Received: 2 June 2019 | Revised: 14 December 2019 | Accepted: 20 December 2019

DOI: 10.1002/ajp.23089

AMERICAN JOURNAL OF PRIMATOLOGY WILEY

COMMENTARY

Howler monkey tolerance to habitat shrinking: Lifetime warranty or death sentence?

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Funding information
Conselho Nacional de Desenvolvimento Científico e Tecnológico, Grant/Award Numbers: 300439/91-1, 303154/2009-8, 303306/2013-0, 304475/2018-1, 306090/2006-6, 404457/88-6; American Society of Primatologists; World Wildlife Fund, Grant/Award Number: 6573/1989; Margot Marsh Biodiversity Foundation; Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, Grant/Award Number: PNPD #2755/2010; Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul, Grant/Award Numbers: 18/2551-0000243-7, PqG #11/1392-3

Abstract

Habitat loss and fragmentation are major threats to the conservation of nonhuman primates. Given that species differ in their responses to fragmented landscapes, identifying the factors that enable them to cope with altered environments or that cause their extirpation is critical to design conservation management strategies. Howler monkeys (*Alouatta* spp.) are good models for studying the strategies of tolerant arboreal taxa and how they cope with spatial restriction, because they live in habitats ranging from vast pristine forests to small disturbed fragments and orchards. While some aspects of their ecology and behavior are conserved, others vary in predictable ways in response to habitat shrinking and decreasing resource availability. We argue that the ability of individual howler monkeys to inhabit low-quality environments does not guarantee the long-term persistence of the small populations that live under these conditions. Their local extirpation explains why few forest fragments below a given area threshold are frequently inhabited in landscapes where recolonization and gene flow are compromised by long isolation distances or less permeable matrices. In sum, howlers' ability to cope with habitat restriction at the individual level in the short-term may mask the inevitable fate of isolated populations, thereby compromising the persistence of the species at a regional scale in the long-term if howlers' need for protection in large forests is undervalued.

KEYWORDS
Alouatta spp., behavioral plasticity, habitat fragmentation, matrix threats, population extirpation, population persistence

1 | HABITAT SHRINKING AND PRIMATE CONSERVATION

Habitat loss and fragmentation are major threats to wildlife conservation worldwide, as human activities such as agriculture, cattle ranching, logging, mining, roads, hydroelectric dams and other infrastructure projects reduce and isolate surviving populations (Haddad et al., 2015). Habitat shrinking and disconnection also threaten the populations of the 700+ nonhuman primate species and subspecies. Approximately 75% of these primate populations are decreasing, and 60% of primate species worldwide are threatened with extinction according to the International Union for the Conservation of Nature/IUCN (Estrada et al., 2017).

Understanding how a taxon responds to the spatial restriction in human-modified landscapes is essential to assess its long-term viability and to design management strategies aimed at the species' conservation. Forest-living, highly arboreal primates, for example, are more sensitive to habitat loss and fragmentation than are semi-terrestrial, terrestrial, or habitat generalist species (Galán-Acedo et al., 2019a). Species requiring large home ranges or specific resources to satisfy their groups' nutritional needs can disappear soon after a disturbance has compromised the quality of a habitat patch, whereas species whose individuals cope with habitat spatial limitation by adapting their needs to the available resources can stay longer (Boyle & Smith, 2010).

