



# Morphological and Behavioral Correlates of Long-Term Bird Survival in Selectively Logged Forest

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The response of biodiversity to land-use change has been a central focus in applied ecological research for close to half a century. However, despite a vast body of literature, our understanding of how species' traits influence demographic vital rates in anthropogenically-modified habitats is remarkably scant. Such an understanding is crucial because vital rates determine population viability in modified habitats, and underlie emergent occupancy, abundance and community-level patterns. I used capture-recapture analyses to estimate variation in survival of birds in intact and logged tropical montane forest in the eastern Himalayas. In general, variation in body mass and alternative behavioral strategies (e.g., mixed-species flocking vs. solitary behavior) were not associated with survival differences in intact forest. However, year-round residents, and species that did not participate in mixed-species flocks had appreciably lower survival in logged forest compared with intact forest. Solitary foragers, for instance, faced a 30% decline in survival in logged forest compared with intact forest. Non-migratory habit and solitary foraging behavior might make species vulnerable to extinction in logged forest through reduced survival, an especially important process in influencing population viability. Identifying how species' traits modulate their response to land-use change is crucial to predict population responses to forest modification, and to better plan and manage biodiversity-friendly forest use.

**Keywords:** apparent survival, body mass, eastern Himalayas, mark-recapture, mixed-species flocks, understory birds, vital rates

## INTRODUCTION

The alteration of tropical forests is globally pervasive. Two of the most widespread forms of forest conversion are fragmentation, which results in isolated forest patches, and selective logging, which involved the extraction of a subset of forest trees. The impacts of fragmentation and logging on the structure and function of ecological communities has received attention since the dawn of conservation biology (reviews in Gibson et al., 2011; Laurance et al., 2016). Further, there is a broad consensus on traits correlated with vulnerability to forest modification (Burivalova et al., 2015). In general, large, long-lived, higher-trophic species decline with logging, and communities in modified forest tend to be dominated by small, highly fecund species at lower trophic levels (Srinivasan, 2013; Hamer et al., 2015). Despite this extensive body of work, surprisingly little is known about how demographic vital rates (e.g., survival and fecundity) are influenced by the interaction between species' traits and habitat change, even in exceptionally well-studied taxa such as birds

(Cossett et al., 2019). Such an understanding is crucial because: (a) vital rates—rather than occupancy or abundance—determine population viability in anthropogenically modified forest, and (b) altered vital rates underpin abundance changes, and therefore community structure and function (Cossett et al., 2019).

In birds, how morphological and behavioral traits influence vital rates is known largely from primary neotropical forest. For instance, body size is positively correlated with survival, but negatively with recruitment (Brawn et al., 1995). A meta-analysis found that species that always foraged in mixed-flocks had higher survival rates than those that did not (Jullien and Clobert, 2000), although several studies from multiple neotropical sites have failed to detect survival differences between flocking and non-flocking species (Brawn et al., 1995; Blake and Loiselle, 2008; Wolfe et al., 2014). There is no compelling evidence that survival rates differ between resident and migratory species (Sandercock and Jaramillo, 2002).

Where demographic vital rates have been compared between intact and modified habitats, such comparisons have been limited to one or few species (Bakermans et al., 2009; Srinivasan et al., 2015; Wolfe et al., 2015), precluding the discovery of generalisable relationships between species' traits and anthropogenically-driven changes in vital rates. For instance, forest fragmentation reduced survival (Doherty and Grubb, 2002) and population growth (Zanette, 2000) in temperate birds, but combined, these studies were able to estimate vital rates for only five species. From the tropics, experimental forest modification did not result in survival differences in two species, but hinted at the survival value of participation in mixed-species flocks (Cruz-Angon et al., 2008). To my knowledge, only Korfanta et al. (2012) compare vital rates for a suite of species in intact and modified (fragmented) forest, concluding that almost all diet guilds are vulnerable to extinction in forest fragments. However, Korfanta et al. (2012) did not test for relationships between vital rates in modified forest and fundamental species' properties such as body mass and migratory behavior, which are crucial determinants of life history. Characterizing such environment-survival relationships—and how these can be modulated by species' traits—is especially important to both understand and mechanistically predict the impacts of land use change on tropical biodiversity (Ruiz-Gutierrez et al., 2012).

