

Conversational Noise Reduction as a Win–Win for Ecotourists and Rain Forest Birds in Peru

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ABSTRACT

For all its positive attributes, the recent expansion of ecotourism has resulted in greater influxes of people into natural areas, causing a range of impacts including behavioral disruptions among wildlife. How animals respond to conversation is poorly understood, but noise reduction may reduce the impact of ecotourists while simultaneously enhancing their experience with higher wildlife encounter rates. We tested the response of a rain forest bird community to noise by playing a recorded conversation while conducting point censuses in a *terra firme* forest in Tambopata, Peru. Fifty decibel conversation (approximately library speaking volume) caused declines of 35 percent in total detections and 33 percent in detected species richness. Birds reacted similarly to 60 dB (approximately the volume of an excited child): average detections declined by 39 percent and detected species richness by 37 percent. Specifically, noise-induced detection declines were manifest both in decreased vocalizations (37% decline) and decreased physical sightings (44% decline). Lowered detection frequencies indicate behavioral shifts. As vocalization is involved in territory defense, breeding behavior, and predator detection, strong noise responsiveness indicates potential harm for birds. Insectivores were the most affected bird guild, raising conservation concerns, as insectivorous birds are sensitive to habitat modification. Birds reacted strongly to noise both near an established ecotourist lodge and in an intact reserve, indicating an absence of habituation. Thus, as a method for reducing ecotourism's footprint on native fauna and improving tourist satisfaction with increased wildlife sightings, noise reduction seems promising, even for well-established ecotourist lodges.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: avian; conversation; ecotourism; guild; habituation; Tambopata.

ECOTOURISM—TRAVEL FOCUSED ON EXPERIENCING NATURAL ENVIRONMENTS—is acclaimed for incentivizing conservation, fostering economic development, and promoting environmental awareness. Yet, in a meta-analysis, Krüger (2005) classifies just 60 percent of ecotourism case studies as ecologically sustainable and 17.6 percent as positively influencing conservation. Besides degrading habitat by expanding infrastructure, promoting ecotourism results in more interactions between humans and wildlife, which in some cases may be quite detrimental (Griffiths & van Schaik 1993, Hidinger 1996, Frid & Dill 2002). The risk-disturbance hypothesis (Frid & Dill 2002) postulates that organisms respond to human disturbance similar to predation, and trade-off continuing normal activity with predation responses such as fleeing, increased vigilance, shifting territories, and vocalization cessation. Engaging in predation responses directly influences fitness. For example, elevated stress hormones can cause cardiovascular problems, reproductive failure, compromised immune systems, and low body weight (Fowler 1999, Müllner *et al.* 2004). These effects may be long lasting: a year after experimentally hunting prairie dogs, hunted colonies still exhibited higher stress levels, worse body conditions, and lower reproductive rates than control colonies (Pauli & Buskirk 2007).

Further, time allocated to predator avoidance is time subtracted from normal activity (Frid & Dill 2002). Burger and Go-

chfeld (1998) found foraging effort decreased when humans walked past waterbirds. Frogs, passerines, and monkeys have been shown to reduce vocalization rates after exposure to human disturbance, which may in turn lower breeding rates (Frid & Dill 2002). Ecotourist avoidance has also been shown to translate into decreased parental investment, resulting in measurable fitness declines (Gillett *et al.* 1975). Because flushing parents may result in egg predation, chick predation, and incubation disruption, nesting success is typically lower when humans are allowed to approach breeding birds (Hunt 1972, Gillett *et al.* 1975, Safina & Burger 1983). So strong are these individual impacts that animals may begin to avoid tourist-frequented trails, resulting in marked abundance decreases near ecotourist areas (Griffiths & van Schaik 1993, Klein *et al.* 1995, Heil *et al.* 2007). This in turn negatively impacts the ecotourism industry by decreasing ecotourists' return on investment as measured by wildlife sighting frequency.

Ecotourism has grown remarkably in the past decades, making impacts of humans on wildlife an increasing concern. Ecotourism grew from a U.S.\$60 billion to U.S.\$175 billion industry from 1989 to 1995, with growth rates double that of tourism in general (Goodwin 1996, Krüger 2005). In our study site, the Tambopata region of southeastern Peru, this has translated into substantial influxes of tourists. From 1995 to 2005, annual visitation expanded from 5665 to 39,565 tourists, with an average annual growth rate of 22 percent (C. Kirkby, unpubl. data). The number of ecotourist lodges has correspondingly grown: from 3 in 1990 to 37 in 2008.

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In Tambopata alone, ecotourism lodges now manage upwards of 54,000 ha (C. Kirkby, unpubl. data).