The long-term persistence of a species that appears to be tolerant to habitat loss and fragmentation depends on the size of the population and the permeability of the matrix to the individuals (Arroyo-Rodríguez, González-Perez, Garmendia, Solà, & Estrada, 2013; Laurance, 1991; Pozo-Montuy, Serio-Silva, Chapman, & Bonilla-Sánchez, 2013). These features determine whether a population has a minimum viable size (Shaffer, 1981). Small habitat patches have higher conservation value when they are integrated into a functional, preferably patchy, metapopulation, in which their frequent role as both recipients and sources of genes creates a single demographic entity, where the extirpation of discrete populations is either absent or unimportant (Harrison, 1991). When small, not self-sustaining populations whose spatial isolation hampers gene flow are fated to disappear as a result of genetic, demographic and environmental stochasticity (Mills, 2007) in addition to human-related threats, the tolerance of individuals to the spatial limitation of habitat fragments is not sufficient to promote the conservation of the species at a regional scale in the long-term. We use the metaphors of "lifetime warranty" and "death sentence" to emphasize this dichotomy. On one hand, we mean by "lifetime warranty" that this individual capacity to cope with habitat restriction would be a guarantee of long-term species persistence in fragmented landscapes. On the other hand, the "death sentence" relates to the aforementioned fate of small and isolated populations, so that relying on them to protect a species would probably lead to its regional extirpation in the long-term.

Not recognizing this dichotomy has practical conservation implications. The contestation of the recommendation by expert primatologists to classify the black-and-gold howler monkey (*Alouatta caraya*) as Near Threatened (NT) in the 2018 IUCN Red List global assessment is an example. IUCN reviewers questioned the NT status in light of the statement that the species "can be found in secondary forest and can adapt to fragmented and degraded habitats" (JC Bicca-Marques, April 2019; pers. comm.).

2 | HOWLER MONKEYS AS MODELS TO ADDRESS THE "LIFETIME WARRANTY" AND "DEATH SENTENCE" DICHOTOMY

Our goal here is to use the Neotropical howler monkeys (*Alouatta* spp.) as models to explore why it is important to consider contrasting interpretations of individual tolerance to habitat shrinking when making conservation decisions. The 12 species and 10 subspecies of howler monkeys (Cortés-Ortiz, Rylands, & Mittermeier, 2015) range from approximately 18°N in Mexico to 31°S in northeastern Argentina and southern Brazil, the widest geographic distribution among all Neotropical primate genera (Crockett & Eisenberg, 1987; Jardim et al., 2020; Neville, Glander, Braza, & Rylands, 1988). They are highly arboreal and found in habitats ranging from pristine continuous forests to small anthropogenically-disturbed forest fragments and orchards (Bicca-Marques, 2003; Fortes, Bicca-Marques, Urbani, Fernández, & Pereira, 2015). Their behavior has been extensively studied for decades (e.g., Glander, 1978; Milton, 1980; see also Bicca-Marques, 2003; Di Fiore, Link, & Campbell, 2011) and their responses to landscape structure are the best known among all primates (Galán-Acedo, Arroyo-Rodríguez, Cudney-Valenzuela, & Fahrig, 2019b). Ten (53%) of the 19 howler monkey taxa assessed for the 2008 IUCN Red List of Threatened Species were classified as Least Concern, four (21%) as Vulnerable, two (11%) as Endangered and three (16%) as Critically Endangered (IUCN, 2019).

3 | RESPONSES OF HOWLER MONKEYS TO HABITAT SPATIAL RESTRICTION

A review of howler monkey ranging behavior (Fortes et al., 2015) shows that they live in habitats varying between <1-ha forest fragments and orchards to vast pristine forests, where their home ranges vary from 0.7 to 182 ha (median = 10 ha; mean = 19 ± *SD* 27 ha; *N* = 85 groups). Except for habitat patches smaller than the normal home range used by groups in large forest fragments or continuous forests, fragment size does not predict home range size (but see Cristóbal-Azkarate & Arroyo-Rodríguez, 2007), whereas population density has a negative influence on it (see also Cristóbal-Azkarate & Arroyo-Rodríguez, 2007). Irrespective of home range size, day ranges are quite conservative (median = 494 m; mean = 506 ± *SD* 190 ha; *N* = 85 groups) and cannot be predicted by fragment size (Fortes et al., 2015). Despite such conservatism, similar to home range, day range is also negatively affected by population density, as it is by the contribution of fruits and leaves to the diet. However, group size has a positive influence on the day range, as larger groups require more food to satiate their members (Fortes et al., 2015).