I asked how morphological and behavioral species' traits interacted with selective logging—a widespread global threat to tropical biodiversity (Edwards and Laurance, 2013)—to influence the survival of birds in the eastern Himalaya global biodiversity hotspot. Specifically, I tested the following predictions, related to three species traits:

- a. Body size. With increasing mass, species should suffer greater survival declines in logged forest, because larger species are more vulnerable to forest modification, and decline in abundance in logged forest (Srinivasan, 2013).
- b. Mixed-species flocking. Logging should cause greater survival reductions in species that forage solitarily or in monospecific flocks, compared with species that forage in mixed-species flocks. This is because mixed-species flock participants receive foraging and anti-predator benefits from other species in

the group (Sridhar et al., 2009), and should therefore be capable of adapting behaviorally (by altering flock size and composition) to logging-induced resource reduction and/or enhanced predation.

- c. Migratory behavior. I remained agnostic about how logging might differentially affect survival for year-round residents vs. elevational migrants. Although migration might allow species to maintain an optimal abiotic environment throughout the year, resident species might benefit through the “local knowledge of food and predator dispersion” on year-round territories (Sandercock and Jaramillo, 2002; Cooper et al., 2015).

I did not test for the effect of diet or vertical stratum because almost all species are understorey insectivores (**Table 1**), a functional guild particularly vulnerable to forest modification (Powell et al., 2015).

## MATERIALS AND METHODS

I sampled montane broadleaf wet evergreen forest (Champion and Seth, 1968) dominated by *Quercus lamellosa* and *Michelia doltsopa* in the canopy, and bamboo (*Chimonobambusa* sp.) in the understorey. Forest patches were selected for sampling based on interviews with persons involved in logging operations, and variation in tree densities on these plots tallied exactly with semi-quantitative estimates of timber extraction (Srinivasan, 2013). Tree densities in intact forest were roughly twofold that in logged forest. I established six sampling plots, three each in intact and logged forest (varying from 2.5 to 4.0 ha in size) at ~2000 m ASL in Eaglenest Wildlife Sanctuary, West Kameng district, Arunachal Pradesh, India (27.07°N; 92.40°E, **Figure 1**). Sampling plots varied in size depending on logging history and accessibility for sampling. Three of these plots were intensively logged until 2002 (“logged forest”; tree densities [DBH ≥ 10 cm] ranging from 76 to 109 trees ha<sup>-1</sup>), while the other three were either never, or very minimally, logged (“intact forest”; tree densities: 168 to 192 trees ha<sup>-1</sup>; Srinivasan, 2013; **Figure 1**). In total, across the three plots in each habitat (intact and logged), I sampled 9 ha each in intact and logged forest separately (**Figure 1**). Arunachal Pradesh has the highest latitudinal extent of tropical forests globally (Proctor and Haridasan, 1998). In each plot, a team operated 24–28 mist nets (12 m length, 4 shelf, 16 mm mesh size; 158 nets in total) from 0500 to 1200 h for three consecutive days in April–May each year, from 2011 to 2017. Nets were set up systematically within a plot, with neighboring nets placed ~40 m apart (**Figure 1**). April–May is the early breeding season for birds in the eastern Himalayas, when the young of most species (and all species included in my analyses) have not fledged. Therefore, all individuals captured are adults. Birds captured in nets were weighed, ringed with numbered aluminum leg rings, and released.

For analysis, I selected species represented by at least 20 individuals in intact and logged forest separately. All species included in the analysis breed on our sampling plots. For each individual bird, I created a capture history spanning seven years. Multiple captures within a year (e.g., on subsequent