As more land becomes managed for ecotourism, it is imperative for research to tease apart the relative harm of specific human actions so that efforts can be made to minimize impact in ecotourist areas. In their risk-disturbance framework, Frid and Dill (2002) identify a variety of specific human actions (*e.g.*, direct approaches, remaining at close distances, fast approaches, and large group sizes) that increase perception of predation threat and result in heightened animal responsiveness. Frid and Dill (2002), however, only address visual cues, though animals may respond strongly to auditory stimuli (Francis *et al.* 2009, Karp & Root 2009).

Conversational noise may serve as another important cue that could provoke the predation responses previously mentioned. Karp and Root (2009) showed that hoatzin (*Opisthocomus hoazin*) agitation and flushing inclination is associated with conversation volume. Further, the authors suggest that hoatzins may not habituate to conversation, making it a significant threat even near long-existing tourist lodges. Such demonstration of noise sensitivity and habituation disinclination could have important conservation implications, but reactions to noise may be species specific. Noise reaction rate and type have been shown to vary among species. Burger and Gochfeld (1998), using foraging rate as the dependent variable, found conversational noise responsiveness varied among waders. Klein (1993) showed behavioral response types also varied by species: some species fled, others emitted alarm calls, and others simply looked up.

Here, we examined sensitivity to conversational noise among a diverse rain forest bird community to determine whether or not conversation-induced behavior change is a general phenomenon. Further, we assessed habituation inclination across the bird community so as to verify whether or not noise is a lasting impact. In analyzing data, we partition species into functional groups (feeding guilds, rain forest strata associations, sensitivities to land disturbance, and taxonomy) to identify particularly noise-sensitive groups. After assessing reactions of tropical birds to conversational noise, we conclude by evaluating the viability of noise reduction as a method for reducing ecotourism's impact and increasing the success of wildlife viewing, a primary objective for most ecotourists.

METHODS

STUDY SITE.—The study was conducted in the Tambopata-Candamo National Reserve in southeastern Peru. We used two transects, one in the protected area and the second in the buffer zone near Refugio Amazonas, an ecotourism lodge opened in 2005. The predominant vegetation at these two sites is *terra firme* tropical forest with three forest strata: understory, mid-story, and canopy. Although both transects were placed in *terra firme* forest, some differences existed presumably associated with the activities in the tourist zone (lodge construction, trail management, and some selective logging). Around the tourist transect, the understory vegetation was denser and trees had smaller diameters than in the

protected zone (Champoux 2008). Canopy height was comparable at both sites (Champoux 2008).

RESEARCH PROTOCOL.—We played a prerecorded ecotourist conversation at different volumes during point-count censuses to test the effects of noise on a *terra firme* bird community. Kroodsma (1989) cautioned that using one recording for playback experiments is pseudoreplication: conclusions regarding behavioral responses can only be drawn with respect to the specific recording utilized. We were concerned, however, with standardizing variations in pitch and frequency across volume treatments, and thus only used one recording. The recording spanned 8 min, and was recorded in a room buffered from potentially confounding ambient rain forest noise that could induce unanticipated behavioral responses. While it is possible birds responded to a hidden cue within our treatments, we feel our treatments are representative of typical human conversation.

We used three volume treatments: 50 dB [Karp & Root's (2009); average speaking volume of ecotourists], 60 dB [Karp & Root's (2009); highest recorded speaking volume], and no noise (control). Fifty decibel is approximately the volume of individuals conversing in a library, and 60 dB is approximately the volume of an excited child. Speakers were calibrated at 3.5 m from a noise meter to the desired treatment volumes (Karp & Root 2009). Community responsiveness to conversational noise was quantified by examining declines in detection rates with noise treatments.

In addition, we examined whether or not birds exhibit signs of noise habituation. We censused birds along two transects, 6 km apart, each with ten point-count census stations. Each point was censused seven times under each noise treatment (total 21 times per point). We progressed through treatments in the following order: control, average noise, and high noise, so as to ensure that temporal changes in the bird community would not confound treatments. In an effort to distribute the highly productive early morning hour across points, we ran transects from both ends. One transect, located in the buffer zone of the Tambopata-Candamo National Reserve, followed the heavily used trails surrounding Refugio Amazonas. The other transect was located in the reserve, and received no tourist foot traffic. If birds habituate to conversation, we expected to detect more noise responsiveness among birds in the reserve transect than birds in the tourist transect. As the majority of censused birds were territorial, it is unlikely that the same individuals moved between transects. All census points in each transect were located in *terra firme* forest to compare similar bird communities and ensure any differences in noise responsiveness would not be attributable to differences in species identity. Indeed, a subsequent analysis of community similarity between the two transects indicated that most of the birds were shared between transects (Sorensen index for bird abundance similarity = 0.78).

Points were spaced 200 m apart, a distance sufficient for each point to function as a statistically independent replicate (Lynch 1995, Haselmeyer & Quinn 2000). We only recorded birds within a 50-m radius of each point, further decreasing the probability of double-counting individuals. Points were also sufficiently spaced so that noise played at one station could not be heard at any others.

