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Assessing Extinction Risk in Small Metapopulations of Golden-headed Lion Tamarins (*Leontopithecus chrysomelas*) in Bahia State, Brazil

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ABSTRACT

Golden-headed lion tamarins (GHLTs; *Leontopithecus chrysomelas*) are endangered primates endemic to the Brazilian Atlantic Forest, where loss of forest and its connectivity threaten species survival. Understanding the role of habitat availability and configuration on population declines is critical for guiding proactive conservation for this, and other, endangered species. We conducted population viability analysis to assess vulnerability of ten GHLT metapopulations to habitat loss and small population size. Seven metapopulations had a low risk of extirpation (or local extinction) over the next 100 years assuming no further forest loss, and even small populations could persist with immediate protection. Three metapopulations had a moderate/high risk of extirpation, suggesting extinction debt may be evident in parts of the species' range. When deforestation was assumed to continue at current rates, extirpation risk significantly increased while abundance and genetic diversity decreased for all metapopulations. Extirpation risk was significantly negatively correlated with the size of the largest patch available to metapopulations, underscoring the importance of large habitat patches for species persistence. Finally, we conducted sensitivity analysis using logistic regression, and our results showed that local extinction risk was sensitive to percentage of females breeding, adult female mortality, and dispersal rate and survival; conservation or research programs that target these aspects of the species' biology/ecology could have a disproportionately important impact on species survival. We stress that efforts to protect populations and tracts of habitat of sufficient size throughout the species' distribution will be important in the near-term to protect the species from continuing decline and extinction.

Abstract in Portuguese is available in the online version of this article.

Key words: Atlantic Forest; habitat fragmentation; habitat loss; logistic sensitivity analysis; population viability analysis; small population size.

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HABITAT LOSS AND FRAGMENTATION ARE MAJOR DRIVERS OF BIODIVERSITY LOSS WORLDWIDE. Species are directly threatened by habitat loss and fragmentation through associated declines in space, resources, and movement of individuals between populations (exogenous threats; Fischer & Lindenmayer 2007). As populations become smaller and more isolated, species become vulnerable to indirect threats of habitat loss related to small population size such as demographic and environmental stochasticity, genetic drift, inbreeding depression, and Alleé effects (endogenous threats; Fischer & Lindenmayer 2007). The ultimate result is decreased survival, reproduction, and gene flow at the individual level and reduced abundance, distribution, and genetic diversity at the population level (reviewed in Fahrig 2003). Cascading effects caused by synergies among direct and indirect threats of habitat loss and fragmentation can radically accelerate population declines and further increase extinction risk (extinction vortex; Gilpin & Soulé 1986).

Brazil's Atlantic Forest provides a prime example of how habitat loss and fragmentation threaten native species. It is one of the world's most endangered biomes while providing habitat for a disproportionate number of species, many of which are endemic (Myers *et al.* 2000). Only 11.73 percent of the Atlantic Forest's original extent remains, the majority of which is found in small fragments (<50 ha; Ribeiro *et al.* 2009). Deforestation has been attributed primarily to clearcutting for timber harvest, charcoal production, cattle ranching, and monoculture plantations (Morellato & Haddad 2000, Pinto & Wey de Brito 2003) and is known to negatively affect several taxonomic groups including small mammals (Pardini 2004), plants (Tabarelli *et al.* 1999), birds (Uezu *et al.* 2005), and amphibians (Becker *et al.* 2007).

One species impacted by the loss and fragmentation of the Atlantic Forest is the golden-headed lion tamarin (GHLT; *Leontopithecus chrysomelas*), an arboreal primate endemic to a small region of southern Bahia, Brazil (Fig. S1) and listed as endangered due to its limited distribution, severely fragmented habitat, continuing decline in extent of occurrence, and small population size (IUCN 2012). GHLTs use lowland mature forest, secondary/regenerating forest, and shade-cocoa agroforest (Pinto & Rylands 1997, Raboy & Dietz 2004). Recent forest mapping efforts demonstrated a 13 percent reduction in the amount of this habitat between 1987 and 2007 (Zeigler *et al.* 2010) and low functional habitat connectivity throughout the GHLT

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distributional range (Zeigler *et al.* 2011). In addition, surveys suggest a population decline and range reduction over a 13-year-period (Raboy *et al.* 2010) since previous estimates made in the early 1990s of at least 6000 GHLTs spanning a geographic range of 19,462 km^2 (Pinto & Rylands 1997). Given that GHLT populations and habitat are declining, understanding the species' vulnerability to continuing habitat loss and risks inherent to small population size is imperative to proactively protect existing habitat and populations and to drive scientifically-informed conservation planning. Here, we highlight trends in extinction probability, population size, and genetic diversity for GHLT metapopulations given both current habitat availability and ongoing forest loss. We also discuss correlations between habitat availability/configuration, life history parameters, and extinction risk.

METHODS

Selection and analysis of metapopulations.—We modeled the viability of GHLT metapopulations inhabiting forest patches known to be occupied according to prior surveys and landscape analyzes. The underlying binary forest map, depicting forest patches and surrounding non-forest matrix, was created using remotely sensed Landsat imagery from 2004 to 2008 (see Zeigler *et al.* 2010 for details). According to Zeigler *et al.* (2010), 21 forest patches on this map were occupied based on recent surveys that established presence/absence of GHLTs on a sample of forest patches throughout the species' range by Raboy *et al.* (2010; Fig. S1). We calculated the Euclidean distance between every pair of forest patches on the forest map in ArcGIS and used Conefor Sensinode v.2.2 (Saura & Torne 2009) to identify groups of patches functionally connected within 1 km (known as a 'component' in graph theory terminology). We chose 1 km as the maximum GHLT dispersal distance based on expert opinion and anecdotal records of long-distance movements (Kierulff & de Oliveira 1994, Grativol *et al.* 2001), and the general observation that GHLTs are rarely seen in open landcover types (Raboy *et al.* 2010).

