


CONTRIBUTED PAPER

Effects of agriculture and nature reserves on avian behavior in northwestern Costa Rica

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Abstract

Behavioral changes are often animals' first responses to environmental change and may act as a bellwether for population viability. Nonetheless, most studies of habitat conversion focus on changes in species occurrences or abundances. We analyzed >14,000 behavioral observations across 55 bird species in communities in northwestern Costa Rica to determine how land use affects reproductive, foraging, and other passive kinds of behaviors not associated with either foraging or reproduction. Specifically, we quantified differences in behaviors between farms, privately owned forests, and protected areas and implemented a novel modeling framework to account for variation in detection among behaviors. This framework entailed estimating abundances of birds performing different behaviors while allowing detection probabilities of individuals to vary by behavior. Birds were 1.2 times more likely to exhibit reproductive behaviors in forest than in agriculture and 1.5 times more likely to exhibit reproductive behaviors in protected areas than in private forests. Species were not always most abundant in the habitats where they were most likely to exhibit foraging or reproductive behaviors. Finally, species of higher conservation concern were less abundant in agriculture than in forest. Together, our results highlight the importance of behavioral analyses for elucidating the conservation value of different land uses.

KEYWORDS

behavioral variation, land-use change, N-mixture model, protected area, tropical ecology

INTRODUCTION

Habitat loss and fragmentation are restructuring wildlife communities, especially in tropical regions, where rates of biodiversity loss and land conversion peak (Gibbs et al., 2010; von Essen & Lambin, 2021; Winkler et al., 2021). Although biodiversity is often higher in intact protected areas than human-dominated landscapes (Newbold et al., 2015), working landscapes can be managed to provide for human needs while sustaining wildlife (Frishkoff et al., 2019; Kremen & Merenlender, 2018). For example, Frishkoff et al. (2014) found that diversified farms in Costa Rica with multiple crop types and natural habitat patches sustain levels of species richness similar to tropical

forest reserves (although reserves support more phylogenetic diversity).

In most studies of land-use change, changes in species occurrences or abundances or both are used to quantify species' tolerances for anthropogenic landscapes (e.g., Ehlers Smith et al., 2018; Hatfield et al., 2018; Newbold et al., 2013). Such studies, however, provide little information about how species actually use the habitats where they occur (Gilroy & Edwards, 2017; Kleijn et al., 2011; Ortega-Álvarez et al., 2021). For example, a species regularly detected in agriculture may be passing through or spilling over from nearby natural habitats (and thus may not actually be resilient to land-use change [Brudvig et al., 2009; Frishkoff et al., 2019; Vickery et al., 2001]). Alternatively,

the species could use working landscapes to forage and reproduce, meaning it is resilient to or can even benefit from land-use change. Finally, a species may use working landscapes but have suboptimal demographic rates in agriculture due to mechanisms such as source–sink dynamics (Pulliam, 1988), buffer effects (Gill et al., 2001), spillover effects (Brudvig et al., 2009), ecological traps (Gates & Gysel, 1978), or extinction debt (Tilman et al., 1994). For example, urban areas in southern Arizona act as ecological traps for Cooper's hawks (*Accipiter cooperii*) that reside and nest in cities but have over 50% nest failure, primarily from trichomoniasis acquired from feeding on urban doves (Boal & Mannan, 1999). Therefore, looking beyond species occurrence is critical for quantifying the conservation value of anthropogenic habitats.

One way to assess how animals use their environments is by examining behavior. Behavioral changes are often an animal's first response to human-induced environmental changes and can indicate whether individuals are able to cope with land-use change (González-Lagos & Quesada, 2017; Wong & Candolin, 2015; Wright et al., 2010). For example, some species can adapt their acoustic signals to maximize transmission in new environments and thus maintain communication between individuals (Graham et al., 2017; Slabbekoorn & Peet, 2003). Alternatively, land-use change can result in behaviors and physiological responses that decrease an individual's fitness, such as reducing foraging due to high risk of predation, (Desrochers et al., 2002) or body mass (Liker et al., 2008). Because behavior can often be linked to demographic parameters (e.g., birth, death, migration), variation in behavior across different environments can have cascading effects on population persistence (Luck, 2002; Lyons, 2005). For example, female great tits (*Parus major*) alter their behavior in response to noise in their environment, which can lead to lower fledgling success (Halfwerk et al., 2012; Slabbekoorn & Peet, 2003). Also, male bird song rate can be used as a proxy for superior male quality and territory defense (Gil & Gahr, 2002; Møller, 1991), and Pillay et al. (2019) measured male per-capita song rate to explore the potential mechanisms underlying tropical bird distributions in selectively logged forest. Therefore, observing changes in behavior can help identify species that are able to exploit anthropogenic resources and act as an early warning signal for populations in trouble (Berger-Tal et al., 2016; Wong & Candolin, 2015). If, however, management decisions rely only on occurrence data, ignoring how species use different habitats, then areas essential to phases of the species' life cycle may not be protected (Ke et al., 2022).

Most studies that measure variation in behavioral use of different environments are limited to a few individuals and species because they require labor-intensive animal monitoring (e.g., focal observations or telemetry [Luck, 2002; Tremblay et al., 2005]). In contrast, survey-type data require fewer resources to collect, can capture a larger portion of the population, and are often suitable for multiple species simultaneously. However, some behaviors are difficult to observe (e.g., sedentary, ambush-oriented feeding behavior in snakes [Durso et al., 2011]). Moreover, the detectability of individuals often depends on the behaviors they perform (Crowe & Longshore, 2010),

which could lead to underestimating the frequency of hard-to-detect behaviors. The detectability of different behaviors may also vary across environments. For example, the probability of observing visually detected behaviors may be lower in dense vegetation compared with open areas. Without accounting for behavior-specific detection, one could risk falsely concluding, for example, that a species forages more often in agriculture than forests simply because the species is more apparent in open environments.