Data collection began on 23 June 2008 and lasted until 25 August 2008, the height of the tourist season but before many species' breeding periods. Each point-count lasted 10 min. Censusing began at 0600 h and continued for *ca* 3 h. Although detections decreased over the 3-h span, enough activity persisted to warrant the existence of ten points per transect.

After arriving at each point, we immediately turned on the conversation tape attached to speakers calibrated with a noise meter to emit noise at one of the volume treatments. Noise played for a 4-min period before censusing, during which we recorded basic weather information including temperature and the qualitative Beaufort scale wind index. After the 4-min period, we stopped the noise tape and began the census. After the first 2 min of censusing, we pulsed noise for 1-min periods at the 2-, 4-, 6-, and 8-min marks. Because noise masks bird calls and songs, we only recorded auditory detections that occurred in the 6 min without noise for both no noise and noise treatments. Visual detections, however, were recorded throughout the 10-min census. Although tourist traffic on the tourist transect was high, tourists rarely passed by active point-counts. On the few occasions when tourists were present during a point-count, the count was suspended and repeated after they left.

To ensure accuracy and consistency in auditory bird identification, we recorded each point census with an omnidirectional microphone and recorder (Sennheiser ME62 microphone and a Zoom H4 digital recorder). We later compared unidentified bird calls and songs with Schulenberg's bird recordings ('Voices of Amazonian Birds'). If a vocalization was not included in Schulenberg's recordings, and local bird guides could not identify the call, we left the detection as unidentified and did not include it in analyses. Most such calls were short chip notes that occurred very frequently. Thus, it is likely that our censuses missed shy, quiet species. We also did not record mixed-canopy flocks and birds in the families Icteridae and Psittacidae, due to difficulty of identification from the forest floor. We included all other canopy birds, however, to test the effect of noise on this guild.

To pinpoint bird groups especially sensitive to noise, species were assigned to feeding guilds, preferred strata, and sensitivity to disturbance. Using Karr *et al.*'s (1990) guild characterization as a template, species were placed into the following feeding guilds: small-insect eaters, large-insect eaters, fruit eaters, small-insect-and-fruit eaters, and large-insect-and-fruit eaters. The few birds that could not be put into these categories (*e.g.*, nectivores and carnivores) were not analyzed due to insufficient frequencies of observation (54 of 993 total detections). Using recommendations from Stotz *et al.* (1996) and Karr *et al.* (1990), all species were also assigned to a preferred rain forest stratum: terrestrial, understory, mid-story, or canopy. Finally, all birds were assigned to an index of sensitivity to land-use disturbance (low, medium, or high), determined for each species in Stotz *et al.* (1996), to test whether or not sensitivity to disturbance correlated with sensitivity to noise.

DATA ANALYSIS.—We analyzed bird detections as a function of noise and transect location. As point-counts were variable, sometimes yielding no detections, and weather was not found to confound noise treatments, we condensed the seven separate censuses into one

master detections list for each point and noise level. Thus, each point, with its seven associated censuses, served as an independent replicate.

To test for differences in diversity between treatments, we calculated individual-based rarefaction curves (Gotelli & Colwell 2001) for the detected fraction of the community under each noise treatment. In addition, we compared similarity and complementarity of the 'communities' as a way to quantify effects on community composition and structure. Complementarity between a pair of sites was composed of a pair of asymmetric reciprocal fractions of species weighted by their abundances in one site relative to the second site, and similarity was defined as one minus the two complementarity fractions (Aguirre *et al.* 2010).

We used generalized linear models (GLM) to test for possible differences in total detections (Gaussian error and link identity function) and species richness (gamma error and link natural log function) between noise levels and transect types. We also used GLM with Poisson error structure and log link function to examine trends in auditory and visual detections associated with the noise treatments. Statistical significance of the analyzed factor and their interaction were established following the model simplification protocol and weighting changes in explained deviance between models at each step using an analysis of variance test, that is, contrasting models. Once no further model simplification was possible factor wise, we proceeded to collapse factor levels and contrast models as described above. In this way, we achieved the simplest model needed to describe changes of community metrics across treatments and transect locations.

Although a concerted effort was made to create linear models including independent random factors such as bird family, guild, stratum, and sensitivity variables, data did not meet model requirements. Instead, analyses were carried out with regression or decision tree models, in which data were subject to recursive binary splitting. Regression trees models can be used elegantly to analyze complex, categorical, ecological data, and their use is increasing in conservation literature (De'ath & Fabricius 2000, Davidson *et al.* 2009). In this case, regression trees were appropriate, as they do not assume normality in predictor variables (Quinn & Keough 2002). Splits were made if > 1 percent of the deviance was explained, and each resulting group contained greater than five observations. As over-fitting is a major drawback with regression tree models, we used random forests (RF), a technique in which random subsets of the data are sampled to generate a 'forest of trees' and the most frequent splits are chosen for the final composite tree (Prasad *et al.* 2006, Davidson *et al.* 2009). For the RF analysis, we repeatedly resampled half of each dataset and created forests of 1000 trees to assess the importance of family, guild, strata, and sensitivity to disturbance predictor variables in structuring bird detections. All statistical analyses were done in R version 2.9.2 (R Development Core Team 2009), and RF were performed with an R code written by R. Guevara.