According to the Conefor Sensinode analysis, ten of the 21 occupied patches were relatively isolated and small, characteristic of the majority of forest patches in the GHLT range (Zeigler *et al.* 2010), and were found within the western portion of the species' range (although we did not specifically select patches in this region). The remaining 11 occupied forest patches were functionally connected to the largest forest patch (741,973 ha) in the study area, which is also occupied by GHLTs and is large enough to support a genetically viable population over 100 years (Zeigler *et al.* 2010). We presumed that GHLT populations in these patches are likely to persist with continuing immigration from a stable source population on the largest patch and that this component group of patches may provide a refuge for the species, protecting it from extinction even if other more isolated patches are clear-cut. We therefore did not focus demographic modeling on these populations at this time but instead focused on the ten small, relatively isolated, occupied forest patches for further demographic analysis.

In ArcGIS, we selected each component containing one of these occupied patches for a total of ten separate components (Figs. S1 and S2; Table 1), with each component comprised of an occupied patch and any other forest patch connected to it within 1 km. We assumed that forest patches within a component supported GHLT populations connected through dispersal, collectively referred to as a 'metapopulation', and we focused demographic modeling on these metapopulations.

TABLE 1. *Physical characteristics of components used to define and model metapopulations of golden-headed lion tamarins in Vortex v.9.98. A 'component' includes a habitat patch known to be occupied by GHLTs and any other patch $\geq$ 36 ha functionally connected to that occupied patch assuming a maximum dispersal distance of 1 km.*

Component	Total forest area (ha)	Number of patches	Number of patches $\geq$ 36 ha[a] (also number of populations)	Area of largest patch (ha)	Number of source patches ($\geq$ 700 ha[b])	Average dispersal probability (% of sub-population)	Total dispersal (% of metapopulation)	Carrying capacity or N_o[c] (# of GHLTs)
1	394	10	1	394	0	0	0	39
2	946	34	4	423	0	1.34	8.06	95
3	551	18	2	440	0	$75e^{-6}$	$75e^{-6}$	55
4	159	20	1	159	0	0	0	16
5	1130	21	4	924	1	0.15	0.92	113
6	849	52	7	244	0	0.49	10.35	85
7	134	4	1	134	0	0	0	13
8	521	13	2	478	0	0.06	0.06	52
9	1231	15	3	896	1	0.10	0.30	123
10	1305	28	4	579	0	0.70	4.23	130

[a] 36 ha is the smallest recorded territory size for GHLTs in primary and secondary forest. Thus, habitat patches smaller than this area are unlikely to support a population of GHLTs.

[b] 700 ha is the size of the smallest habitat patch able to support a viable population of GHLTs according to Zeigler *et al.* 2010.

[c] N_0 = initial population size (which we assumed to be equal to carrying capacity because actual population sizes are unknown).

Within each of the ten components identified, we defined forest patches ≥ 36 ha, the smallest known territory size for GHLTs in primary or secondary forest (Rylands 1989), as a 'population patch'. We considered any patch <36 ha as a 'stepping stone patch' (*i.e.,* a small habitat patch that reduces transit time in non-forested matrix and promotes dispersal between larger habitat patches but, by itself, is too small to support a population of GHLTs). We then analyzed all components separately in Conefor Sensinode to determine the maximum product probability that any pair of population patches in the component was connected by dispersal (Saura & Pascual-Hortal 2007), modeled as a decreasing negative exponential function of distance (Appendix S1). The patch area and maximum product probability of dispersal between pairs of population patches were then used to structurally characterize our focal metapopulations for demographic analysis.

Demographic analysis.—We conducted population viability analysis (PVA) in Vortex ver9.98 (Miller & Lacy 2005, Fig. S3). Vortex is an individual-based PVA program that simulates effects of both deterministic forces and demographic, environmental, and genetic stochastic events to assess extinction risk (Miller & Lacy 2005).

For each component and its corresponding metapopulation, we characterized sub-populations in Vortex such that they could occur only on population patches and that initial population size was equal to patch area (calculated in ArcGIS) multiplied by a density of 0.1 GHLTs/ha (*i.e.,* the average density of GHLTs in both primary and degraded forest). Thus, by our definition, a sub-population included all individuals found within the same habitat patch, and a metapopulation included all individuals in sub-populations found within the same component.

Dispersal was modeled in Vortex as the proportion of individuals from Sub-Population i that disperse to Sub-Population j per year. We calculated dispersal between sub-populations by multiplying the distance-dependent probability of dispersal (as calculated by Conefor Sensinode) by 5 percent, the average estimated maximum proportion of individuals that emigrate from territorial groups within a population per year based on social factors. In summary, the dispersal probability between sub-populations was a negative exponential function of distance ranging from 0 percent (>1 km between sub-populations) to 5 percent (0 m between sub-populations).We also assumed that the proportion of individuals dispersing from a population was at its highest as the source sub-population approached carrying capacity and that dispersal did not occur when the target sub-population was already saturated.