We evaluated how land use affects the likelihood of birds exhibiting reproductive, foraging, and passive behaviors (e.g., perching, preening, roosting) (details in Appendix S2) over 4 years in northwestern Costa Rica. We extended a single-species behavior N-mixture model (Ke et al., 2022) to a community model to quantify differences in behaviors between farms, privately owned forest patches, and formal nature reserves, and accounted for variation in detection between behaviors, species, and habitats.

Our work was guided by 3 core questions. First, how do bird communities vary in abundance and behavior between land uses? We hypothesized that because high-intensity agricultural habitats contain fewer trees and fewer bird species that utilize the habitat (Luck & Daily, 2003), birds are less abundant and perform foraging and reproductive behaviors less frequently in agriculture than in forest. Based on prior work (Karp et al., 2019), we also hypothesized that protected areas have similar bird abundances but higher probabilities of exhibiting reproductive behaviors than privately owned forests, due to higher rates of disturbance from logging, fires, and hunting in private forests. Second, do species that peak in abundance in one habitat also forage and reproduce there more often? We predicted that most species would exhibit reproductive and foraging behaviors in the habitats where they peak in abundance (as long as they are selecting their habitats correctly and are not subject to ecological traps [Gates & Gysel, 1978]). However, we predicted that some species would have inconsistent responses in abundance and behavior, for example, if individuals were more likely to perform reproductive behaviors in one habitat but were equally or less abundant in that habitat. That is, a species could have equal abundances in forest and agriculture but perform more reproductive behaviors in forest. Finally, do species of higher conservation concern (i.e., range-restricted or declining species) react differently than less sensitive species? Given prior research documenting the sensitivity of range-restricted species to habitat conversion (Karp et al., 2019; Sykes et al., 2020), we predicted that species of higher conservation concern would be more abundant and perform foraging and reproductive behaviors more frequently in protected areas than in agriculture and private forests.

METHODS

Study area

We investigated how land use affects bird behavior and abundance in the Guanacaste Province of northwest Costa Rica

(Appendix S13). Our study region was a mosaic of tropical forest ranging from coastal wet forests to inland dry forests (protected and privately owned forests) and agriculture (pastures and crop fields). Guanacaste experiences a dry season from December to April, 2 rainy seasons (May to June and September to November), and a midsummer dry period in July and August (Hund et al., 2021). We selected sites across a network of 5 formally protected areas and 20 farms, which were composed of pasture ($n = 12$), rice ($n = 6$), sugarcane ($n = 1$), and Taiwan grass (a forage crop, $n = 1$). These agricultural types were representative of the broad study region. Prior tree surveys in our study plots suggest that some of the most common tree species in our study region were *Guaizuma ulmifolia*, *Semialarium mexicanum*, *Ardisia revoluta*, *Lysiloma divaricatum*, and *Luehea candida* (Karp et al., 2019). Protected areas were under government administration and experienced regular tourist visitation and occasional illegal hunting. All work was conducted with approval from the Costa Rican government (permits: SINAC-SE-CUS-PI-R-036-2016, SINAC-SE-CUS-PI-R-030-2017, SINAC-PNI-ACAT-043-2019, and SINAC-PNA-ACAT-039-2021).

We selected specific point-count locations on farms so that local forest cover within 50 m varied independently from the surrounding landscape context (i.e., amount of forest within the surrounding landscape). On each farm or protected area, birds were surveyed at 6 point-count locations (150 points total). On average, point-count locations in the same farm or protected area were located 500 m apart. On farms, half of the point-count locations were in agriculture and the other half in privately owned forests. On farms, we chose locations in forest interiors, forest edges, small forest fragments, agricultural field centers, fields bordering forest, and fields surrounded by forest. For protected areas, 4 point-count locations were placed in forest interiors and 2 were in forest edges. Privately owned forests were twice as fragmented as protected areas (based on total forest edge length); they were also regularly logged, which led to significantly shorter tree heights than in protected areas (Karp et al., 2019).

Bird surveys

At each point-count location, the same expert observer (J.Z.) recorded all birds by sight and sound in 20-min, 50-m fixed-radius point counts from 2016 to 2019 during the breeding season for most bird species in the region (i.e., May–July). This length of point count allowed detection of rare behaviors, and the observer has decades of expertise to draw from when differentiating among individuals, which avoided double counting (Hendershot et al., 2020). J.Z. sampled half of the point-count locations 3 times within 1–2 weeks. The other half were sampled once to increase spatial replication while still providing sufficient replication to estimate detection probabilities (see below). One farm or protected area (6 points) was surveyed each day beginning at sunrise and continuing for ~5 h. Information concerning species identity, number of individuals observed, time

of day, and whether noise exceeded typical background levels (e.g., farm machinery, cicadas) was recorded.

Each observation was also associated with one of 32 behaviors that we placed in one of 3 categories: reproductive, foraging, and passive behaviors (details in Appendix S2). If only a vocalization was heard, the observation was recorded as singing or calling behavior. When an individual performed more than one behavior during a point count, we randomly selected one of the behaviors observed because the structure of our model allowed for only one behavior per individual observation (see “Modeling behavior”). Although this could slightly affect conclusions about infrequently detected species exhibiting infrequently detected behaviors, only 10.5% of bird observations were associated with more than one behavior. Further, to ensure we had enough observations of each species for the model to effectively estimate behaviors, we restricted analyses to species that were observed at least 20 times and had at least one observation in each behavior category. This resulted in 55 species for our first analysis that compared bird behaviors between forest and agricultural sites and 40 species for the second analysis, for which we used a subset of the data to compare bird behavior between privately owned forests and protected areas (but not agricultural areas).