RESULTS

COMMUNITY RESPONSE TO NOISE AND HABITUATION POTENTIAL.—After simplification, models for total detection and species richness

accounted for 56 and 48 percent of observed variability, respectively. The interaction term between noise level and transect location had no significant effect ($\chi^2 < 1.35$, $df=2$, $P > 0.51$) on total detections or species richness. In contrast, noise treatments affected significantly total detections and species richness ($\chi^2 > 8.25$, $df=2$, $P < 0.02$). In both models, 50 and 60 dB noise treatments did not differ significantly ($\chi^2 < 0.40$, $df=1$, $P > 0.53$), but both noise levels did differ significantly from the control ($\chi^2 > 4.93$, $df=1$, $P < 0.03$). Total detections and species richness declined by 37 and 35 percent, respectively, for both noise treatments compared with the no noise level (Fig. 1).

Diversity of subsets of the community of birds detected under each treatment did not differ, as individual-based rarefaction curves overlapped completely (Fig. 2). Complementarity and similarity indices, however, indicated that compositions of birds sampled under each treatment were distinct. Complementarity of the subset of the community detected under no noise on that detected under mean noise was 0.33, whereas the reverse complementarity was 0.21 with an overall similarity of 0.46. In the same way, the complementarities between no noise and high noise were 0.38 and 0.25 with an overall similarity of 0.38. Complementarities between mean noise and high noise were 0.26 and 0.24 with an overall similarity of 0.49.

Model simplification showed no effects of the interaction between noise level and transect location on visual and vocal detection ($\chi^2 < 3.16$, $df=2$, $P > 0.21$). Transect location affected significantly vocal detections ($\chi^2 = 41.8$, $df=1$, $P < 0.01$), but not visual ones ($\chi^2 = 2.30$, $df=1$, $P = 0.13$). Vocal detections were 1.72 times higher in the tourist transect compared with the control transect (Fig. 3). Hence, birds reached higher abundances near the tourist transect than near the control transect. Congruently with results on community metrics, noise treatments significantly affected visual and vocal detections ($\chi^2 > 5.49$, $df=2$, $P < 0.02$). Again, mean and high noise treatments were found to be indistinguishable ($\chi^2 < 1.73$, $df=2$, $P > 0.19$). Simplified vocal and visual detec-

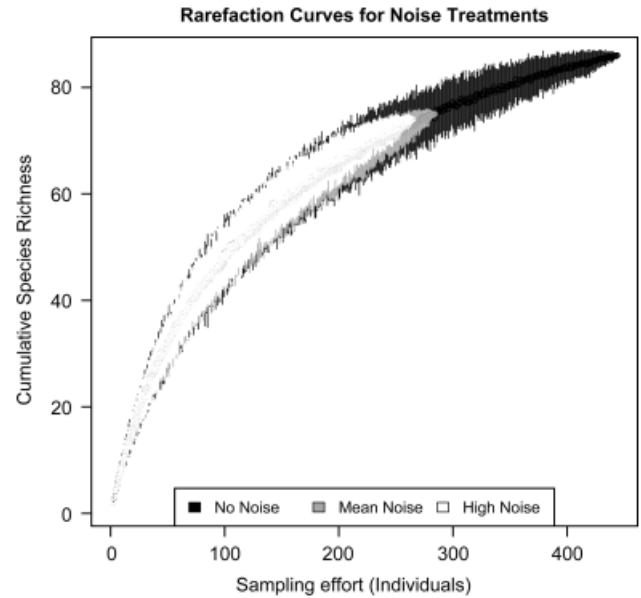


FIGURE 2. Individual-based rarefaction curves for each noise treatment showing range covered by 50 random repetitions.

tions models accounted for 57 and 12 percent of the total deviance, respectively. Total detections for each encountered species and noise level are listed in Table S1.

COMMUNITY PATTERNS OF NOISE SUSCEPTIBILITY.—We used the RF statistical test to reveal patterns of noise responsiveness within the bird community. Uncovering particularly noise-sensitive groups within (1) guilds, (2) families, (3) sensitivities to disturbance, and (4) preferred strata was accomplished by analyzing the four composite trees.