We then parameterized demographic rates in Vortex based on field observations as part of long-term monitoring projects by Raboy and Dietz (Maruim population; 1995–2007) and De Vleeschouwer (Piedade population; 2003–2010) in Una Biological Reserve (see Table S1 for parameter list; Table S2 for information relating to datasets). Demographic rates were calculated according to Zeigler *et al.* (2010), and the standard deviation in these parameters attributable to environmental variation was calculated according to Akcakaya (2002; Table S2). Mortality was further increased for dispersers such that the probability of an individual dying during dispersal was 25 percent, and this dispersal mortality was imposed after and in addition to the baseline age- and sex-based average mortality. We also incorporated demographic and environmental stochasticity as well as inbreeding depression, which decreased the baseline probability of survival for inbred offspring during their first year according to species-specific values calculated by Ballou *et al.* (1998). We initialized metapopulations in a stable age distribution and an initial population size at carrying capacity because actual population sizes and age distributions were unknown.

We modeled metapopulation dynamics for each component under three landscape scenarios in Vortex to explore the ramifications of varying levels of continued forest loss:

1. Forest cover does not change in the future.
2. Forest continues to be lost at the recent deforestation rate of 0.65 percent per year (Zeigler *et al.* 2010).
3. Forest continues to be lost at twice the recent deforestation rate per year at 1.3 percent. This rate was selected to explore the impact of drastic increases in deforestation that may occur in the Atlantic Forest in the coming decades (see Discussion).

Forest loss was modeled by decreasing carrying capacity by 0, 0.65 or 1.3 percent per year depending on the scenario for every sub-population within each metapopulation.

We modeled stochastic population dynamics over 100 years for 1000 iterations. We noted the deterministic rate of population growth as well as the stochastic average probability of local extinction, mean and median time to local extinction, percentage genetic heterozygosity remaining, and average final population abundance after 100 years.

Sensitivity analysis.—We conducted sensitivity analysis in Vortex using logistic regression to explore the importance of certain parameters on estimates of extinction risk (McCarthy *et al.* 1995). In a modified version of Vortex, we created 100 parameter sets by randomly choosing input values from uniform distributions within reasonable parameter ranges for population correlation (range: 0–1), percentage females breeding (range: 0–100%), disperser survival rate (range: 0–100%), dispersal rate (range: 0–25%), infant mortality for both sexes (range: 20–35%), female mortality for the 1- to 2-year age class (range: 8–15%), and adult female mortality (range: 10–28%).

We ran 1000 iterations in Vortex for each parameter set, resulting in 100,000 binary observations of population persistence or extinction by year 100. Using parameter set values as independent variables and whether the population goes extinct or not by year 100 as the binary dependent variable, we conducted logistic regression in R (R Development Core Team 2011) and compared the standardized regression coefficients to rank each independent variable's importance in relation to extinction risk (McCarthy *et al.* 1995). The standardized regression coefficient is a unitless value, scaled by parameter uncertainty, which expresses the contribution of each independent variable to changes in the dependent variable (Cross & Beissinger 2001) and establishes to which parameters Vortex models were most sensitive. This process was repeated using Vortex models for metapopulations on Components 2, 3, 6, and 7, chosen to reflect different combinations of GHLT carrying capacities, dispersal rates, and extinction risks.

OTHER STATISTICAL ANALYZES.—We were also interested in determining which physical characteristics of components were associated with high probabilities of local metapopulation extinction and early times to extinction. In ArcGIS, we determined the following landscape metrics for each component: total area of forest (ha), area of the largest patch (ha), number of patches ≥ 36 ha (which is also the number of populations), the number of patches ≥ 700 ha (*i.e.,* the minimum area required to support a self-sustaining population of GHLTs according to Zeigler *et al.* 2010), the average proportion of individuals across patches in a metapopulation/component that will disperse each year, and the total proportion of individuals that will disperse from all sub-populations in a metapopulation/component each year (Table 1). From these variables, we selected three ('area of largest patch', 'number of patches ≥ 36 ha', and 'average dispersal between populations') that were the least correlated with any other variable (Table S3) and that also characterized an element of forest availability, degree of patchiness, and degree of connectivity between populations in a metapopulation/component. We then used the Spearman rank correlation coefficient to test for a relationship between these variables and both the extinction probability and the average time to extinction for each metapopulation under the baseline scenario. Correlations were considered significant at $P < 0.017$ following Bonferonni adjustment to account for the three separate analyzes conducted on the dependent variable datasets. Statistical analyzes were conducted in *R*.

In addition, to determine if continuing forest loss significantly impacted the viability of metapopulations, we compared probability of extinction at 100 years between baseline, 0.65 percent forest loss, and 1.3 percent forest loss scenarios for each metapopulation/component using Fisher's exact test ($P < 0.05$).

RESULTS

METAPOPULATION VIABILITY.—In the baseline stochastic model, which assumed no additional forest loss, three metapopulations had a moderate to high risk of extirpation (or local extinction) over 100 years (Fig. S4). In determining the structural characteristics of metapopulations associated with higher local extinction risks, we found that the size of the largest patch was significantly correlated with both the probability of metapopulation extinction (*rho* = −0.81, $P = 0.004$) and the time to metapopulation extinction (*rho* = −0.75, $P = 0.012$). No other variables tested were significant (Table 2). Despite low local extinction risks for the majority of metapopulations, population size for all metapopulations declined over 100 years, ranging from a 3.15 percent decline for the metapopulation on Component 1 to an 86 percent decline for the metapopulation on Component 6 (Fig. S5; Table 3). In addition, no metapopulation was able to retain more than 88 percent of its original genetic heterozygosity (Fig. S6).