Covariates

To quantify local forest cover, we classified tree cover within 50 m of all point-count locations with cloud-free Google Earth images available from 2013 to 2017. We also extracted multiple species’ traits as covariates to determine whether rare species behaved differently from common species. Because many Neotropical species are understudied and population sizes are often uncertain, we assessed multiple dimensions of rarity. One way rarity can be defined is by geographic range size (Sykes et al., 2020). We obtained species’ range sizes from BirdLife Data Zone (BirdLife Data Zone, 2021). Although all species included in our model were least concern, we also obtained global population trend information (i.e., whether each species is declining, stable, or increasing) from the International Union for the Conservation of Nature Red List of Threatened Species (IUCN, 2022).

Modeling behavior

To quantify how birds change their behavioral use of habitats, we developed a community extension of a behavior N-mixture model (Ke et al., 2022). The N-mixture model uses spatially and temporally replicated surveys in which the number of individuals is counted to estimate abundance while accounting for detection probability (Kéry, 2018; Royle, 2004). Behavior N-mixture models quantify the probability of individuals exhibiting different behaviors while accounting for the fact that the detectability of a behavior depends on behavior performed and surrounding environment (e.g., a foraging bird is likely

easier to detect in an open field vs. a dense forest) (Ke et al., 2022). We extended the single-species behavior N-mixture model such that the probabilities of many species exhibiting different behaviors could be estimated jointly. Species-specific parameters were derived from community-wide hyperdistributions governed by (community-level) hyperparameters estimated from the data. This parameterization allows estimating parameters of species with fewer observations by sharing information among species in the community, although rare species' parameters tend to shrink toward the community mean (Dorazio & Royle, 2005; Kéry & Royle, 2015).

In summary, the number of individuals of species (i) performing a certain behavior (b) at site (j) was modeled using a negative binomial distribution (Appendix S1) in which the expected abundance $\lambda_{i,j}$ was modeled as

$$\log(\lambda_{i,j}) = \alpha 0_i + \alpha 1_i \times \text{forest cover}_j + \delta 0_{i,\text{farm}[j]} + \delta 1_{i,\text{year}[k]} + \delta 2_{i,\text{point}[j]}. \quad (1)$$

Forest cover is the local forest cover within 50 m of the point-count location. Parameters in the α family were estimated for each species, and the δ terms represent random effects included to account for spatial and temporal autocorrelation in bird abundances and explain variation among species, point-count locations, farms, or years that was not explained by the other parameters. We modeled the probabilities of species performing each behavior as a function of habitat with multinomial logistic regression. Finally, we modeled the detection probability of an individual of a certain species performing a certain behavior at a given site and visit ($P_{i,j,b,k}$) as

$$\text{logit}(P_{i,j,b,k}) = \gamma 0_{i,b} + \gamma 1_b \times \text{noise}_{j,k} + \gamma 2_{i,b} \times \text{habitat}_j + \gamma 3 \times \text{time}_{j,k}, \quad (2)$$

where noise is a binary variable indicating whether noise levels exceeded typical background noises and time is time of day of the point count. Parameters $\gamma 0$ and $\gamma 2$ were species-level random effects, and parameters $\gamma 1$ and $\gamma 3$ were constant over species (detailed modeling methods in Appendix S1).

To compare shifts in behaviors between protected areas and private forests (Questions 1 and 2), we conducted a second analysis in which all sites in agriculture were omitted and habitat and forest cover variables were replaced with a binary variable indicating whether the forest site was in a protected area or not. We also excluded $\gamma 2_{i,b}$ (i.e., habitat type) from the detection process because all sites were in forests.

Behavioral N-mixture models can be used to estimate effects of environmental covariates on abundance, but the actual abundance estimates generated from them can be biased because when an individual is observed performing different behaviors between visits, it contributes to overall abundance estimates multiple times (Ke et al., 2022). Thus, to model abundances (Questions 1 and 2), we constructed a traditional N-mixture model for each analysis (forest vs. agriculture and protected vs.

private forest [Kéry, 2018; Royle, 2004]). The models retained all parameters above except the behavior index and the behavior components involving π .

All models were implemented in R 4.0.0 with the package nimble, which runs Markov chain Monte Carlo (MCMC) algorithms (de Valpine et al., 2017; R Core Team, 2021). We ran 3 chains starting at random initial values and 5000 burn-in iterations. We included 20,000 post burn-in iterations thinned at a rate of 15. We assessed convergence by examining Gelman–Rubin statistics of the chains of every parameter and considered chains to converge if Gelman–Rubin statistics were ≤ 1.1 (Gelman et al., 2004). To assess model fit, we also calculated the Bayesian p values of the probabilities of species performing each behavior (Conn et al., 2018) (Appendix S1).

Interpreting behavioral coefficients

We derived the probability of a species performing a behavior and the number of individuals performing each behavior in each habitat. We compared the resulting Bayesian credible intervals (BCIs) for each species to assess whether behavior probabilities were significantly different between habitats. We used a 90% BCI cutoff because each parameter was estimated with less data than the community means (details in Appendix S1). To understand how bird communities change in abundance and behavior with changes in land use (Question 1), we extracted community-wide mean effects of forest cover (or protection status) on abundance ($\alpha 1$) and the mean predicted differences in behavior between habitats with the community-wide means for the behavior probability intercept ($\beta 0$) and the effect of habitat on behavior ($\beta 1$). For community-wide effects, we used a BCI cutoff of 95% to determine statistical significance because we had more data available to estimate them (Kruschke, 2014; McElreath, 2020). For the effects of forest cover and protected area on abundance, we calculated their statistical significance with a 5% cutoff with the MCMC p value or with the proportion of posterior samples above or below zero from the MCMC.qpcr package (Matz, 2020).