The guild composite tree shows small-insect eaters to be the most noise responsive guild (Fig. 4A). In this guild, the majority of

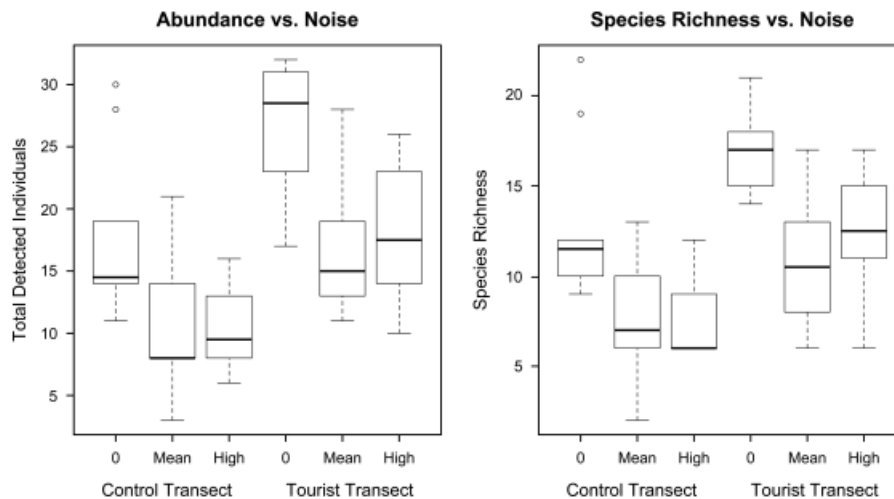


FIGURE 1. Effects of noise level treatments on *terra firme* bird community indices for control and tourist transects in southeastern Peru. Whiskers represent minimum and maximum values when no outliers are present or twice the interquartile range subtracted and added from the first and third quartile (the bounds of boxes).

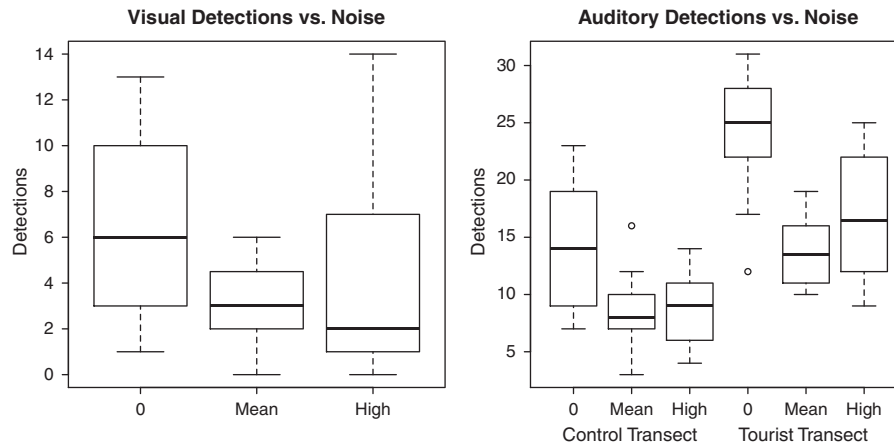


FIGURE 3. Effects of noise treatment on bird detection type for control and tourist transects in southeastern Peru (definition of boxplot in Fig. 1).

resampled trees split the control noise treatment from the mean and high noise treatments in both the control and tourist transects (control transect: 56.3% of trees; tourist transect: 50.0%; Fig. 4A). In 34.8 percent of trees, large-insect eaters and large-insect-and-fruit eaters were left un-split by noise. Noise treatments, however, explained deviance in these guilds for only a slightly smaller percentage of trees (32.1%), indicating that these guilds are the next most likely feeding groups to respond to noise. In contrast, noise explained the deviance for fruit eaters and small-insect-and-fruit eaters in only 0.14 percent of trees.

Using RF to examine bird families yielded few results. The only group to show significant noise responsiveness was *Thamnophilidae* (antbirds). In the tourist transect, thamnophilids were detected significantly more often in the absence of noise, with 67.6 percent of the trees exhibiting splits (Fig. 4B). Antbirds clearly exhibited no sign of habituation, reacting to noise more frequently on tourist trails than in the reserve.

As expected, high sensitivity to disturbance correlated with increased noise responsiveness: in 87.2 percent of trees, noise split highly sensitive birds from the birds less sensitive to disturbance (Fig. 4C). Interestingly, for noise treatments, more birds were observed on average in the tourist transect than in the reserve transect (65.9% of trees). For no noise treatments, birds were seen equally frequently in both transects. Hence, birds with a high sensitivity index may habituate to noise. A disproportionate number of highly sensitive birds, however, were located in the control transect relative to the tourist transect. χ^2 analysis showed sensitivity index and transect location were not independent ($\chi^2 = 21.2$, $P < 0.01$). Approximately 80 percent of the χ^2 statistic was due to an unexpectedly low proportion of 'high' sensitive birds and high proportion of 'medium' sensitive birds in the tourist transect. As no other test lends evidence for bird habituation, the bird sensitivity incongruity between transects is probably the best explanation for the potential habituation fingerprint.