TABLE 2. *Spearman rank correlation coefficients (rho) and significance levels linking landscape characteristics of component groups with the local extinction probability and average time to extinction for metapopulations on those components. Correlations were considered significant at* $P < 0.017$.

Landscape characteristic (independent variable)	Probability of extinction		Time to extinction	
	Spearman rank correlation coefficient	*P*-value	Spearman rank correlation coefficient	*P*-value
Largest patch	−0.81	0.004	−0.75	0.01
Patches ≥ 36 ha	−0.31	0.38	−0.07	0.85
Average dispersal	−0.43	0.21	−0.25	0.49

When deforestation was considered at its current rate of 0.65 percent loss per year, three metapopulations had a >90 percent chance of local extinction by year 100, and only three metapopulations had ≤ 2 percent probability of local extinction in 100 years (Fig. S4). Deforestation at the current level of forest loss significantly increased local extinction risk compared with the baseline scenario for seven of the metapopulations. All metapopulations experienced at least a 70 percent reduction in population abundance under this scenario (Fig. S5; Table 3), and no metapopulation retained more than 80 percent of its original genetic heterozygosity (Fig. S6).

Finally, when we assumed that deforestation would double to a rate of 1.3 percent per year, all metapopulations were extirpated by year 100 (Fig. S4). Seven of the metapopulations had a mean time to local extinction between 70 and 76 years, and the remaining three metapopulations were extirpated, on average, between years 38 and 54 (Fig. S4; Table 3). All metapopulations had a significantly higher risk of local extinction with deforestation rates of 1.3 percent per year compared with both the baseline and the 0.65 percent deforestation rate scenarios ($P < 0.01$).

SENSITIVITY ANALYSIS.—The magnitude and relative importance of standardized regression coefficients differed depending on the metapopulation analyzed; however, all metapopulations displayed similar general patterns of parameter sensitivity (Table S4). Models were consistently insensitive to population correlation and infant mortality. For all metapopulations, however, extinction risk was significantly positively correlated with adult female mortality and dispersal rate but negatively correlated with the percentage of females breeding and the probability of disperser survival.

DISCUSSION

DIRECT THREATS: VULNERABILITY FROM HABITAT LOSS.—Populations of GHLTs are at risk due to both direct and indirect threats associated with habitat loss and fragmentation, especially in the western portion of their range. Although seven of the ten metapopulations modeled in this study had no risk of extirpation

TABLE 3. *Mean time to extinction and percentage population decline over 100 years for metapopulations of golden-headed lion tamarins assuming no additional forest loss, 0.65 percent forest loss per year (current deforestation rate), and 1.3 percent forest loss per year (double the current deforestation rate).*

	Baseline (No deforestation)		0.65% deforestation per year		1.3% deforestation per year	
Component	Population decline (% change)	Mean time to extinction (year)	Population decline (% change)	Mean time to extinction (year)	Population decline (% change)	Mean time to extinction (year)
1	3.15	>100	70.46	88	100	70
2	3.78	>100	72.96	98	100	74
3	20.07	>100	75.45	91	100	71
4	56.13	64	96.63	63	100	46
5	19.00	>100	71.73	>100	100	76
6	85.67	83	99.62	73	100	54
7	78.69	56	99.15	51	100	38
8	9.06	>100	70.42	94	100	72
9	5.23	>100	69.50	>100	100	76
10	34.49	>100	86.66	93	100	73

over the next 100 years given current forest availability, seven metapopulations had a significantly higher risk of extirpation assuming that forest loss continues at the current rate, and the remaining three already had a high risk of extinction under the baseline scenario. All metapopulations had at least a 70 percent decline in population abundance given this ongoing deforestation. If deforestation continues at double the current rate, all metapopulations modeled here have a 100 percent probability of local extinction within the next 100 years. Given current trends in forest loss, our results suggest that the species is vulnerable to extirpation on forest patches of similar size and isolation, characteristic of the majority of habitat patches particularly in the western portion of the species' range (Zeigler *et al.* 2010, 2011), and we expect to see a continuation of the range contraction suggested by Raboy *et al.* (2010).

These trends are particularly worrisome given that deforestation rates are projected to increase as shade-cocoa plantations are converted to open cattle pasture (Schroth & Harvey 2007). Although this land conversion will not have a large impact on the metapopulations evaluated here as the western portion of the species' range contains very little available habitat in the form of shade-cocoa agroforest, it would drastically reduce the amount of available habitat in the large eastern forest patch previously thought to be a safe-haven for the species. In addition, changes to Brazil's Forest Act (1989) under Law No 12.651 (as of 25 May 2012) will eliminate enforced protection of certain areas of existing forest (Calmon *et al.* 2011). This change in the country's forest law could increase extinction risk for more than 100,000 species and is being touted as the biggest environmental set-back in the country's history (Metzger *et al.* 2010). GHLT populations, both on forest patches like those modeled here as well as on the large eastern patch, will likely be impacted by the loss of protected habitat that would occur under a reduction in the mandates of the Forest Act.