To understand how individual species' abundance responses to forest cover (or protection status) related to their behavioral responses (Question 2), we compared differences in abundance across forest cover (or protection statuses) with differences in behavior probabilities between habitats and measured the strength of relationships with Spearman's correlation coefficient. We then categorized species based on their abundance response to local forest cover (or protection status) and their behavioral response to habitat. For example, when individuals of a species were more likely to exhibit reproductive or foraging behaviors in one habitat (e.g., forests) but they were equally or less abundant in that habitat, we termed this an inconsistent response. This is because the abundance pattern indicates that forest is not more important than agriculture for the species, but the behavior information implies the opposite. Because passive behaviors were considered the least important for survival and reproduction, we considered species that were more likely

to exhibit passive behaviors in one habitat than the other habitat but were equally or more abundant in that habitat to have an inconsistent response (e.g., more passive behaviors in forest than in agriculture and more abundant in forest than in agriculture).

In contrast, we considered responses consistent when a species was more abundant in one habitat and was also more or equally likely to exhibit reproductive or foraging behaviors (or less likely to exhibit passive behaviors) in that habitat. We labeled these species as affiliated with a habitat. Finally, species with no significant differences in abundance or behavior between habitats were labeled nonsignificant response. Species that have similar abundance and behavioral use in different habitats (i.e., habitat generalists) or high uncertainty in the abundance or behavior estimates could have led to them not being statistically significant.

Finally, to understand whether species of higher conservation concern exhibited greater sensitivity to agriculture or privately owned forests (Question 3), we calculated Spearman's correlation coefficients between species' global range sizes and differences in abundance across forest cover (or protection statuses) and differences in behavior probabilities between habitats. We also used pairwise Wilcoxon rank sum tests to determine whether differences in abundance across forest cover (or protection statuses) and differences in behavior probabilities between habitats differed between categories of global population trends (decreasing, stable, or increasing). We used the more conservative nonparametric tests because linear model assumptions were not met.

RESULTS

After filtering out infrequently observed species (see methods), we retained 14,051 behavioral observations of 55 species for our analyses comparing forest and agriculture and 9,145 behavioral observations of 40 species for comparing protected and private forests (Appendix S3). Thirty species were passerines, and the others were nonpasserines (e.g., Columbiformes, Apodiformes). There was a negative effect of loud ambient noise on detecting reproductive behaviors, and a negative effect of time of day on detection probability. On average, foraging behaviors had the highest detection probability, followed by reproductive and passive behaviors. We do not report mean detection probabilities by species because the behavior N-mixture model underestimates detection probability, even when estimates of behavior parameters are unbiased (Ke et al., 2022). Chains for all but 31 (out of 637) parameters for the land-use analyses converged (Gelman–Rubin statistics <1.1), and the parameters that did not converge still had Gelman–Rubin statistics <1.5. Chains for all but 8 (out of 386) parameters for the protected area analysis converged, and the parameters that did not converge had Gelman–Rubin statistics <1.33. For the land-use analysis, 82% of species' behavior probabilities had Bayesian p values from 0.1 to 0.9. However, for the protected area analysis, 59% of species' behavior probabilities had Bayesian p values from 0.1 to 0.9.

Abundance and behavior trends between land-use types

Results from the regular N-mixture model supported our hypothesis that the community-average species abundance significantly increased with forest cover (effect size = 0.34, p MCMC = 0.006, 95% BCI: 0.10 to 0.59) (Appendices S8 & S14). However, there was no significant effect of protection status on average abundance (effect size = 0.11, p MCMC = 0.37, 95% BCI: -0.14 to 0.37) or abundance of any species (Appendices S9 & S15).

We also found evidence to support our predictions that on average across all species birds were more likely to exhibit reproductive behaviors in forest than agriculture. Specifically, individuals were 1.2 times more likely to perform reproductive behaviors in forest than agriculture (statistically significant; Figure 1; Appendices S9 & S15). Likewise, models predicted 3 times more individuals performing reproductive behaviors in forest than agriculture (statistically significant). At the species level, many more species had significantly higher probabilities and numbers of individuals exhibiting reproductive behaviors in forest than agriculture (e.g., elegant trogon [*Trogon elegans*]) (Table 1; Appendices S8, S10, & S16). In contrast, although there was no significant difference in the number of individuals performing foraging behaviors between forest and agriculture (Figure 1; Appendix S4), individual birds were 1.8 times more likely to perform foraging behaviors in agriculture than in forest. On average, individuals were more likely to perform passive behaviors in agriculture than in forest; however, we observed no significant differences between land-use types in the number of individuals performing these behaviors (Figure 1; Appendix S4).

Conforming to our expectations, when comparing protected and privately owned forests, the average species was significantly more likely to perform reproductive behaviors in protected forest (Figure 1; Appendix S4). Correspondingly, 10 species had higher probabilities of exhibiting reproductive behaviors in protected forest than in private forest (e.g., stripe-throated hermit [*Phaethornis striigularis*]), whereas only one species had a higher probability of exhibiting reproductive behaviors in private forest (white-collared seedeater [*Sporophila torqueola*]) (Table 1; Appendices S9 & S17). However, the total number of individuals performing reproductive behaviors was not significantly different between protected and privately owned forests across all species and at the species level (Table 1; Figure 1; Appendices S4, S11, & S19). Finally, there was a higher average probability and number of individuals performing foraging and passive behaviors in privately owned forest than in protected forest (Figure 1; Appendix S4).