Surprisingly, of the four recorded strata, canopy-associated birds reacted strongest to noise. Noise explained deviance in canopy birds for 59.2 percent of iterations (Fig. 4D).

The RF composite tree contained no other noise splits. A subsequent χ^2 analysis showed that strata and sensitivity to disturbance were not independent ($\chi^2 = 171.5$, $P < 0.01$), and 64 percent of the χ^2 statistic was due to two cells: fewer 'high' sensitive birds and more 'medium' sensitive birds were located in the terrestrial layer than would be expected. Canopy birds exhibited the expected ratio of sensitive to insensitive birds. Mid-story birds, however, contained more sensitive birds than was expected.

DISCUSSION

REACTION TO CONVERSATIONAL NOISE.—Although ecotourism incentivizes conservation, the influx of tourists into natural areas may impact wildlife. Karp and Root (2009) found louder conversations resulted in increased Hoatzin agitation and susceptibility for flushing. In this study, the rain forest bird community also responded strongly to conversational noise. Detected abundance and species richness declined similarly for both mean and high noise treatments. Diversity did not change between the treatments, probably because all birds were sampled from the same community. Therefore, species accumulated at the same rate. Nevertheless, complementarity and similarity indices among noise treatments suggest marked changes in the detected community structure, likely due to changes in behavior within the bird community. In addition, strong declines in species richness and abundance also indicate behavioral responses to noise. Woodland birds began declining in abundance in response to an average car noise volume of 42 dB, with the most sensitive birds showing responsiveness at 35 dB (Forman & Alexander 1998). That species richness and total abundance declined in this study for the average (50 dB) and high (60 dB) noise treatments is consistent.

Observed responsiveness of birds to conversational noise is likely a predation response. Birds were seen and heard less often when exposed to conversational noise treatments. These increased physical secrecy and decreased vocalization rates may evidence predator avoidance behavior. Further, the observation that birds react similarly to mean and high noise treatments is consistent with