Continued forest loss and fragmentation expected in the coming years would leave the GHLT landscape lacking in contiguous forest cover and would increase the vulnerability of individual populations, and eventually the entire species, to extinction. The modeling exercise described here as well as other case studies of related primates (*e.g., Alouatta palliata mexicana*, Mandujano & Escobedo-Morales 2008) provide further evidence that continued forest loss and fragmentation will lead to drastic population declines from which a species may not be able to recover. It cannot be stressed enough that forest within the GHLT range must be proactively protected now while it still exists. The majority of native vegetation throughout Brazil, including the GHLT range, is found on private land where extreme pressure for agricultural expansion is highest (Ferreira *et al.* 2012). Given the historical rate and patterns of deforestation in this region, forest will undoubtedly continue to disappear, and its enforced protection will be the only means through which habitat for GHLTs and other Atlantic Forest species will be able to persist. In addition, it is important to protect forested areas throughout the species' range in an effort to preserve redundant populations and the species' full complement of genetic variability. Various mechanisms for protecting habitat include the creation of federally mandated protected areas, the promotion of private reserves, and the implementation of positive incentives for farmers to continue biodiversity-friendly agroforestry practices (reviews in Langholz & Lassoie 2001, Tabarelli *et al.* 2005, Cassano *et al.* 2009).

In addition, we found that the variable describing the amount of forest available to the metapopulation, specifically the size of the largest patch, was significantly negatively correlated with probability of local extinction. Larger patches are more likely to have resources to support self-sustaining source populations (Pulliam 1988), which is especially important in this highly fragmented landscape where successful immigration may be low (Zeigler *et al.* 2011). Large populations have a lower risk of local extinction than their smaller counterparts, can produce individuals that then contribute to the entire regional population through dispersal and metapopulation dynamics in paired source-sink systems (Hanski 1991, Radford & Bennett 2004), and can ultimately provide a stabilizing effect on metapopulation size and persistence (Howe *et al.* 1991). Large forest patches and their corresponding large populations have been shown to be important for a variety of Atlantic Forest species (Chiarello 1999, Chiarello & de Melo 2001, Brito & Fernandez 2002, Brito & Grelle 2006, Metzger *et al.* 2009, Vieira *et al.* 2009). Given the importance of large patches for the persistence of GHLTs, protecting habitat and metapopulations on the largest remaining forest patches throughout the GHLT range (as identified in Zeigler *et al.* 2010) will be critical for the persistence of the species.

INDIRECT THREATS: VULNERABILITY INHERENT TO SMALL POPULATIONS.—Although extinction risk was significantly higher for GHLT metapopulations due to continuing forest loss, some metapopulations were also at risk due to indirect threats associated with small population size. Despite the fact that GHLT populations should be stable ($\lambda_{\text{deterministic}} = 1.02$), we found that three metapopulations had a probability of local extinction ≥ 24 percent within the next 100 years even when no further deforestation occurred. Many species exhibit time lags in their response to reductions in forest area and connectivity (Tilman *et al.* 1994), particularly when those reductions occur very quickly as seen in the Atlantic Forest (Brooks & Balmford 1996, Fahrig 2005, Metzger *et al.* 2009). The current presence of some GHLT metapopulations modeled here despite high probabilities of extinction may simply reflect extinction debt (Tilman *et al.* 1994), and continuing local population extinctions like those already observed for the species (Raboy *et al.* 2010) may be expected as population dynamics catch up with habitat loss.

Metapopulations that exhibit relatively high local extinction probabilities even when the direct pressures of forest loss and fragmentation are removed could be experiencing pressure from processes like demographic and environmental stochasticity, genetic deterioration, and social dysfunction (Simberloff 1986). Genetic deterioration may be of particular concern for small populations of GHLTs. Lion tamarins have the lowest levels of genetic diversity reported for any primate (Forman *et al.* 1986), likely due to the species' propensity for twins, monogamous mating system, and social structure (small family groups with a single breeding pair) which reduce the number of possible allelic combinations (Forman *et al.* 1986). In addition, moderate levels of inbreeding have been linked to significantly higher juvenile mortality rates (Ballou 1985, Ralls *et al.* 1988, Dietz *et al.* 2000). Thus, genetic drift and inbreeding depression may cause a reduction in already low genetic diversity for GHLTs, ultimately reducing survival of offspring and reproductive success. We found that populations are likely to lose, at a minimum, 20 percent genetic heterozygosity assuming that deforestation continues at its current rate.

In addition to genetic deterioration, small GHLT metapopulations are also vulnerable to Allee effects (Alleé *et al.* 1949), which describe the reduction in *per capita* growth rate at low population densities. Allee effects can occur when a population size falls below a critical number of individuals required for behaviors like anti-predator defense, inbreeding avoidance, mate attraction, or conspecific enhancement of reproduction (Stephens & Sutherland 1999). GHLTs and other cooperatively-breeding species are predicted to be especially vulnerable to Allee effects because offspring survival is dependent on the presence of helpers (Dobson & Lyles 1989, Courchamp *et al.* 1999). Allee effects were not included in our models, and GHLT metapopulations may be at a higher risk of local extinction than we predicted if Allee effects are in fact impacting populations.

PARAMETER UNCERTAINTY AND MODEL LIMITATIONS.—Sensitivity analysis showed that PVA models were impacted by variation in parameters for the percentage of females breeding, disperser survival, dispersal rate, and adult female mortality. These results are important because there is an uncertainty surrounding the values used for these parameters. Information about GHLT dispersal behavior is especially lacking, including how far and how often individuals are willing to travel over what types of matrix. Furthermore research on these areas of GHLT ecology and behavior, especially dispersal rate (Fahrig 1990), will improve the predictive accuracy of PVA models in the future. Sensitivity results showed that local extinction risk was negatively correlated with the rate of dispersal and positively correlated with the survival rate of dispersers. We assumed very low rates of dispersal for our baseline models, and, should dispersal between populations actually be higher, extirpation risk for GHLT metapopulations would also be substantially higher as individuals enter non-forest matrix where mortality is higher. Likewise, if dispersal survivorship is lower than 75 percent as estimated here, metapopulation extinction risk would also increase.