The activity budget is also conservative wherever howlers live and is not predicted by habitat size (Bicca-Marques, 2003). Howlers spend most of their time resting (often >60% of the daytime), followed by similar proportions of feeding and traveling (frequently between 15% and 20% each) and a low investment in socializing (<5% of the day; Bicca-Marques, 2003; Di Fiore et al., 2011).

Howlers' ability to live in the aforementioned wide range of forested habitats has been related to their flexible folivorous-frugivorous diet, of which the contribution of leaves and fruits varies between seasons and sites (Bicca-Marques, 2003; Bonilla-Sánchez, Serio-Silva, Pozo-Montuy, & Chapman, 2012; Chaves & Bicca-Marques, 2016; Dias & Rangel-Negrín, 2015; Prates & Bicca-Marques, 2011). Howlers are the most folivorous Neotropical primates (Neville et al., 1988). Although both the richness of sources of fruits and leaves tends to decrease with habitat shrinking (Bicca-Marques, 2003), howlers may need to diversify their diet under conditions of high population density in small forest fragments (Cristóbal-Azkarate & Arroyo-Rodríguez, 2007). The consumption of plant items from non-tree growth forms was reported to increase in small fragments in *A. palliata* (Cristóbal-Azkarate & Arroyo-Rodríguez, 2007), but not in *A. guariba clamitans* (Chaves & Bicca-Marques, 2016). Depending on the habitat and the sampling effort, diet richness at the group level can range from around a dozen to almost 200 plant species (see revision by Dias & Rangel-Negrín, 2015). We found in a review of studies on brown howler monkeys (*A. guariba clamitans*) along the taxon's distribution that they exploit 402 plant species as food sources. We further estimated that 720 species (±*SD* 157) represent the actual richness for all populations, illustrating the variable diet at the species level (Chaves & Bicca-Marques, 2013; see also Cristóbal-Azkarate & Arroyo-Rodríguez, 2007).

Groups living in forest fragments near human settlements eat fruits from cultivated species (Bicca-Marques & Calegaro-Marques, 1994; Chaves & Bicca-Marques, 2017; Pozo-Montuy et al., 2013) and, more rarely, food supplemented by local people (Back & Bicca-Marques, 2019). Alien, potentially invasive, plant species can be important sources of fruits (e.g., *Psidium guayava* and *Eriobotrya japonica*, Chaves & Bicca-Marques, 2017) and leaves (e.g., *Ceiba speciosa* and *Melia azedarach*; Bicca-Marques & Calegaro-Marques, 1994), thereby compensating for the often lower diversity of native species in small habitat patches (Bicca-Marques & Calegaro-Marques, 1994; Chaves & Bicca-Marques, 2016). Howlers have also been reported to feed on resources found on the ground (Pozo-Montuy & Serio-Silva, 2007; Prates & Bicca-Marques, 2011). However, the most striking example of their dietary plasticity probably comes from a few groups that have been shown to raid wild or domestic bird nests to feed on eggs or nestlings (Bicca-Marques, Muhle, Prates, Oliveira, & Calegaro-Marques, 2009; Bicca-Marques, Silveira, Martins, & Rabelo, 2014).

Under some circumstances, howlers can also take advantage of permanent sources of water available to livestock (Bicca-Marques, 1992). Sources of water and cultivated fruit can be found inside the habitat patch or in the surrounding matrix (Bicca-Marques, 1992; Pozo-Montuy & Serio-Silva, 2007; Pozo-Montuy et al., 2013).

4 | DETERMINANTS OF THE OCCURRENCE OF HOWLER MONKEYS IN FOREST FRAGMENTS

The findings above on the behavior of groups living in small habitat patches can lead to the misinterpretation that howler monkeys can be found in any forest fragment and, therefore, are of least conservation concern. Researchers surveying howler monkeys in forest fragments at the landscape-level have identified factors that influence their occurrence.