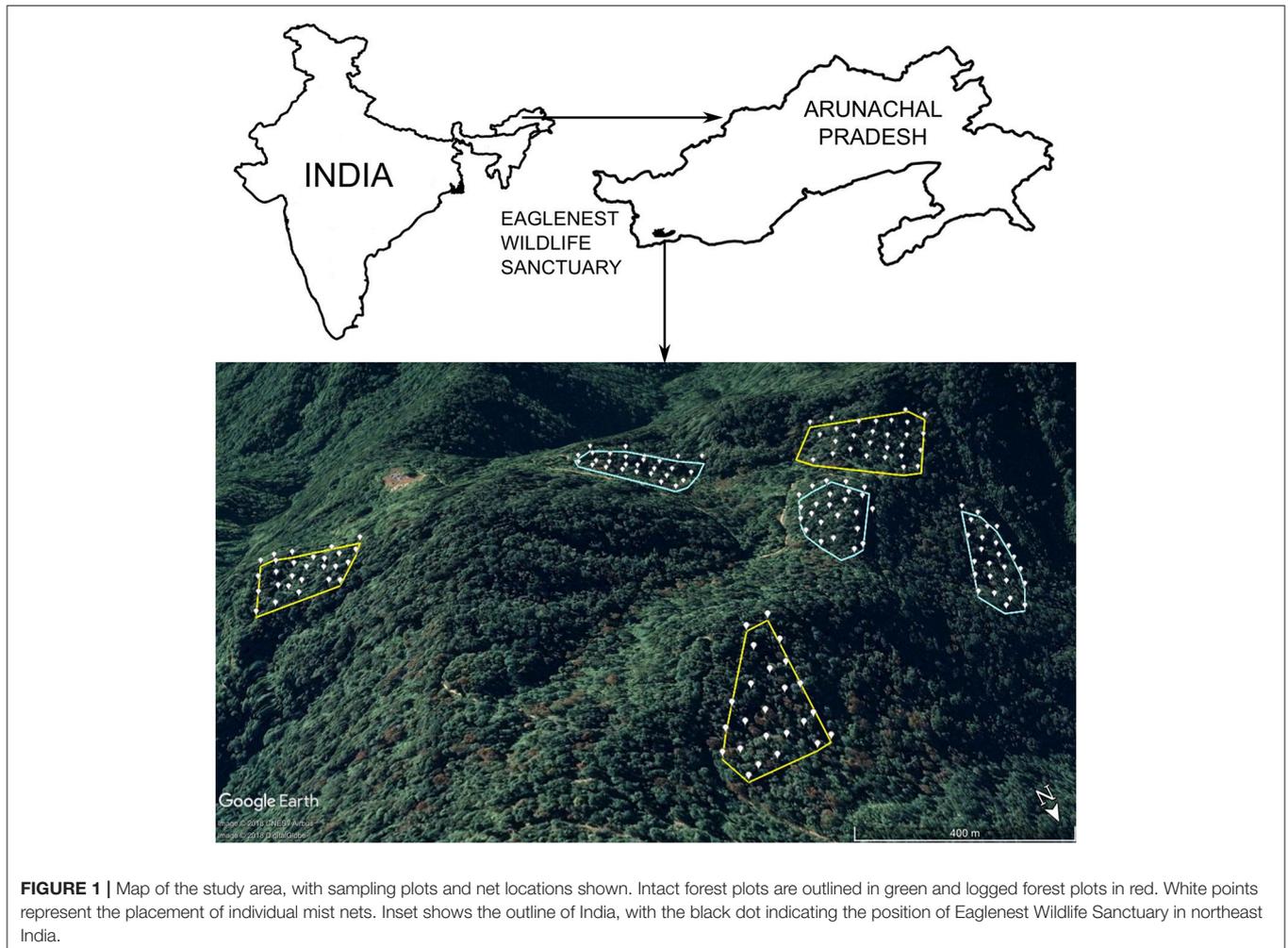
**TABLE 1** | List of species analyzed, with relevant life-history traits and estimates of apparent survival in intact and logged forest.