Relationships between abundance and behavioral responses to land use

We did not find evidence to support our second hypothesis. Specifically, species were not always more likely to forage

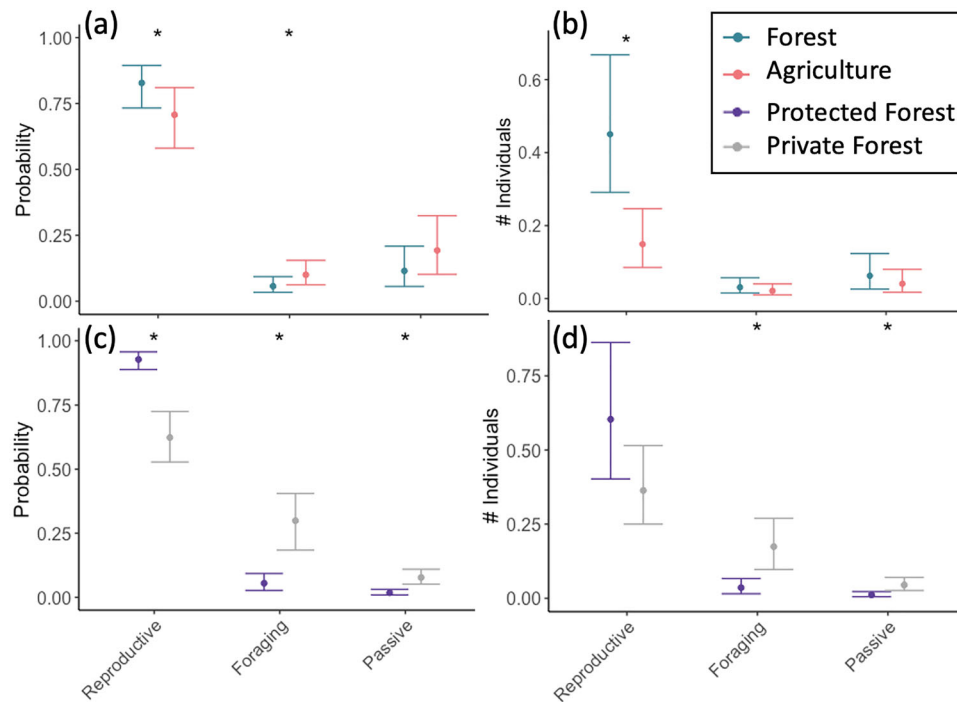


FIGURE 1 Mean predicted probability and 95% Bayesian credible intervals of reproductive, foraging, and passive behaviors occurring in (a) forest and agriculture and (c) private and protected forest and mean predicted number of individuals performing foraging, passive, and reproductive behaviors in (b) agriculture versus forest and (d) protected versus private forest (asterisk, significant differences between habitats such that the 95% intervals do not overlap zero).

TABLE 1 Number of bird species that had a positive, negative, or nonsignificant (NS) behavioral response to forest relative to agriculture and protected area relative to private forest and whether the response was associated with the probability of exhibiting a behavior or the number of individuals exhibiting a behavior.

Area type	Behavior	Probability of exhibiting a behavior			No. of individuals exhibiting a behavior		
		Positive	NS ^a	Negative	Positive	NS ^a	Negative
Forest (relative to agriculture)	Reproductive	17	38	0	25	24	6
	Foraging	0	46	9	14	32	9
	Passive	0	50	5	12	39	4
Protected areas (relative to private forest)	Reproductive	10	29	1	0	40	0
	Foraging	1	36	3	0	40	0
	Passive	1	31	8	0	40	0

^aNo significant response.

or reproduce in the habitats where they were most abundant. Although most species had consistent abundance and behavioral responses, species' abundance responses to forest cover (or protection status) were not statistically correlated with their behavioral responses (Appendix S5). This could happen because many species had a significant abundance response but no significant behavioral response to habitat, and these responses were considered to be consistent.

At the species level, 37 species had consistent abundance and reproductive responses to forest versus agriculture (29 affiliated with forest and 8 affiliated with agriculture), 8 had inconsistent responses, and 10 species had nonsignificant responses (Table 2; Figure 2). Species exhibiting inconsistent responses were more likely to perform reproductive behaviors in forest but were

either less or equally abundant as local forest cover increased (e.g., great kiskadee [*Pitangus sulphuratus*]). In the protected area analysis, there were 11 species with inconsistent responses but no species with consistent responses (likely because no species had a significant abundance response to protected forest vs. private forest; Appendix S20). In terms of foraging behavior, 5 species exhibited inconsistent responses. These species were more likely to forage in agriculture but were either less or equally abundant as agriculture increased (e.g., yellow-green vireo [*Vireo flavoviridis*]) (Figure 3). In terms of passive behavior, 3 species exhibited inconsistent responses. These species performed passive behaviors more frequently in agriculture but were either less or equally abundant with increasing forest cover (Figure 4).

TABLE 2 Number of bird species in each behavior category relative to their presence in forest versus agriculture and private versus protected forest.

Habitat comparison	Affiliation	Behavior		
		Reproductive	Foraging	Passive
Forest versus agriculture	Forest	29	26	28
	Agriculture	8	12	11
	NS ^a	10	12	13
	Inconsistent response	8	5	3
Protected versus private forest	Forest	0	0	0
	Agriculture	0	0	0
	NS ^a	29	36	31
	Inconsistent response	11	4	9

^aNo significant response.