In addition, we could not assess variation in matrix habitat separating forested habitat patches because of difficulties in reliably separating certain classes (*e.g.,* monoculture plantations from native forest) in this region of Brazil (Lawrence *et al.* 1995). The nature of this variation can strongly influence occupancy, movement patterns, and disperser survivorship (*e.g.*, Anderson *et al.* 2007), and our estimates of local extinction risk could vary as described in the previous paragraph if disparities in the suitability of different matrix habitats result in varying dispersal rate and survivorship.

Finally, PVA models conducted here may represent overly optimistic predictions of local extinction risk for reasons other than underestimation of dispersal rate and survivorship. Survival and reproductive rates for GHLTs were based on studies of populations in forested areas in and around Una Biological Reserve, an area of optimal habitat for GHLTs with high structural forest connectivity. No long-term published data on the demographic rates and group dynamics of GHLTs in very small, degraded forest patches characteristic of the western portion of the species' range (and the components explored in this study) are currently available. We also did not incorporate the effects of catastrophes or other threats beyond habitat loss. Fire and disease are both major threats to GHLTs and would increase extirpation risk, particularly for populations in the west that are surrounded by pasture that is routinely burned (Holst *et al.* 2006). In addition, we assumed that all habitat patches ≥ 36 ha surrounding habitat patches known to be occupied by GHLTs were also inhabited by the species and that these populations were at carrying capacity.

Our models were thus initiated at what could be inflated metapopulation sizes. For these reasons, our models represented GHLT metapopulations at optimal conditions (with larger metapopulation sizes, high vital rates, and no catastrophes), and local extinction risk for the metapopulations described herein may be higher than our results portrayed.

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SUPPORTING INFORMATION

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

TABLE S1. *Life history parameters used for population viability analysis modeling in Vortex.*

TABLE S2. *Background on field observations.*

TABLE S3. *Spearman correlation coefficients between physical characteristics of forest components/metapopulations.*

TABLE S4. *Model sensitivity to selected metapopulation parameters for four components according to logistic regression.*

FIGURE S1. Location of the geographic distribution of the golden-headed lion tamarins in Bahia, Brazil.

FIGURE S2. Component groups modeled in this study.

FIGURE S3. Program algorithm detailing order of events in the population viability analysis program Vortex.

FIGURE S4. Extinction risk curves for metapopulations of golden-headed lion tamarins on components of functionally connected habitat patches.

FIGURE S5. Population abundance curves for metapopulations of golden-headed lion tamarins on components of functionally connected habitat patches.

FIGURE S6. Percentage of the original heterozygosity remaining for metapopulations of golden-headed lion tamarins on components of functionally connected habitat patches through time. Curves correspond to models that assume (1) no further deforestation (circles), (2) 0.65% forest loss per year (current rate in the region; triangles), and (3) 1.3% forest loss per year (double current rate; squares). Gray dashed lines correspond to the 95% confidence intervals associated with stochastic simulation.

APPENDIX S1. Methodology used in Conefor Sensinode.

LITERATURE CITED

AKCAKAYA, H. R. 2002. Estimating the variance of survival rates and fecundities. Anim. Conserv. 5: 333–336.

ALLEÉ, W. C., A. E. EMERSON, O. PARK, AND K. P. SCHMIDT. 1949. Principles of Animal Ecology. W.B. Saunders, Philadelphia, PA.

ANDERSON, J., J. M. ROWCLIFFE, AND G. COWLISHAW. 2007. Does the matrix matter? A forest primate in a complex agricultural landscape. Biol. Conserv. 135: 212–222.

BALLOU, J. 1985. International Studbook for the Golden-Lion Tamarin, *Leontopithecus rosalia rosalia* (1984). National Zoological Park, Washington DC.

BALLOU, J., R. C. LACY, K. KLEIMAN, A. RYLANDS, AND S. ELLIS. 1998. *Leontopithecus* II: the second population and habitat viability assessment for lion tamarins: final report. Conservation Breeding Specialist Group (SSC/IUCN), Apple Valley, MN.

BECKER, C., C. FONSECA, C. HADDAD, R. BATISTA, AND P. PRADO. 2007. Habitat split and the global decline of amphibians. Science 318: 1775–1777.

BRITO, D., AND F. A. S. FERNANDEZ. 2002. Patch relative importance to metapopulation viability: the neotropical marsupial *Micoureus demerarae* as a case study. Anim. Conserv. 5: 45–51.

BRITO, D., AND C. E. V. GRELLE. 2006. Estimating minimum area of suitable habitat and viable population size for the northern muriqui (*Brachyteles hypoxanthus*). Biodivers. Conserv. 15: 4197–4210.

BROOKS, T., AND A. BALMFORD. 1996. Atlantic Forest extinctions. Nature 380: 115.

CALMON, M., P. BRANCALION, A. PAESE, J. ARONSON, P. CASTRO, S. da SILVA, AND R. RODRIGUES. 2011. Emerging threats and opportunities for large-scale ecological restoration in the Atlantic forest of Brazil. Restor. Ecol. 19: 154–158.

CASSANO, C., G. SCHROTH, D. FARIA, J. DELABIE, AND L. BEDE. 2009. Landscape and farm scale management to enhance biodiversity conservation in the cocoa producing region of southern Bahia, Brazil. Biodivers. Conserv. 18: 577–603.