Family	English name	Scientific name	Mass (g)	Flock	Migrant	$\Phi_{\text{intact}}$	$\Phi_{\text{logged}}$
Phylloscopidae	Blyth's Leaf Warbler	<i>Phylloscopus reguloides</i>	7.5	Y	Y	0.56 ± 0.11	0.82 ± 0.19
Phylloscopidae	Chestnut-crowned Warbler	<i>Seicercus castaniceps</i>	5.3	Y	Y	0.35 ± 0.13	0.48 ± 0.20
Phylloscopidae	White-spectacled Warbler	<i>Seicercus affinis</i>	7.0	Y	Y	0.58 ± 0.08	0.49 ± 0.13
Phylloscopidae	Gray-cheeked Warbler	<i>Seicercus polioygenys</i>	6.3	Y	Y	0.59 ± 0.10	0.32 ± 0.11
Cettiidae	Black-faced Warbler	<i>Abroscopus schisticeps</i>	4.7	Y	Y	0.75 ± 0.13	0.68 ± 0.14
Cettiidae	Gray-bellied Tesia	<i>Tesia cyaniventer</i>	9.7	N	Y	0.61 ± 0.16	0.31 ± 0.12
Cettiidae	Slaty-bellied Tesia	<i>Tesia olivea</i>	7.0	N	Y	0.18 ± 0.09	0.18 ± 0.10
Muscicapidae	Snowy-browed Flycatcher	<i>Ficedula hyperythra</i>	8.2	N	Y	0.64 ± 0.10	0.28 ± 0.09
Muscicapidae	Large Niltava	<i>Niltava grandis</i>	30.3	N	Y	0.58 ± 0.16	0.36 ± 0.27
Muscicapidae	Rufous-bellied Niltava	<i>Niltava sundara</i>	21.1	N	Y	0.55 ± 0.10	0.62 ± 0.13
Muscicapidae	White-tailed Robin	<i>Cinclidium leucurum</i>	27.0	N	Y	0.43 ± 0.11	0.35 ± 0.15
Sylviidae	Golden-breasted Fulvetta	<i>Lioparus chrysotis</i>	5.5	Y	N	0.63 ± 0.05	0.61 ± 0.04
Sylviidae	Black-throated Parrotbill	<i>Suthora nipalensis</i>	5.5	Y	N	0.49 ± 0.05	0.46 ± 0.05
Pellorneidae	Yellow-throated Fulvetta	<i>Pseudominla cinerea</i>	11.0	Y	N	0.50 ± 0.05	0.50 ± 0.04
Pellorneidae	Rufous-winged Fulvetta	<i>Pseudominla castaneiceps</i>	12.5	Y	N	0.57 ± 0.06	0.50 ± 0.06
Timaliidae	Rufous-capped Babbler	<i>Stachyridopsis ruficeps</i>	10.3	Y	N	0.48 ± 0.06	0.50 ± 0.06
Timaliidae	Golden Babbler	<i>Stachyridopsis chrysaea</i>	9.0	Y	N	0.51 ± 0.09	0.53 ± 0.07
Timaliidae	Streak-breasted Scimitar Babbler	<i>Pomatorhinus ruficollis</i>	32.0	Y	N	0.46 ± 0.26	0.55 ± 0.14
Leiothrichidae	Rusty-fronted Barwing	<i>Actinodura egeroni</i>	36.0	Y	N	0.74 ± 0.16	0.30 ± 0.14
Leiothrichidae	Chestnut-crowned Laughingthrush	<i>Trochaloferon erythrocephalum</i>	71.1	Y	N	0.64 ± 0.16	0.48 ± 0.35

"Flock" indicates whether a species forages in mixed-species bird flocks in winter (Y) or solitary or in monospecific groups (N); "Migrant" indicates whether a species is resident year-round (N) or an elevational migrant (Y). The last two columns represent estimates of apparent survival in intact and logged forest with associated standard errors.

sampling days) were not considered recaptures for analytical purposes. Therefore, in capture histories, all captures within a sampling season (i.e., year) were collapsed into a single occurrence. Because logged forest plots were, on average, closer to each other than intact forest plots, recapture rates in logged forest might be higher than those in intact forest. I therefore calculated plot-level proportion of individuals recaptured for each species (i.e., number of individuals recaptured divided

by total number of individuals ringed), and then calculated the mean and standard deviation of capture rate for plot-level information for each species in each habitat (**Table S1**). For 19 of 20 species analyzed, there were no differences in the proportion of individuals recaptured between intact and logged forest (overlapping standard errors, **Figure S1**), and no consistent habitat-dependent direction in the mean of recapture rates across species (**Figure S1**).



**FIGURE 1** | Map of the study area, with sampling plots and net locations shown. Intact forest plots are outlined in green and logged forest plots in red. White points represent the placement of individual mist nets. Inset shows the outline of India, with the black dot indicating the position of Eaglenest Wildlife Sanctuary in northeast India.

