and adult female were recorded, in addition to the length of each visit, plus the duration between visits and the time lapsed until first provisioning event (latency time).

Statistical Analysis- Provisioning behaviors were analyzed using multiple regression or, for single predictor models (latency time and duration between visits), *t*-tests. We conducted Shapiro-Wilk's test for normality on all variables, and data were log transformed when necessary to meet assumption of normality (transformed variables include latency time, average duration between visits, average time in box). Number of chicks and video length were included in the initial linear model for number of visits to account for potential discrepancies in feeding rates among different brood sizes (i.e. Stauss et al. 2005, Rytkönen et al. 1996) and slight differences in video length. Because latency time significantly differed between treatment and control boxes (see Results section), we also replaced total video length for adjusted video length in initial models.

Adjusted video length was calculated as the difference between total video length and time to first provisioning event for each box. For average time spent in the nest box during visits, number of visits as well as brood size were included in the initial model. Final models were selected using backward selection, removing least informative variables ($P > 0.1$) stepwise. After final model selection, we used $\alpha = 0.05$ to determine variable significance. All statistical analyses were performed in R v. 3.2.2.

2.3 Results

We recorded western bluebird provisioning behavior at eight control and five treatment boxes and ash-throated flycatcher provisioning behavior at three control and four treatment boxes. For western bluebirds, the number of total visits by parents to the nest box during the provisioning stage was significantly greater at control boxes than noise-exposed boxes ($\beta = -4.67 \pm 1.83$, $t = -2.55$, $P = 0.03$, Figure 7). Total video length, adjusted video length, and brood size were uninformative in predicting number of visits (for all, $P > 0.25$). Although western bluebird parents in noise-exposed had fewer visits than those in quiet control boxes, average duration between visits did not explain this difference because it did not differ significantly between noise-exposed and quiet control boxes ($t = -0.95$, $df = 5.19$, $P = 0.38$). Additionally, average time spent in the box during visits did not differ between treatment types ($\beta = -0.21 \pm 0.21$ SE, $t = -1.02$, $P = 0.33$), but time spent in the box decreased significantly with number of visits ($\beta = -0.56 \pm 0.26$ SE, $t = -2.18$, $P = 0.05$, Figure 8) and declined with number of chicks ($\beta = -0.26 \pm 0.09$ SE, $t = -2.98$, $P = 0.01$, Figure 9). Latency time, or time lapsed before first provisioning event, was significantly longer for noise-exposed nests than for controls ($t = -5.14$, $df =$

10.40, $P < 0.001$, Figure 10) and accounts for the difference in number of visits between treatment types.

For ash-throated flycatchers, number of visits did not significantly differ between treatment and control nests ($\beta = -0.70 \pm 0.449$ SE, $t = -1.551$, $P = 0.20$). Total video length, adjusted video length, and brood size were uninformative in predicting number of visits (all, $P > 0.11$). There was no significant difference in latency time, or time upon first provisioning event, between treatments and controls ($t = 0.07$, $df = 2.67$, $P = 0.95$). Average duration between visits did not differ significantly between treatments and controls ($t = -1.32$, $df = 4.99$, $P = 0.24$). Similarly, the duration of provisioning visits within the box did not differ significantly between treatment and control boxes ($\beta = -0.33 \pm 0.40$ SE, $t = -0.83$, $P = 0.47$). Number of chicks did not influence the duration of provisioning visits ($\beta = -0.31 \pm 0.22$ SE, $t = -1.40$, $P = 0.23$). However, average time spent in the box during provisioning visits was negatively related to number of visits ($\beta = -0.92 \pm 0.26$ SE, $t = -3.49$, $P = 0.02$), which appears to be heavily influenced by one outlier (Figure 11). As such, we reran the analysis with the point removed (avg. time in box > 40 s) and found a marginally significant negative relationship between average time spent in the box and number of visits ($\beta = -0.26 \pm 0.10$ SE, $t = -2.58$, $P = 0.06$).

2.4 Discussion

Traffic from roads is a ubiquitous and chronic disturbance that has recently been tied to changes in animal's foraging patterns (Shannon et al. 2014), vocalizations (Francis 2015), and reproductive success (Halfwerk et al. 2011, Kight et al. 2012, Chapter 1). We examined potential changes in provisioning behaviors in response to anthropogenic noise pollution in two secondary-cavity nesting species and found that western bluebirds

altered provisioning behaviors when exposed to chronic traffic noise. Individuals nesting in noise-treated boxes made fewer visits, which was explained by an increase in time lapsed before first provisioning event compared to individuals nesting in control boxes. Conversely, there was no difference in provisioning rates between ash-throated flycatcher individuals nesting in treatment and control boxes. We elaborate on the contrasting results between species and discuss potential explanations below.