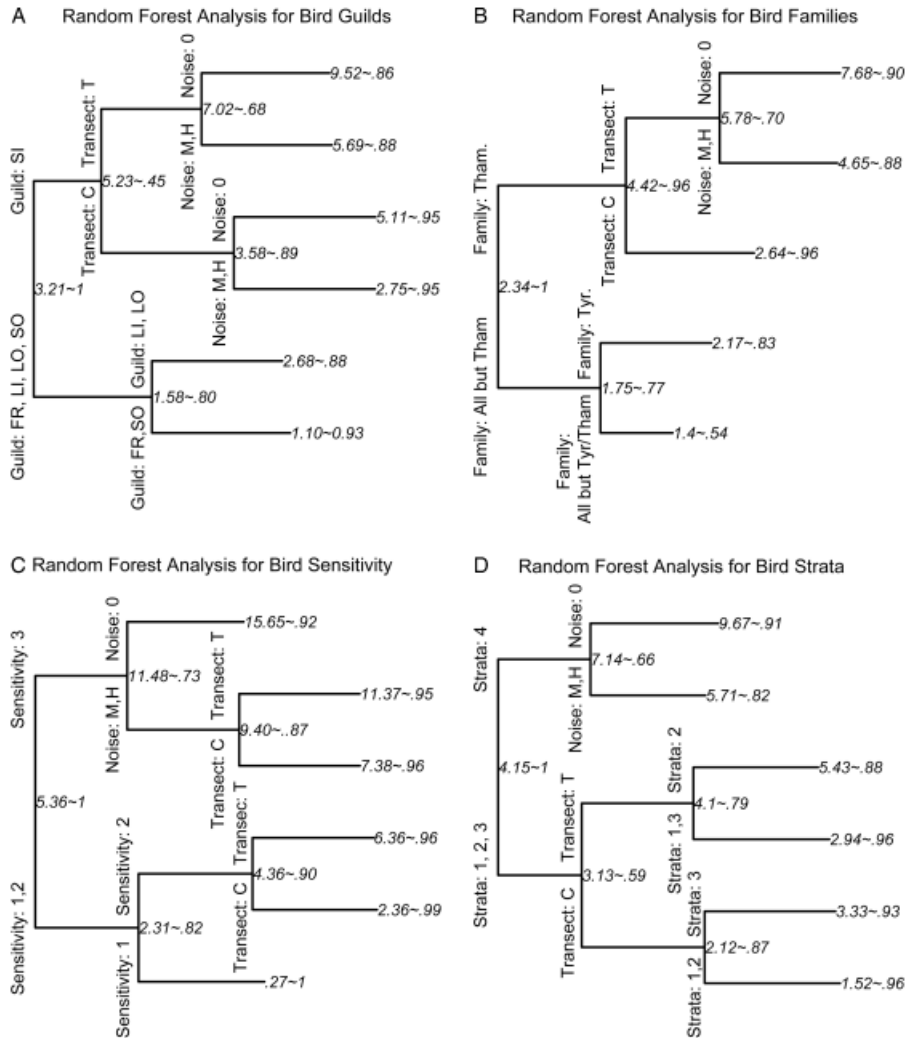


FIGURE 4. Composite trees representing the most frequent splits from four random forest analyses examining whether or not noise responsiveness is structured by bird feeding guild (A), taxonomic family (B), sensitivity to disturbance (C), and preferred strata (D) (mean explained deviance: 0.91, 0.96, 0.91, and 0.91, respectively). The length of each branch is proportional to the node’s percentage of total deviance reduction. At each node, the average number of individuals belonging to each of the previous predictor variable groups followed by the percentage of total deviance reduction is reported. For example, birds of the family Thamnophilidae in the tourist transect were detected on average 7.68 times at each point without noise. Graph A shows small-insect (SI) eaters were more responsive to noise than large-insect (LI), large-insect-and-fruit (LO), small-insect-and-fruit (SO), and fruit (FR) eaters. Small-insect eaters were encountered less frequently for mean (M) and high (H) noise treatments in both the tourist (T) and control (C) transects. Graph B shows that Thamnophilidae is the most responsive bird family, but it exhibits no sign of habituation, reacting strongly to noise in the tourist transect. Graph C indicates birds with high sensitivity to disturbance (3) reacted stronger to noise than those with low (1) and medium sensitivity (2). Highly sensitive birds show signs of habituation, with more individuals being encountered in the tourist transect than the control transect for both noise treatments. Graph D indicates canopy birds (4) were more responsive to noise than mid-story (3), understory (2), and terrestrial (1) birds in both transects.

predator avoidance. If birds can detect mean noise, there is no reason to believe they would react differently to an increase in volume.

It is possible, however, that decreases in detection rate were not predator driven. Many studies have found birds exhibit strong reactions to mechanical noise (e.g., Delaney *et al.* 1999, Canaday & Rivadeneyra 2001, Francis *et al.* 2009). Forman and Alexander (1998) suggest hearing loss, stress hormone release, or communication disruption may elicit bird sensitivity to mechanical noise.

Francis *et al.* (2009) found birds whose vocalizations overlap with mechanical noise abandon noise-polluted areas. Many of the observed species forage in mixed-species flocks, which rely on inter-specific communication for predator detection (Goodale & Kotagama 2005). Secretive behavior could be a preventative measure used when noise masks birds’ ability to quickly relay a predator threat. It seems unlikely, however, that a 50-dB conversation would interfere with bird communication, and vociferous ambient noise

(from howler monkeys, insects, parrots, etc.) would not. Further analysis of noise frequency overlap and sensitivity to human conversation is needed.

COMMUNITY HABITUATION POTENTIAL.—Vocal detection rates were higher in the tourist transect compared with the reserve transect, a fact in agreement with Champoux (2008), who argues that intermediate disturbance near the lodge fostered higher bird densities. Despite this, little evidence for bird habituation to conversational noise was found in this study. Although separated by only 6 km, the Tambopata-Candamo National Reserve experiences much less foot traffic than the trails surrounding Refugio Amazonas lodge: only the occasional researcher or Brazil nut harvester uses the area. Habituation to noise would have been evidenced if birds had exhibited increased responsiveness in the control transect relative to the tourist transect. This trend does not appear. In fact, antbirds (Thamnophilidae) were more secretive on the tourist trails than in the reserve. The only sign of increased noise responsiveness in the reserve was for birds sensitive to human land use; however, this trend was confounded by the occurrence of more sensitive birds in the reserve. Although both transects were placed in *terra firme* forest, Champoux (2008) measured significant increases in understory vegetation density, slightly significant decreases in tree diameter, and comparable tree heights in the tourist transect relative to the reserve transect. Our finding of no habituation is robust to the possibility that differences in habitat structure confounded our ‘treatment’ of tourist presence. Because noise travels farther in open habitats, birds would have been expected to be more responsive in the more open, control transect.

Conversation may represent such a strong predation cue that birds have not yet habituated. The area surrounding Refugio Amazonas (both the tourist and reserve transects) was heavily hunted until the lodge’s construction. For game birds like tinamids or cracids, human conversation may be an important signal to begin avoidance behavior. Less intuitive is why small birds would also respond strongly to conversation. In fact, humans do not restrict hunting to large game birds. The Maraca tribe of Colombia has been recorded using over 50 species of birds, some quite small (Redford 1992). Studies show raptors, game birds, insectivorous birds, and others all suffer substantial hunting pressure (Thiollay 1985, 1999; Canaday 1997). Besides direct hunting, the native Ese Eja tribe traditionally sought out bird eggs for consumption. With heavy hunting pressure continuing until 3–4 yr ago, some hunting continuing today, and traditional egg collection, the bird community may still view humans as predators, indicated by the absence of noise habituation. Alternatively, if noise has physiological ramifications, then decreasing detectability would be expected, even for birds with previous noise exposure. Similarly, habituation would not be expected if noise masks bird communication.