I pooled capture histories from the three intact forest plots to represent individuals sampled in intact forest, and did the same with capture histories from the three logged forest plots. I pooled data to enable the robust estimation of apparent survival ( $\Phi$ ) in intact and logged forest for each species, because plot-level data was inadequate to enable survival estimation for each species in each plot. (Separate plots were initially established to span the gradient in logging intensity, ranging from 76 to 192 trees per ha). I used the Cormack-Jolly-Seber (CJS) open-population mark-recapture model to estimate adult survival (Cormack, 1964; Jolly, 1965; Seber, 1965) for each of 20 species in intact and logged forest separately (**Table 1**), an approach that simultaneously accounts for imperfect detection ( $p$ )-situations in which only a proportion of individuals are observed/captured (Seber, 1965). For each species in each habitat (i.e., 40 different sets of capture histories), I first ran tests to ensure that CJS models fitted the capture history data well, using the *R2ucare* package (Gimenez et al., 2017) in Program R (R Core Team, 2018), and following the decision tree outlined in **Figure 1** in Gimenez et al. (2017). For each species, I ran two models each in intact and logged forest separately; one in which recapture probability was constant across all sampling occasions, and another in which recapture

probability varied with time. I constrained apparent survival to be invariant across the six annual inter-breeding intervals in both models. For each species, I selected the best model (of the two considered, i.e., time-varying and time-invariant recapture probability) as determined by the small sample size-corrected Akaike's Information Criterion (AICc), and I report survival estimates from the best model (**Table 1**).

I used ordinary least squares regression models to relate survival estimates in intact and logged forest to the natural log of body size (in grams; averaged from our measurements), a continuous predictor. Species' body masses ranged from 4.5 to 69.0 g (**Table 1**). I obtained data on other species' traits (mixed-species flocking, migratory and foraging behavior) from published sources (Rasmussen and Anderton, 2012). These traits were both binary categorical predictors. Fourteen species participate in winter mixed-species bird flocks, while six forage either solitary or in monospecific groups. Ten species hold year-round territories, whereas 10 were elevational migrants, breeding at higher elevations and wintering at lower elevations (**Table 1**). I compared the survival of species with mutually exclusive strategies for a particular trait (e.g., resident vs. elevational migrant) in intact forest, in logged forest, and between intact

and logged forest. For these comparisons, I calculated mean annual survival (and standard errors) across all species sharing a strategy for a given trait, separately for intact and logged forest. To account for uncertainty in the estimation of survival rates, I assessed whether survival means differed from each other using weighted ordinary least-squares ANOVAs (with model weights as the inverse of the standard error of survival estimates).

I used Pagel's  $\lambda$  to initially assess whether differences in survival between intact and logged forest showed any relationship to evolutionary relatedness using a phylogenetic tree constructed using data from Jetz et al. (2012).

## RESULTS

I recorded 5,298 captures of 3,310 individuals of 20 species. Overall, 34.4% of individuals were captured more than once (see **Table S1** for species-specific capture rates in intact and logged forest separately). The total effort was 278,712 net-meter-hours. Overall, 93.4% of individuals were recaptured only on the plots on which they were initially captured. In other words, only 6.6% of individuals were captured in more than one sampling plot despite the relative proximity of plots (**Figure 1**), indicating that populations on each plot were representative of the demographic processes operating on them, and were minimally influenced by the habitats surrounding a plot. Further, only 3.4% of individuals captured initially on one habitat type (intact or logged) were subsequently recaptured in a different habitat type. These individuals were excluded from the analyses. Goodness-of-fit testing indicated that standard CJS models were appropriate for each species in each habitat, and did not require correcting for either overdispersion or the presence of transient individuals ( $p$ -value for  $\chi^2$  goodness-of-fit tests  $> 0.05$  for all species in both habitats).

Across species, the model with time-varying capture probability was a better fit than the model with constant capture probability (based on the small sample size-corrected Akaike's Information Criterion) for only three species, in both intact and logged forest. These species were *Niltava sundara* (Rufous-bellied Niltava), *Pseudominla castaneiceps* (Rufous-winged Fulvetta) and *Pseudominla cinerea* (Yellow-throated Fulvetta). For all other (i.e., 17) species, the model with constant capture probability performed better than time-varying capture probability in both intact and logged forest.

Ten species had higher survival in intact than in logged forest, six species had roughly equal survival in both habitats, while for four species, survival increased with logging (**Table 1**).