CHIARELLO, A. 1999. Effects of fragmentation of the Atlantic Forest on mammal communities in south-eastern Brazil. Biol. Conserv. 89: 71–82.

CHIARELLO, A. G., AND F. R. de MELO. 2001. Primate population densities and sizes in Atlantic forest remnants of Northern Espirito Santo, Brazil. Int. J. Primatol. 22: 379–395.

COURCHAMP, F., B. GRENFELL, AND T. H. CLUTTON-BROCK. 1999. Population dynamics of obligate cooperators. Proc. R. Soc. Lond., Ser. B: Biol. Sci. 266: 557–563.

CROSS, P. C., AND S. BEISSINGER. 2001. Using logistic regression to analyze the sensitivity of PVA models: a comparison of methods based on African wild dog models. Conserv. Biol. 15: 1335–1346.

DIETZ, J., A. BAKER, AND JD BALLOU. 2000. Demographic evidence of inbreeding depression in wild golden lion tamarins. In A. Young, and G. Clarke (Eds.). Genetics, Demography, and the Viability of Fragmented Populations, pp. 203–211. Cambridge University Press, Cambridge, UK.

DOBSON, A., AND A. M. LYLES. 1989. The population dynamics and conservation of primate populations. Conserv. Biol. 3: 362–380.

FAHRIG, L. 1990. Simulation methods for developing general landscape-level hypotheses of single-species dynamics. In M. Turner, and R. Gardner (Eds.). Quantitative Methods in Landscape Ecology. Springer-Verlag, New York.

FAHRIG, L. 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Evol. Syst. 34: 487–515.

FAHRIG, L. 2005. When is landscape perspective important? In J. A. Wiens, and M. R. Moss (Eds.). Issues and Perspectives in Landscape Ecology. Cambridge University Press, Cambridge.

FERREIRA, J., R. PARDINI, J. METZGER, C. FONSECA, P. POMPEU, G. SPAROVEK, AND J. LOUZADA. 2012. Towards environmentally sustainable agriculture in Brazil: challenges and opportunities for applied ecological research. J. Appl. Ecol. 49: 535–541.

FISCHER, J., AND D. B. LINDENMAYER. 2007. Landscape modification and habitat fragmentation: a synthesis. Glob. Ecol. Biogeogr. 16: 265–280.

FORMAN, L., D. G. KLEIMAN, R. M. BUSH, J. M. DEITZ, J. D. BALLOU, L. G. PHILLIPS, A. F. COIMBRA-FILHO, AND S. J. O'BRIEN. 1986. Genetic variation within and among lion tamarins. Am. J. Phys. Anthropol. 71: 1–11.

Gilpin, M., and M. E. Soulé. 1986. Minimum viable populations: processes of extinction. In M. E. Soulé (Ed.). Conservation Biology: the Science of Scarcity and Diversity. Sinauer Associates, Sunderland, MA.

Grativol, A., J. Ballou, and R. Fleischer. 2001. Microsatellite variation within and among recently fragmented populations of the golden lion tamarin (*Leontopithecus rosalia*). Conserv. Genet. 2: 1–9.

Hanski, I. 1991. Metapopulation dynamics: brief history and conceptual domain. Biol. J. Linn. Soc. 42: 3–16.

Holst, B., E. Medici, O. Marino-Filho, D. Kleiman, K. Leus, A. Pissinatti, G. Vivekananda, J. Ballou, K. Traylor-Holzer, B. Raboy, F. Passos, K. Vleeschouwer, and M. Montenegro. 2006. Lion Tamarin Population and Habitat Viability Assessment Workshop 2005, Final Report. IUCN/SSC Conservation Breeding Specialist Group, Apple Valley, MN.

Howe, R., G. Davis, and V. Mosca. 1991. The demographic significance of sink populations. Biol. Conserv. 57: 239–255.

IUCN. 2012. The IUCN Red List of Threatened Species. Version 2012.2. Available at http://www.iucnredlist.org (accessed 17 October 2012).

Kierulff, M., and P. de Oliveira. 1994. Habitat preservation and the translocation of threatened groups of golden lion tamarins, *Leontopithecus rosalia*. Neotrop. Primates 2(supplement): 15–18.

Langholz, J., and J. Lassoie. 2001. Perils and promise of privately owned protected areas. Bioscience 51: 1079–1085.

Lawrence, W., S. Saatchi, R. Defries, J. Dietz, R. Rice, L. Dietz, M. de Araujo, and K. Alger. 1995. Utilization of SAR and optical remote sensing data for habitat conservation in the tropical forest of Brazil. Geoscience and Remote Sensing Symposium, Firenze, Italy.

Mandujano, S., and L. Escobedo-Morales. 2008. Population viability analysis of howler monkeys (*Alouatta palliata mexicana*) in a highly fragmented landscape in Los Tuxtlas, Mexico. Tropical Conservation Science 1: 43–62.

McCarthy, M., M. Burgman, and S. Ferson. 1995. Sensitivity analysis for models of population viability. Biol. Conserv. 73: 93–100.

Metzger, J., T. Lewinsohn, C. Joly, L. Verdade, L. Martinelli, and R. Rodrigues. 2010. Brazilian law: full speed in reverse? Science 329: 276–277.

Metzger, J. P., A. C. Martensen, M. Dixo, L. C. Bernacci, M. C. Ribeiro, A. M. G. Teixeira, and R. Pardini. 2009. Time-lag in biological reponses to landscape changes in a highly dynamic Atlantic forest region. Biol. Conserv. 142: 1166–1177.