Our results indicate no effect of noise exposure on ash-throated flycatcher provisioning behaviors, despite previous findings of decreased fitness in response to noise (see Chapter 1) and reduced nest site selection in noisy areas compared to quiet habitats (Kleist et al. *in review*). In the latter study (Kleist et al.), noise was experienced throughout the landscape (i.e. outside the box) and caused a reduction in nest occupancy for the species. This suggests that noise across a territory where foraging occurs, may be more influential on provisioning behavior than noise played inside the box. Additionally, our previous findings of decreased reproductive success in treatment individuals compared to controls was attributed to nest abandonment during the incubation stage, suggesting noise may be more influential in initial nest site selection and during early stages of nesting rather than during the provisioning stage. However, our results should be interpreted with caution due to the small sample size. Still, we recognize sensitivity to noise for this species may result in changes to critical nesting behaviors (i.e. mate selection and/or incubation patterns) other than the provisioning behaviors measured in this study, and further studies should attempt to address potential changes at these various stages.

The decrease in number of provisioning events, explained by an increase in latency time, for noise-treated western bluebird nests compared to controls may provide further evidence of increased vigilance at the cost of feeding behaviors, similar to those found in mammals (e.g., Gavin and Komers 2006). A previous study examining risk assessment in multiple passerine species found that adults were able to alter their parental investment in response to perceived predation risks (Fontaine and Martin 2006), and trade-offs between foraging and vigilance in response to traffic noise have been observed in adult white-crowned sparrows (*Zonotrichia leucophrys*; Ware et al. 2015). Increased perceived predation risks, brought on by reduced acoustic surveillance with noise exposure, is a likely mechanism that could account for longer, more cautious approaches to the nest. For example, because each three decibel increase in background noise can reduce an organisms listening area by as much as 50% (reviewed in Barber et al. 2010, Kleist et al. 2016), birds may be cautious when approaching nests due to an inability to acoustically detect the presence of eavesdropping nest predators and other threats. However, in our study traffic noise was broadcast inside the nest box and potential heightened perceived risk due to impaired surveillance capabilities can be excluded.

A probable alternative explanation could be altered internal physiology in the form of a heightened stress response due to the influence of multiple stressors. Because chronic stressors can promote acclimation and may result in disrupted hypothalamic–pituitary – adrenal (HPA) axis physiology, baseline corticosteroid (CORT) levels can remain higher than normal and animals may experience a hypersensitive response to a novel stressor, a process known as facilitation (*reviewed in* Romero 2004). Thus, in this study, for individuals exposed to chronic traffic noise in the box, the presentation of a

novel stressor, such as human encroachment and camera installation, could result in facilitation, whereby parent physiology and behavior reflects a hypersensitive response to a threatening stimulus. Male greater sage-grouse (*Centrocercus urophasianus*) experience elevated CORT levels at courtship grounds (i.e., leks) treated with experimental noise playback compared to comparable quiet sites (Blickley et al. 2012), thus altered physiology and resulting behavioral responses to additional stressors may be likely. Clearly, future work must determine whether western bluebirds exposed to noise experience elevated CORT that could support this possible explanation.

As expected, number of visits was inversely correlated to average time spent in the box for both species. This is likely because individuals making frequent visits to the nest box are spending less time in the box per visit, as opposed to individuals making less frequent, longer visits. However, in contrast to our prediction, the average time western bluebirds spent in the box significantly declined with an increase in brood size. This may be due to an energetic trade-off between adult energy demands and fledgling survival, which increases with increased nestling weight, such that parents with large broods are unable to find enough sizable prey worth transferring to the nest (Smith et al. 1988). Smith et al. experimentally manipulated brood size in great tits (*Parus major*) and found that adults did not increase their feeding frequency in response to enlarged broods. That being said, in our study, brood size was not significantly correlated to number of visits, which may have been expected with an energetic trade-off. Alternatively, it is possible that an increase in competition among larger broods may lead to dominant individuals begging or displaying more than others. If so, adults may make an easier decision on which nestling to feed and thus spend less time in the box. Collectively, our results

indicate that it may be inappropriate to assume that all species are able to behaviorally increase their provisioning efforts in relation to brood size (Martin 1995).

Although previous work has documented no apparent, immediate fitness consequence of traffic noise for western bluebirds (Chapter 1) and it appears not to alter settlement patterns (Kleist et al. *in review*), traffic noise does affect provisioning behavior, and these changes could be explained by an altered physiological response. Changes in stress physiology have been tied to alterations in provisioning behaviors in male white-throated sparrows (*Zonotrichia albicollis*; Horton and Holberton 2009), as males with experimentally raised CORT levels provisioned less often than control males. However, whether these changes in provisioning behaviors are directly tied to a decrease in fitness remains unknown, but sufficient evidence points towards a correlation. For example, female house sparrows (*Passer domesticus*) breeding in noisy areas provisioned their broods significantly less than in quiet areas, and chicks from noisy areas experienced reduced body mass and lower probabilities of successfully fledging and recruiting into the population (Schroeder et al. 2012). Long-term studies such as these help to identify whether observed changes in provisioning behaviors ultimately correlate with fitness consequences. Because of the various and complex influences of noise pollution on animal behavior and physiology (*reviewed in* Kight and Swaddle 2010), future research should seek to understand the longer-term consequences of noise exposure for birds.

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APPENDIX A: FIGURES

Figure 1: Nest boxes (n=217) placed roughly 60 meters apart (mean = 61.66 ± 1.58 SE) within the study area of Poly Canyon in San Luis Obispo, California.