### Body Mass and Survival

I found no relationship between the natural log of body mass and inherent survival (i.e., survival in intact forest;  $\beta_{\text{intact}} = 0.02 \pm 0.04$  SE), and also no relationship between the natural log of body mass and survival differences between intact and logged forest ( $\beta_{\text{logged}} = -0.06 \pm 0.04$ ;  $R^2 = 0.1$ ;  $p = 0.22$ ; **Figure 2A**).

### Mixed-Species Flocking and Survival

Flocking behavior was related to the manner in which logging influenced survival ( $R^2 = 0.28$ ;  $p = 0.01$ ; **Figure 2B**). In intact

forest, the apparent survival of species that foraged in winter mixed-species flocks ( $0.56 \pm 0.03$  SE) did not differ from that of non-flocking species ( $0.50 \pm 0.07$ ; **Figure 2B**). In logged forest, however, the survival of flocking species ( $0.51 \pm 0.04$ ) was higher than that of non-flocking species ( $0.35 \pm 0.06$ ; **Figure 2B**). While there was no difference in the survival of flocking species between intact ( $0.56 \pm 0.03$ ) and logged forest ( $0.51 \pm 0.04$ ), as expected, non-flocking species had lower survival in logged forest than in intact forest; on average, the survival of non-flocking species in logged forest (0.35) was 30% lower than in intact forest (0.50; **Figure 2B**).

### Elevational Migration and Survival

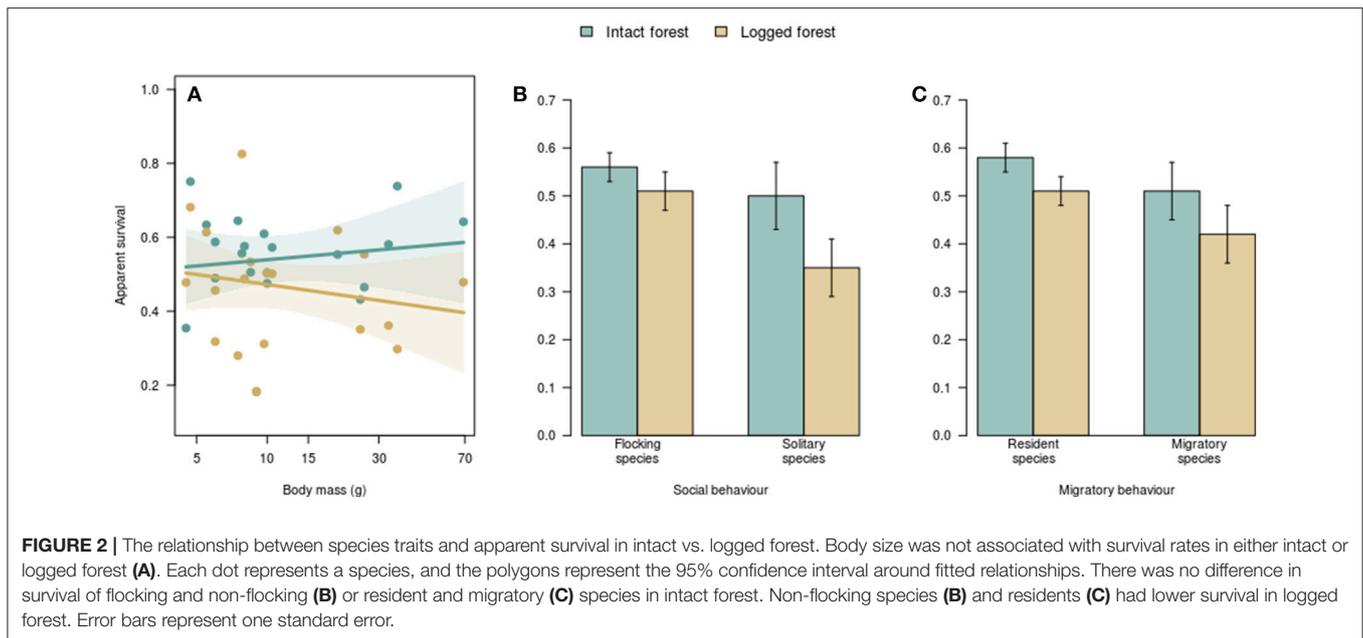
Migratory behavior was appreciably related to changes in survival with logging ( $R^2 = 0.22$ ;  $p = 0.03$ ). Residents and elevational migrants had similar survival in intact forest ( $0.58 \pm 0.03$  and  $0.51 \pm 0.05$ , respectively; **Figure 2C**) and logged forest ( $0.51 \pm 0.03$  and  $0.42 \pm 0.06$ ; **Figure 2C**). However, while the survival of elevational migrants did not differ between intact ( $0.51 \pm 0.05$ ) and logged ( $0.42 \pm 0.06$ ) forest, resident species had, on average, 12% lower survival in logged forest (0.51) compared with intact forest (0.58; **Figure 2C**).