NOISE SENSITIVITY AMONG INSECTIVORES.—Within bird guilds, the small-insect eating birds were the most sensitive to noise, followed by large-insect and large-insect-and-fruit eaters. Congruently, thamnophilids (antbirds), a group entirely composed of insectivores, were the most responsive bird family. Our results are consis-

tent with Canaday and Rivadeneyra (2001), who found terrestrial insectivores declined more than all other examined guilds near a petroleum operation and implicated mechanical noise as the primary driver. That insectivores would be most susceptible to conversational noise is somewhat surprising. If noise responsiveness were governed by hunting pressure, large game birds would be expected to be most sensitive. Game birds, including tinamids (tinamous), cracids (guans), and columbids (pigeons), were frequently detected, but still belonged to the comparatively least sensitive bird guild (frugivores).

Insectivores may respond most strongly to noise due to acute hearing, explaining their sensitivity to both mechanical and conversational noise. The first to detect a possible threat may be the first to respond. Some insect eaters locate prey auditorily, and may thus have more developed hearing than visual fruit searchers. Percussion feeders, for example, tap on wood and listen for resonance changes to locate their insect prey (Kilham 1972). Focused physiological research that compares the hearing of insect and fruit eaters is needed.

RAIN FOREST STRATA ASSOCIATIONS AND NOISE RESPONSIVENESS.—During noise treatments, detections declined most for canopy birds. Raucous calls of parrots and booming howler monkeys make the canopy among the noisiest of strata. As the noise stimulus was farthest away from the canopy, it is surprising that ambient noise did not mask the noise treatments and make canopy species the least noise sensitive. One possible explanation of the trend is strata plasticity. We assigned each species to one stratum, but, in reality, birds frequent many parts of the forest. In future studies, bird positions should be noted during noise treatments to clarify whether or not canopy birds are most noise sensitive.

CONCLUSION

The bird community around Refugio Amazonas responded strongly to noise treatments. Apparent species richness and abundance of rain forest birds declined for both noise treatments. Both visibility and vocalization frequency were shown to decrease in response to noise. Increasing secretive behavior may have negative consequences for birds. Although this study did not pinpoint specific behavioral shifts when birds were seen, natural behavior must have changed as birds became less apparent. As tourist activity often coincides with the dawn chorus (D. Karp, pers. obs.), birds may often lower rates of vocalization in response to tourists. Vocalization can increase energy expenditure (Thomas 2002); however, vocalization is key for procuring breeding opportunities and repelling rival conspecifics. Although we can conclude noise elicits strong bird responsiveness, we do not know if fitness impacts exist. It seems more likely, however, that if fitness impacts are present, they are negative.

Ecotourism is sometimes destructive, and conserving rare or sensitive birds by promoting ecotourism may not always be effective. Insectivores, consistently shown to be among the most sensitive of bird guilds (Canaday 1997, Canaday & Rivadeneyra 2001), also respond negatively to ecotourism. Heil *et al.* (2007) found that

abundance of insectivores declined conspicuously on trails frequented by ecotourists in the Cordoba Mountains of Argentina. Here, conversational noise is shown to impact insectivores strongly. Because birds sensitive to land use are also most affected by noise, as currently practiced, ecotourism may not be the savior of sensitive species. Ecotourism, however, still has much worth, and is clearly preferable to large-scale, exploitive practices such as commercial agriculture, mining, and timber harvesting that result in widespread deforestation. While sensitive birds respond strongest to noise, they are still encountered frequently near lodges like Refugio Amazonas. Noise reduction may mitigate current behavioral impacts.

Although sometimes the interests of ecotourists and wildlife are at odds, noise reduction is a win-win, where the interests of wildlife, lodge owners, and tourists align. In general, bird detections decrease markedly with elevated noise, silence would probably result in tourists encountering more wildlife, increasing their perceived return on investment. Further, wildlife may continue to frequent tourist areas, benefiting the lodges' future economic viability. As it appears that the bird community does not habituate to noise, reducing noise volume may make a difference for even long-standing lodges. As ecotourism continues to increase in popularity, seeking mechanisms for mitigating its consequences will become progressively more imperative. With clear benefits for wildlife and tourists alike, noise reduction seems to be an effective and easy first step.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

TABLE S1. *Number of detections per noise treatment by species.*

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