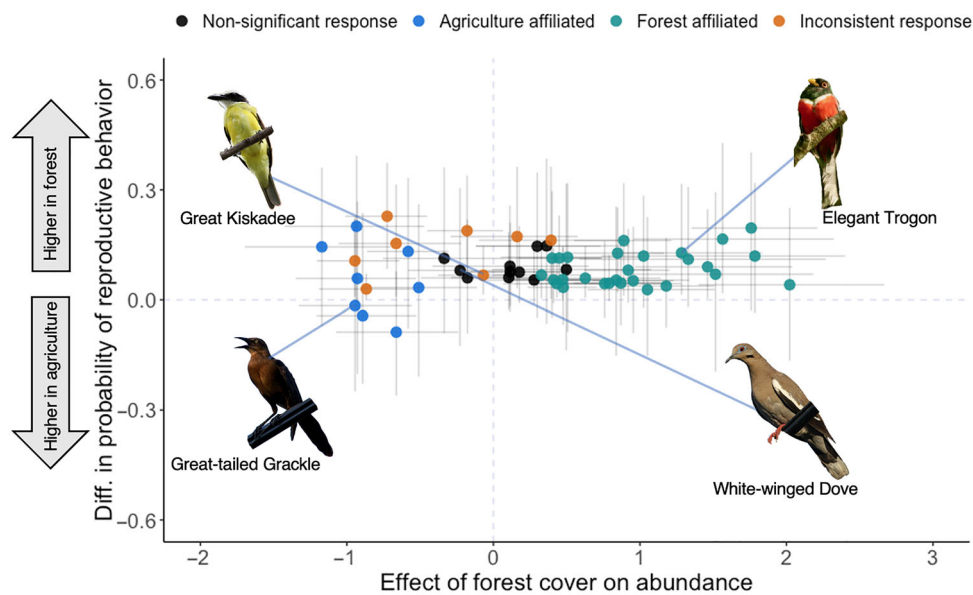


FIGURE 2 Relationship between the effect of local forest cover (range: 0–100%, centered and scaled) on a species’ abundance and the predicted difference in species’ probability of performing reproductive behaviors between habitats (gray lines, 90% Bayesian credible intervals; birds pictured, representative species in each category). Species with inconsistent responses (orange) preferentially exhibited reproductive behaviors in forest but did not significantly increase in abundance with forest cover.

Species of conservation concern

Our hypothesis that species of higher conservation concern would disproportionately rely on forest and protected areas was partially supported. Based on correlation analyses, species with smaller range sizes and decreasing global population trends tended to be more abundant in forest (Appendices S6 & S7). Species with stable population trends tended to have a more positive association with protected areas than species with increasing population trends (Appendix S7). There were some negative relationships between range size (and global population trends) and the numbers of individuals performing each behavior in forest versus agriculture, likely driven by the strong negative relationships with the abundance response (Appendices S6 & S7). However, we observed no significant

relationships between species’ range sizes (or global population trends) and the probability of individuals exhibiting any behavior between any habitats (Appendices S6 & S7).

DISCUSSION

Our community behavioral N-mixture model elucidated how bird communities and individual species vary in abundance and behavior across land-use types, while accounting for differences in detection probability between species, behaviors, and habitats. On average, Costa Rican bird species were more abundant and more likely to perform reproductive behaviors in forest than agriculture. Species were also more likely to perform reproductive behaviors in protected forest, despite there being

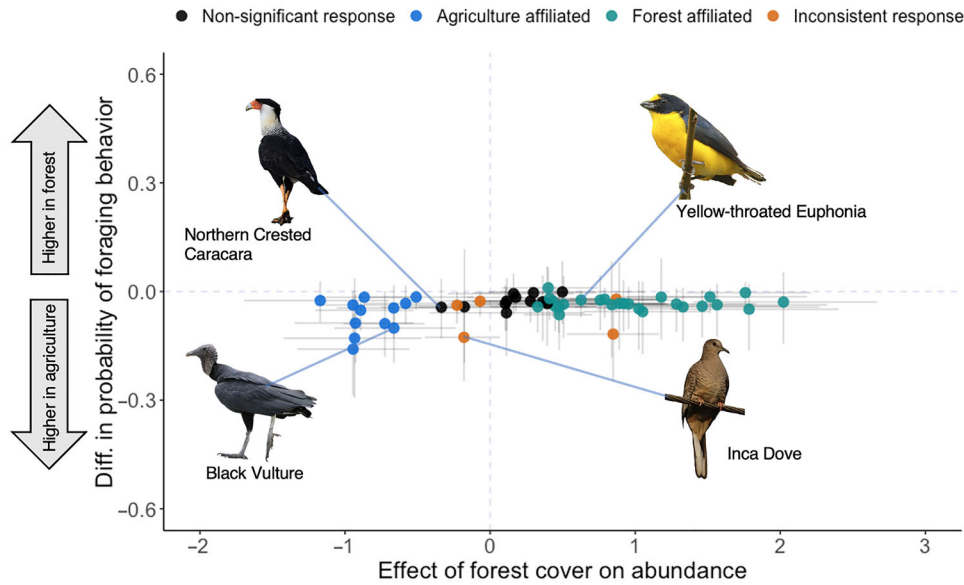


FIGURE 3 Relationship between the effect of local forest cover (range: 0–100%, centered and scaled) on a species' abundance and the predicted difference in species' probability of performing foraging behaviors between habitats (gray lines, 90% Bayesian credible intervals; birds pictured, representative species in each category). Species with inconsistent responses (orange) preferentially exhibited foraging behaviors in agriculture but did not significantly increase in abundance as agriculture increased.