Pagel's  $\lambda$  indicated that survival differences of between intact and logged forest were not phylogenetically structured (probability of difference from Brownian motion,  $\chi^2$  test = 0.99).

## DISCUSSION

I estimated adult survival rates for 20 eastern Himalayan species in intact and logged forest separately. Based on the small sample size-corrected Akaike's Information Criterion, capture probabilities remained constant across years (in intact and logged forest separately) for 17 of 20 species. For three species, capture probabilities were time-varying in both intact and logged forest. This indicates that land use change did not result in heterogeneity in capture probabilities over time, but that for these three species, capture probabilities might be inherently variable across time. For these species, variation in capture probability might be related to greater flexibility in foraging height compared with other species.

I expected that logging would cause changes in survival in different ways for different species. Indeed, of the 20 species I analyzed, the survival of 10 species was lower in logged forest, did not appear to be influenced by logging for six species, and was associated with increased survival for four species. Variation in how survival is impacted by logging is likely to be driven by the interaction between species' traits and changes to forest structure following logging. Selective logging causes structural changes to forest, including canopy thinning and increased volume of understorey vegetation. In turn, these structural changes can modify resource availability (Zanette, 2000) and predation risk (Hua and Sieving, 2016). Individuals in logged forest would therefore need to adapt to these changes to optimize survival in logged forest. The results of this study show that the degree to which species are capable of surviving such environmental changes hinge on their traits.



For eastern Himalayan tropical montane birds, selective logging did not result in altered survival for species that foraged in winter mixed species flocks or for migratory species. However, non-flocking species and year-round residents showed survival declines in logged forest (Figure 2).

### Mixed-Species Flocking and Survival

From a meta-analysis of survival rates of neotropical birds, Jullien and Clobert (2000) concluded that obligate flocking species (i.e., species that always foraged in mixed-species flocks) had higher annual survival than either facultative flocking species or solitary foragers. However, such patterns might be confounded by significant within-species variation in survival over large geographical scales (Wolfe et al., 2014), making across-site species comparisons problematic. Like several prior studies (Brawn et al., 1995; Blake and Loiselle, 2008; Wolfe et al., 2014), I found no evidence for any site-specific survival differences between flocking and non-flocking species in intact forest. The lack of survival differences between flocking and non-flocking species in intact habitat should perhaps not be surprising, given that both types of species might adopt different life-history strategies to maximize survival (Ghalambor and Martin, 2001).

For instance, while flocking species might rely on enhanced resource availability and predator avoidance in flocks (Sridhar et al., 2009) to increase survival probability, non-flocking species might vary reproductive investment between males and females to differentially prioritize sex-specific survival (Santos and Nakagawa, 2012), with consequences for overall species' survival. In this dataset, none of the flocking species are sexually dimorphic; however, males and females of two-thirds of non-flocking species differ in plumage, indicating that flocking and non-flocking species might allocate resources differentially to sex-specific reproduction and survival. Estimating and evaluating sex-specific survival rates for both flocking and non-flocking

species will be important to test for such potentially different life-history strategies.

For flocking species, survival was not altered by selective logging (Figure 2B), despite some evidence that flocking species decline in abundance with habitat change (Stouffer et al., 2006; Sigel et al., 2010). Further, the structure and composition of mixed-species bird flocks is sensitive to forest modification; flock richness (number of species) and size (number of individuals) declines with forest fragmentation and degradation (Lee et al., 2005; Cordeiro et al., 2015). Recent evidence also points to the breakdown of interspecific associations in mixed flocks, and therefore, the reduced stability of mixed-species flocks in altered forest (Mokross et al., 2014; Mammides et al., 2015). Predictable changes in flock structure and composition in logged forest, including on the plots I sampled (Borah et al., 2018) are likely a response to altered resource availability and predation risk (Ewers et al., 2015; Hua and Sieving, 2016).