Contrasting results have been reported for the importance of metrics concerning the spatial isolation of forest fragments in the matrix, with some authors finding support for it (Boyle & Smith, 2010; Estrada & Coates-Estrada, 1996; Mandujano, Escobedo-Morales, Palacios-Silva, Arroyo-Rodríguez, & Rodríguez-Toledo, 2006; Mandujano & Estrada, 2005; Pozo-Montuy, Serio-Silva, & Bonilla-Sánchez, 2011), while others do not (Anzures-Dadda & Manson, 2007; Arroyo-Rodríguez, Mandujano, & Benítez-Malvido, 2008; Arroyo-Rodríguez, Mandujano, Benítez-Malvido, & Cuende-Fanton, 2007; Cristóbal-Azkarate, Veà, Asensio, & Rodríguez-Luna, 2005; Ribeiro & Bicca-Marques, 2005; Silva & Bicca-Marques, 2013). For example, the proximity of the habitat patch to human settlements, a metric often related to the risk of hunting and selective logging among other anthropogenic influences, has been shown to negatively affect the occurrence of howlers in a Mexican fragmented landscape (Arroyo-Rodríguez et al., 2008), but to have no influence on their occurrence in a south Brazilian landscape (Ribeiro & Bicca-Marques, 2005).

All researchers that have measured the abundance of food resources in forest fragments have concluded that this variable is a critical modulator of howlers' presence (Anzures-Dadda & Manson, 2007; Arroyo-Rodríguez et al., 2007; Cristóbal-Azkarate et al., 2005; Estrada & Coates-Estrada, 1996; Mandujano et al., 2006; Pozo-Montuy et al., 2011; Zunino, Gonzalez, Kowalewski, & Bravo, 2001). However, results on other vegetation metrics often correlated with food availability are controversial: basal area (positive influence: Arroyo-Rodríguez et al., 2007; no influence: Anzures-Dadda & Manson, 2007; Pozo-Montuy et al., 2011), canopy height or mean tree height (positive influence: Pozo-Montuy et al., 2011; no influence: Anzures-Dadda & Manson, 2007; Ribeiro & Bicca-Marques, 2005).

Also related to food availability and a habitat patch's carrying capacity, the influence of fragment size on species occurrence has varied among studies. Authors did not find size differences between occupied and vacant fragments in six studies (Arroyo-Rodríguez et al., 2007; Chiarello, 2003; Estrada et al., 2002; Kowalewski & Zunino, 1999; Ribeiro & Bicca-Marques, 2005; Silva & Bicca-Marques, 2013), but smaller fragments were less likely to be inhabited than larger ones in ten other studies (Anzures-Dadda & Manson, 2007; Arroyo-Rodríguez & Dias, 2010; Arroyo-Rodríguez et al., 2008; Benchimol & Peres, 2015; Benchimol & Venticinque, 2014; Boyle & Smith, 2010; Cristóbal-Azkarate et al., 2005; Gilbert, 2003; Mandujano et al., 2006; Mandujano & Estrada, 2005; Michalski & Peres, 2005). When size mattered and the threshold of habitat suitability was estimated, it was 4.5 ha (Benchimol & Peres, 2015) and 10 ha for *A. macconnelli* (Boyle & Smith, 2010), and 20 ha (Mandujano et al., 2006) and 32 ha (Arroyo-Rodríguez et al., 2008) for *A. palliata*.

5 | MAJOR THREATS TO HOWLER MONKEYS IN FRAGMENTED LANDSCAPES

In addition to resource scarcity, diverse factors can contribute to the extirpation of howler monkeys, particularly from smaller habitat patches immersed in human-altered landscapes. Howlers are killed by domestic dogs and people or are run over by cars when they descend to the ground to cross canopy gaps or to move between discrete habitat patches to feed, or they are electrocuted when they move along power lines (Bicca-Marques & Calegaro-Marques, 1995; Chaves, Fernandes, Oliveira, & Bicca-Marques, 2019; Corrêa, Chaves, Printes, & Romanowski, 2018; Jerusalinsky et al., 2010; Lokschin, Printes, Cabral, & Buss, 2007; Pozo-Montuy & Serio-Silva, 2007; Pozo-Montuy et al., 2011, 2013; Prates & Bicca-Marques, 2008).