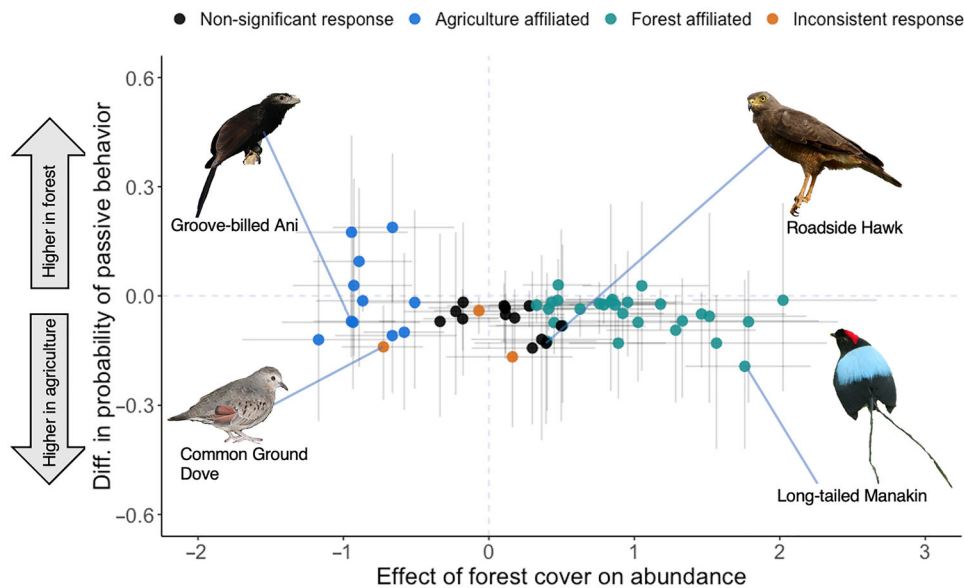


FIGURE 4 Relationship between the effect of local forest cover (ranging from 0% to 100%, and then centered and scaled) on a species' abundance and the predicted difference in species' probability of performing passive behaviors between habitats (gray lines, 90% Bayesian credible intervals; birds pictured, representative species in each category). Species with inconsistent responses (orange) preferentially exhibited reproductive behaviors in agriculture but did not significantly increase in abundance with agriculture.

no significant abundance differences between protected versus privately owned forest. Moreover, abundance and behavioral responses to land use were largely uncorrelated and sometimes inconsistent at the species level. These results highlight the importance of behavioral analyses for elucidating the conservation value of different habitat types and identifying species that may have the least behavioral flexibility for coping with human-induced changes (Wong & Candolin, 2015).

Behavior and abundance differences between forest and agriculture

Across the community, Costa Rican birds on average increased in abundance, were more likely to perform reproductive behaviors, and were less likely to forage in forest than in agriculture. We also estimated over 3 times as many individuals engaging in reproductive behaviors in forest than in agriculture (Figure 2).

This implies that forests host better reproductive territories and resources for the average bird species, which is unsurprising given that Costa Rica was forested historically (Sader & Joyce, 1988).

At the species level, some behavioral responses to habitat were consistent with their abundance responses. For example, agriculture specialist species that occurred and foraged more in agriculture tended to be granivorous (e.g., blue-black grassquit [*Volatinia jacarina*], common crested bobwhite [*Colinus cristatus*]). Meanwhile, forest specialist species tended to be those known to primarily occur and nest in forest (e.g., lesson's motmot [*Momotus lessonii*], elegant trogon) (del Hoyo et al., 2020; Kunzmann et al., 2020). Importantly, there were no species that significantly increased their reproduction or decreased their foraging behaviors in agriculture. Even the species with consistent responses primarily showed no significant differences in behavior but with the majority of the posterior density being in favor of forest for reproduction and agriculture for foraging. As such, most of the species with inconsistent responses were agriculture affiliates that reproduce in forest, and some (but fewer) species were forest affiliates that forage in agriculture.

Correlations between species' abundance and behavioral responses to land use were often low (Appendix S5), and, for some species, abundances did not peak where the species was most likely to exhibit reproductive or foraging behaviors. Thus, combining abundance and behavior information proved essential to understanding how species respond to land use. For example, tropical kingbirds (*Tyrannus melancholicus*) were more abundant in agriculture and were more likely to perform reproductive behaviors in forest. The greater number of individuals in agriculture was balanced by a greater fraction of individuals performing reproductive behaviors in forest, leading to a similar number of individuals engaging in reproductive behaviors between the 2 habitat types. In contrast, Inca doves (*Columbina inca*) were equally abundant across habitat types but had a higher likelihood and number of individuals foraging in agriculture. This indicates that Inca doves can likely find more food resources in agriculture but may still need forest for other reasons (e.g., nesting).

Finally, for several species, our results suggested the possibility that agriculture may act as an ecological trap (Robinson et al., 1995). Specifically, common ground-dove and masked tityra (*Tityra semifasciata*) showed more reproductive behaviors in forest and more passive behaviors in agriculture, despite being more or equally abundant in agriculture. There is evidence that land-use change causes declines in common ground-dove. The species used to be highly abundant in gardens and open areas in San Jose, Costa Rica, until the late 1990s, but it has now almost disappeared from urban areas in this region (Biamonte et al., 2011). Ecological traps have been observed through behavioral studies of other species. For example, Ben-Aharon et al. (2020) tracked the territories of mourning wheatears (*Oenanthe lugens*) to find that roads in southern Israel reduced survival and acted as an ecological trap. Rufous treecreepers (*Climacteris rufus*) had significantly lower density but significantly higher reproductive success in ungrazed habitats compared with grazed and fragmented habitats in southwestern Australia (Luck, 2003),

suggesting that habitat quality may be higher in ungrazed areas and that the other habitats may act as ecological traps.