Taken together, unchanged survival but changing flock structure indicate that flocking species possess a degree of behavioral flexibility, allowing them to alter the strength and nature of interspecific associations to maintain survival in the face of modified resources and predation in altered forest. Therefore, participation in mixed flocks might be a trait that reduces, rather than enhances, vulnerability to selective logging, and changes in the structure and composition of mixed flocks in logged forest (Borah et al., 2018) need not necessarily mean that flocking species are demographically particularly vulnerable to logging. With fragmentation, however, isolation might lead to the outright loss of species important for flock cohesion in forest fragments, leading to severely disrupted flock networks (Mokross et al., 2014), and declining survival of species regardless of flocking behavior (Korfanta et al., 2012). Non-flocking species, lacking the ability to forage with other species (and therefore potentially alter interspecific associations to adapt to

habitat change) might be behaviorally disadvantaged to deal with increased predation and resource scarcity in logged forest, resulting in depressed survival with habitat change (Figure 2B).

## Elevational Migration and Survival

The time-allocation hypothesis proposes that survivorship should increase with time spent on climatically favorable wintering grounds (Greenberg, 1980); this would predict that elevational migrants should have higher survival rates than residents, because year-round residents are likely to face harsher winters. However, the survival of resident and migrant species did not differ in either intact or in logged forest (Figure 2C), contradicting the time-allocation hypothesis. Although elevational migration might serve to maximize year-round constancy in the climatic niche (Srinivasan et al., 2018), migration can also carry energetic and predation costs that offset benefits from enhanced resource availability in milder wintering grounds (Alerstam et al., 2003; Cooper et al., 2015; Rushing et al., 2017). At the same time, residents, despite being subject to food shortages in winter (Ghosh et al., 2011), might benefit from enhanced knowledge of resource and predators distribution on their territories (Sandercock and Jaramillo, 2002). Combined, these trade-offs might result in the lack of survival differences between residents and migrants in both intact and logged forest (Figure 2D).

Resident species had higher survival in intact than in logged forest, while the survival of elevational migrants did not differ with logging (Figure 2D). This pattern might point to the importance of winter habitat quality in seasonal environments in influencing annual survival. Migratory species breeding in logged forest can potentially search for, and winter in, optimal habitats; on the other hand, species resident in logged forest are likely to face resource shortages and enhanced predation year-round (Cooper et al., 2015; Ewers et al., 2015; Hua and Sieving, 2016). Differences in survival between residents and migrants are consistent with the predictions of the time-allocation hypothesis (Greenberg, 1980)—for resident insectivorous birds, winters in logged forest might be harsher than winters in intact forest, because of higher predation and reduced food resources (Ewers et al., 2015; Hua and Sieving, 2016). Characterizing summer and winter habitat quality for residents and migrants using telemetry-based approaches with concomitant habitat quality data would be essential to test this mechanism.

## CONCLUSIONS

This study is one of the first to examine how species' traits influence demographic vital rates in anthropogenically modified

forest. I identify attributes—, solitary foraging and year-round residency—that predispose eastern Himalayan bird species to vulnerability to selective logging, via reductions in annual survival. Existing long-term demographic data (e.g., Blake and Loiselle, 2001; Korfanta et al., 2012; Wolfe et al., 2014, 2015) should be analyzed to test whether these traits are correlated with reduced survival in fragmented and logged forest across the tropics. Given the importance of annual survival in determining the population persistence in disturbed habitats (Karr, 1990; Korfanta et al., 2012), identifying general relationships between species' traits and anthropogenically altered survival rates is crucial to both predict species responses to forest modification, and to better plan and manage biodiversity-friendly forest use.

## ETHICS STATEMENT

This study was carried out in accordance with the recommendations of the Arunachal Pradesh Forest Department, Government of India.

## AUTHOR CONTRIBUTIONS

US designed the study, collected the data, conducted the analyses, and wrote the manuscript.

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## SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2019.00017/full#supplementary-material>

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