Figure 2: Treatments fixed to the roof of each nest box: (a) Control, (b) Satachi system and (c) StormMp3 system. The majority of treatment boxes contained system (c), and all treatments broadcasted a unique (for each species) playback file, standardized at approximately 65 dB(A) (mean $L_{eq} = 65.23 \pm 0.22$ SE dB(A) at 10 cm).

Figure 3: Power Spectra of original traffic recordings taken 10 meters from the road (red, solid line, $n=11$), playback (StorMp3 system) of original traffic recordings within the nest box (blue, dotted line, $n=11$), traffic recordings taken 20 meters from the road at original locations (green, solid line, $n=5$), and recordings made inside control boxes (black, dotted line, $n=4$). Systems significantly raised the amplitude within the boxes within the frequency range most audible to birds (i.e., 0.5-10 kHz). All in-box recordings were made using Roland R05 recorders.

Figure 4: Average Sound levels (dB(A)) in control (blue) versus treatment (red) boxes for western bluebirds (a) and ash-throated flycatchers (b). (a) Control average $L_{eq} = 46.19 \pm 3.99$ SE dB(A) at 10 cm, Treatment average $L_{eq} = 65.38 \pm 0.55$ SE dB(A) (b) Control average $L_{eq} = 42.99 \pm 1.67$ SE, Treatment average $L_{eq} = 64.91 \pm 0.11$ SE. Solid black lines represent the median, upper box is the 75th percentile and the bottom of the box is the 25th percentile. Whiskers represent the minimum and maximum values (extremes) of the data.

Figure 5: Decline in tarsus length (mm) of western bluebird nestlings with an increase in clutch initiation date (Julian Date Number, JDN) ($P < 0.001$).

Figure 6a,b,c: Ash-throated flycatcher fitness metrics as it relates to treatment by year. Control boxes are in navy blue. Treatment boxes are shown yellow. (a) Treatment individuals in year 1 experienced significantly fewer chicks per nest ($df=11$, $z = -2.06$, $P = 0.04$), but no significant difference between chicks among treatment individuals was detected in year 2 ($z = 1.70$, $P = 0.09$). There was no difference in number of chicks between control individuals in year 1 and year 2 ($P = 1.00$). (b) There was a significant negative effect of treatment on number of fledglings ($\beta = -1.87 \pm 0.76$ SE, $z = -2.46$, $P = 0.01$). No significant difference in number of fledglings was detected between years ($\beta = -0.62 \pm 0.47$ SE, $z = -1.32$, $P = 0.19$), but an interaction effect was found between treatment and year ($\beta = 2.49 \pm 0.89$ SE, $z = 2.79$, $P = 0.005$). (c) There was a significant positive influence of the noise treatment on nestling weight ($\beta = 5.73 \pm 1.18$ SE, $t = 4.84$, $P = 0.005$). There was no overall difference in nestling weight between year one and two ($\beta = -0.98 \pm 0.73$ SE, $t = -1.35$, $P = 0.24$); however, there was a significant interaction between treatment and year ($\beta = -4.13 \pm 1.39$ SE, $t = -2.97$, $P = 0.03$). Solid black lines represent the median, upper box is the 75th percentile and the bottom of the box is the 25th percentile. Whiskers represent the minimum and maximum values (extremes) of the data.

Figure 7: Number of visits for western bluebird treatment and control boxes. Treatment individuals visited the nest box during the provisioning stage significantly less than control individuals ($\beta = -4.68$, $t = -2.55$, $P = 0.03$), and this difference was explained by an increase in latency time (see Figure 10). Solid black lines represent the median, upper box is the 75th percentile and the bottom of the box is the 25th percentile. Whiskers represent the minimum and maximum values of the data.

Figure 8: Average time in box (s) as it relates to number of visits for western bluebirds. Duration spent in the box significantly decreased with increasing number of visits ($\beta = -0.56 \pm 0.26$ SE, $t = -2.18$, $P = 0.05$).

Figure 9: Average time western bluebirds spent in the nest box during visits as it relates to brood size. Duration spent in the box significantly decreased with increasing brood size ($\beta = -0.26 \pm 0.09$ SE, $t = -2.95$, $P = 0.01$).

Figure 10: Latency time, or time upon first visit to the nest box after video set-up, in western bluebird treatment and control boxes. Treatment individuals had a significantly longer latency period ($t=-5.14$, $df= 10.4$, $P < 0.001$). Solid black lines represent the median, upper box is the 75th percentile and the bottom of the box is the 25th percentile. Whiskers represent the minimum and maximum values of the data.

Figure 11: Average time ash-throated flycatchers spent in the box (s) as it relates to the number of visits. Duration spent in the box significantly decreased with increasing number of visits ($\beta = -0.92 \pm 0.26$ SE, $t = -3.49$, $P = 0.02$). Because the relationship might be heavily influenced by one data point, we reran the analysis with the point removed (avg. time in box > 40 s) and found marginal significance ($\beta = -0.26 \pm 0.10$ SE, $t = -2.58$, $P = 0.06$).