Miller, P. S., and R. C. Lacy. 2005. Vortex: a Stochastic Simulation of the Extinction Process. Version 9.50 User's Manual. Conservation Breeding Specialist Group (SSC/IUCN), Apple Valley, MN.

Morellato, L., and C. Haddad. 2000. Introduction: the Brazilian Atlantic forest. Biotropica 32: 786–792.

Myers, N., R. Mittermeier, C. Mittermeier, G. D. Fonseca, and J. Kent. 2000. Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

Pardini, R. 2004. Effects of forest fragmentation on small mammals in an Atlantic Forest landscape. Biodivers. Conserv. 13: 2567–2586.

Pinto, L., and A. Rylands. 1997. Geographic distribution of the golden-headed lion tamarin, *Leontopithecus chrysomelas*: implications for its management and conservation. Folia Primatol. 68: 161–180.

Pinto, L. P., and M. C. Wey de Brito. 2003. Dynamics of biodiversity loss in the Brazilian Atlantic Forest: an Introduction. In C. Galindo-Leal, and I. de Gusmao Camara (Eds.). The Atlantic Forest of South America: biodiversity status, trends, and outlook, pp. 27–30. Center for Applied Biodiversity Science and Island Press, Washington, DC.

Pulliam, H. 1988. Sources, sinks, and population regulation. Am. Nat. 132: 652–661.

R Development Core Team. 2011. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Raboy, B., and J. Dietz. 2004. Diet, foraging, and the use of space in wild golden-headed lion tamarins. Am. J. Primatol. 63: 1–15.

Raboy, B., L. Neves, S. Zeigler, N. Saraiva, N. Cardoso, G. Santos, J. Ballou, and P. Leimgruber. 2010. Strength of habitat and landscape metrics in predicting golden-headed lion tamarin presence or absence in forest patches in southern Bahia, Brazil. Biotropica 42: 388–397.

Radford, J. Q., and A. F. Bennett. 2004. Thresholds in landscape parameters: occurrence of the white-browed treecreeper *Climacteris affinis* in Victoria, Australia. Biol. Conserv. 117: 375–391.

Ralls, K., J. Ballou, and A. Templeton. 1988. Estimates of lethal equivalents and the cost of inbreeding in mammals. Conserv. Biol. 2: 185–193.

Ribeiro, M. C., J. P. Metzger, A. C. Martensen, F. J. Ponzoni, and M. M. Hirota. 2009. The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. Biol. Conserv. 142: 1141–1153.

Rylands, A. B. 1989. Sympatric Brazilian callitrichids: the black tufted-ear marmoset, *Callithrix kuhli*, and the golden-headed lion tamarin, *Leontopithecus chrysomelas*. J. Hum. Evol. 18: 679–695.

Saura, S., and L. Pascual-Hortal. 2007. Conefor Sensinode 2.2 User Manual: software for quantifying the importance of habitat patches for maintaining landscape connectivity through graphs and habitat availability indices. University of Lleida, Spain.

Saura, S., and J. Torne. 2009. Confor Sensinode 2.2: a software package for quantifying the importance of habitat patches for landscape connectivity. Environ. Modell. Softw. 24: 135–139.

Schroth, G., and C. A. Harvey. 2007. Biodiversity conservation in cocoa production landscapes: an overview. Biodivers. Conserv. 16: 2237–2244.

Simberloff, D. 1986. The proximate causes of extinction. In D. M. Raup, and D. Jablonski (Eds.). Patterns and Processes in the History of Life. Springer-Verlag Berlin, Heidelberg.

Stephens, P. A., and W. J. Sutherland. 1999. Consequences of the Alleé effect for behaviour, ecology, and conservation. Trends Ecol. Evol. 14: 401–405.

Tabarelli, M., W. Mantovani, and C. Peres. 1999. Effects of habitat fragmentation on plant guild structure in the montane Atlantic Forest of southeastern Brazil. Biol. Conserv. 91: 119–127.

Tabarelli, M., L. Pinto, J. Silva, M. Hirota, and L. Bede. 2005. Challenges and opportunities for biodiversity conservation in the Brazilian Atlantic Forest. Conserv. Biol. 19: 695–700.

Tilman, D., R. M. May, C. L. Lehman, and M. A. Nowak. 1994. Habitat destruction and the extinction debt. Nature 371: 65–66.

Uezu, A., J. P. Metzger, and J. M. E. Vielliard. 2005. Effects of structural and functional connectivity and patch size on the abundance of seven Atlantic Forest bird species. Biol. Conserv. 123: 507–519.

Vieira, M. V., N. Olifiers, A. C. Delciellos, V. Z. Antunes, L. R. Bernardo, C. E. V. Grelle, and R. Cerqueira. 2009. Land use vs. forest fragment size and isolation as determinants of small mammal composition and richness in Atlantic Forest remnants. Biol. Conserv. 142: 1191–1200.

Zeigler, S., W. Fagan, R. Defries, and B. Raboy. 2010. Identifying important forest patches for the long-term persistence of the endangered golden-headed lion tamarin (*Leontopithecus chrysomelas*). Trop. Conserv. Sci. 3: 63–77.

Zeigler, S., M. Neel, L. Oliveira, B. Raboy, and W. Fagan. 2011. Conspecific and heterospecific attraction in assessments of functional connectivity. Biodivers. Conserv. 20: 2779–2796.