While the effects of these factors on population (or metapopulation) viability are often subtle and can take a long time to reach the extreme consequence, namely species extirpation (i.e., extinction debt; Haddad et al., 2015), infectious diseases can also have drastic lethal effects that are perceived in real-time during epizootics (see Estrada et al., 2018). This is the case of African-borne yellow fever (hereafter YF), a recurring threat to howler monkeys, whose susceptibility to the virus has long been known (Balfour, 1914; Collias & Southwick, 1952).

Recent epizootics of sylvatic YF in extra-Amazonian Brazilian biomes (2007–2009 and 2016-at least up to June 2019) have caused the death of large numbers of primates (e.g., Almeida, Santos, Cardoso, Silva et al., 2019; Almeida et al., 2012; Bicca-Marques & Freitas, 2010; Bicca-Marques et al., 2017; Holzmann et al., 2010; Strier et al., 2019). The 2007–2009 epizootic extirpated ca. 80% of the *A. caraya* (Freitas & Bicca-Marques, 2011) and *A. guariba clamitans* (Veiga, Fortes, & Bicca-Marques, 2014) populations in two regions of the southern Brazilian state of Rio Grande do Sul. A similar impact on the *A. guariba clamitans* population of Caratinga in the southeastern Brazilian state of Minas Gerais was recorded during the epizootics that began in 2016 (Possamai, Mendes, & Strier, 2019).

Extirpations in highly fragmented landscapes increase the distance between surviving populations and between those and newly unoccupied habitat patches, thereby further compromising gene flow and recolonization (Freitas & Bicca-Marques, 2011). In the absence of gene flow, there are very low likelihoods of survival in Vortex population viability analyses for some of the remaining populations of *A. guariba clamitans* of the state of Rio Grande do Sul. Additionally, metapopulation recovery to pre-epizootic levels are expected to take more than 100 years even if there is gene flow between the surviving populations and no other YF epizootic during this time (Veiga et al., 2014; see also Agostini et al., 2014; Moreno et al., 2015).

The recognition of the serious consequences of the YF epizootics of the last two decades in Brazil and Argentina on howler monkey populations has informed the revision of the conservation status of *A. guariba clamitans* and *A. caraya*. *Alouatta guariba clamitans* was uplisted from Endangered to Critically Endangered in Argentina (Agostini et al., 2012) and from Near Threatened to Vulnerable in Brazil (Bicca-Marques et al., 2018). Given the estimated and continuing impact of these epizootics on both subspecies, *A. guariba* was included in the 2018–2020 list of the 25 world's most endangered primates (Buss et al., 2019). The conservation status of *A. caraya* was also uplisted from Least Concern to Vulnerable in Argentina (Agostini et al., 2012) and to Near Threatened in Brazil (Ludwig et al., 2015).

6 | THE ROLE OF SMALL HABITAT PATCHES IN AVOIDING OR DELAYING THE EXECUTION OF THE "DEATH SENTENCE"

Recognizing the "lifetime warranty" and "death sentence" dichotomy resulting from partial interpretations of the research findings that we have described above (see Table 1) does not mean that we should devalue the importance of small habitat patches for the conservation of their inhabitants, although it means that we cannot rely on them alone to secure the conservation of a species. Given that habitat fragmentation limits howler monkey dispersal (Oklander, Kowalewski, & Corach, 2010; Oklander, Miño, Fernández, Caputo, & Corach, 2017; see also Calegaro-Marques & Bicca-Marques, 1996), even vacant small habitat patches can decrease the distance between isolated populations by serving as stepping stones and sources of food for dispersing individuals (Bicca-Marques & Calegaro-Marques, 1994; Galán-Acedo et al., 2019b; Pozo-Montuy et al., 2011).