However, more data are needed before conclusively determining that agriculture is acting as an ecological trap for the species we surveyed. Another possibility is that one habitat is insufficient to fulfill all the needs of a species (e.g., Fiss et al., 2021). For example, a species may forage in agriculture and reproduce in forest. This could be the case for the Inca dove. In this scenario, a mosaic of land-use types could result in larger populations than if only one habitat was present. Conversely, it is also possible that ecological traps are present, even for species that we deemed to have consistent responses to land use. For example, a species may exhibit more reproductive behaviors in a habitat, but reproduction in that habitat may still be unsuccessful due to factors such as food availability, nest predation, and parasitism. Thus, to truly understand habitat quality for foraging and reproduction, more data would be needed, ideally from experiments that manipulate food availability, nest site locations, or reproductive success between habitat types to determine how birds change their behaviors and habitat selection (Bélisle, 2005; Knowlton & Graham, 2010).

Behavior and abundance differences between privately owned and protected forest

Consistent with our prior work (Karp et al., 2019), we found that species did not differ in abundance between protected and privately owned forests. Nonetheless, species were, on average, more likely to perform reproductive behaviors and less likely to perform foraging and passive behaviors in protected forest. At the species level, 10 species were more likely to exhibit reproductive behaviors in protected areas versus only one for which reproductive behaviors were more likely in private forests. These differences may result from differences in habitat quality. In our study system, privately owned forests are embedded in more fragmented landscapes and have less canopy cover, shorter tree heights, lower tree richness, and less dense understories than protected forests, likely due to regular logging, fires, hunting, and other disturbances (Karp et al., 2019). Thus, although bird abundances were not different between privately owned forests and protected areas in northwestern Costa Rica in our prior work (Karp et al., 2019), here we found that the behaviors may differ between protection statuses.

Species of conservation concern

We found that species with smaller geographic range sizes and decreasing global populations tended to be more abundant in forest (as in Karp et al. [2019]). Small range sizes are especially related to higher extinction vulnerability, lower dispersal ability, and heightened sensitivity to land-use change (Böhning-Gaese et al., 2006; Sykes et al., 2020). This suggests that habitat conversion to agriculture is most likely to threaten species that are already declining and to favor species that are more adapted to different or novel food resources. However, we found little

evidence that species of conservation concern were more dependent on protected areas than privately owned forests.

Limitations

Like any study of behavior, it is important to acknowledge that the frequency at which a species performs a behavior during surveys may not reflect the behaviors it performs consistently. Animal behavior varies based on seasons, time of day, which other species are present, and individual personalities (Bailey et al., 2004; Chambert et al., 2012; Merrick & Koprowski, 2017; Veech et al., 2016). This limitation could be reduced with more behavioral observations, potentially spread throughout the day. We assumed that if animals are spending more time foraging (or engaging in reproductive behaviors) in one location, then they have selected a habitat with more abundant food (or reproductive) resources. However, it is possible that areas with fewer food resources force individuals to forage more often or that the individuals foraging may be less skilled at finding food (Lescroël et al., 2010). In both cases, the ecological trap may be where individuals spend more time foraging. Similarly, a higher rate of reproductive behavior does not necessarily lead to more successful reproduction, and comparing reproductive success and fledgling survival between habitat types would be needed to link behavioral patterns to fitness.

Another caveat is that because we had to restrict analyses to the most easily observed species, we could have missed the rarest and most forest-restricted species. Indeed, compared with included species, species excluded from analyses were observed 3 times more often in each forested site than in each agriculture site on average and 1.5 times more often in each protected area site than each private forest site on average. Thus, if anything, our finding that species are more likely to exhibit reproductive behaviors in forests (especially protected areas) is likely conservative. Including only species that were observed at least 20 times was sufficient to identify species that had inconsistent abundance and behavior patterns between forest and agriculture. However, we found fewer significant patterns when comparing private and protected forests. The fewer significant effects may have arisen because the effect sizes of protected status on abundance and behavior were weaker than the effects of agriculture and because the estimates had higher uncertainty (due to the fact that fewer sites and observations were included in the protected area model). Increasing the number of sites and observations per species could have allowed us to statistically resolve the weaker effects of protected area status, and, as such, we recommend other researchers consider sampling effort based on the predicted magnitude of habitat effects.

Finally, protected area models did not fit the data as well as the land-use analysis, again possibly due to fewer sites and observations included in the analysis. However, all community-level effects of protection status on abundance and behavior and most species' behavior probabilities had appropriate Bayesian p values that were <1.1 . In addition, when only including species that had at least 2 of the 3 behavior probabilities with Bayesian

p values from 0.1 to 0.9, results did not change—the mean effect of protection status on abundance was near zero (mean [SD] = 0.014 [0.294]), and the mean differences in species' behavior probabilities between habitats were similar, changing by $<1\%$.

Conservation implications

Our results suggest that habitat conversion to agriculture can have strong effects on avian behavior. These changes may have cascading implications for individual fitness and future population viability, given the strong negative effects on reproductive behavior. Moreover, our finding that reproductive behaviors are, on average, more likely in protected areas than private forests suggests that studying behaviors can unmask differences in habitat value, even when community composition and abundance exhibit little differences between habitat types. Another benefit of the community behavior N-mixture model is that it can be used to identify the species that are most likely to shift their behaviors across land-use types, and, as such, most likely to be caught in ecological traps, unable to adjust to anthropogenic changes, or, alternatively, able to exploit novel resources and thrive in new environments (Sih et al., 2011; Tuomainen & Candolin, 2011). We recommend that scientists incorporate behavioral observations in their survey protocols when possible, given that the models presented here can be flexibly adapted to quantify how animal behaviors change across a wide variety of environmental stressors while accounting for imperfect detection. Doing so could not only help provide early warning signals for species in trouble, but may also point to key mechanisms underlying habitat selection and the ecological and evolutionary consequences of behavioral changes.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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