Small populations can also be important sources of uncommon genetic variability (Oklander et al., 2010, 2017) and individuals resistant to YF (Almeida et al., 2016; Almeida, Santos, Cardoso, Noll, et al., 2019). Assuming that the offspring of these individuals inherit resistance and breed either in their natal or in other populations, the proportion of resistant alleles might increase in the metapopulation, potentially promoting the lowering of the impact of future disease outbreaks.

However, given the growing loss and fragmentation of forest ecosystems and the impact of human economic activities on them (Estrada et al., 2017, 2018), the negative influence of land-use changes on the conservation of highly arboreal primates can be much stronger than normally perceived for those species capable of surviving in small habitat patches. Simulations of *A. palliata mexicana* population viability predict a drastic decrease in the number of individuals 30 years after an event of habitat fragmentation and a probability of extinction greater than 60% for populations isolated in <15-ha forest fragments (Mandujano & Escobedo-Morales, 2008). Monitoring data for two African highly arboreal and folivorous primates (*Procolobus rufomitratus* and *Colobus guereza*) show even faster and sharper population declines in small forest fragments. Whereas *C. guereza* populations experienced a reduction of 60% in a period of 15 years, *P. rufomitratus* populations declined by 83% in just 10 years (Chapman et al., 2013). These examples illustrate the concept of extinction lag; that is, the time elapsed between the occurrence of an event that compromises the long-term viability of a given population and its actual extirpation (Jackson & Sax, 2010). The kind and intensity of the disturbance event and the resulting habitat quality, the cultural differences in the way that local people perceive and exploit primates, the inter-patch connectivity and other landscape structuring characteristics that affect dispersal are examples of factors that influence the extinction lag. The extinction lag might explain the differences in the area threshold of habitat suitability mentioned above for *A. macconnelli* and *A. palliata*.

Therefore, restoring and reconnecting small habitat patches to promote metapopulation functioning can increase the odds of the persistence of a species in highly fragmented landscapes (Bonilla-Sánchez et al., 2012; Boyle & Smith, 2010; Chapman et al., 2013; Cristóbal-Azkarate & Arroyo-Rodríguez, 2007; Galán-Acedo et al., 2019b; Mandujano et al., 2006; Marsh et al., 2013; Oklander et al., 2017; Silva & Bicca-Marques, 2013). It is also critical to highlight that primates sometimes represent the largest remaining frugivores of the

TABLE 1 Summary of the main aspects of the behavior and ecology of howler monkeys living in fragmented landscapes supporting the proposed lifetime warranty vs. death sentence dichotomy

Research subject	Finding(s)	References
Use of space	Groups can live in habitat patches as small as 1-ha	1
	Forest fragment size does not predict home range	1
	Forest fragment size predicts home range	2
	Population density has a negative influence on home range	1–2
	Day ranges are quite conservative (often below 1,000 m)	1
	Forest fragment size does not predict day range	1
	Population density, group size, and diet composition affect day range	1
Activity budget	Conservative (resting > feeding~moving > socializing)	3–4
	Fragment size does not predict the activity budget	3
Feeding behavior	Flexible folivorous-frugivorous diet	3, 5–8
	Most folivorous New World monkeys	9
	Variable diet richness that responds to local resource availability	3, 6, 7
	Exploit cultivated and alien species as food sources	10–13
	Exploit cultivated fruit and man-made sources of water in the surrounding matrix	13–15
Determinants of occurrence	The spatial isolation of forest fragments predicts occurrence	16–20
	The spatial isolation of forest fragments does not predict occurrence	21–26
	Abundance of food resources is critical for occurrence	17–18, 20–22, 24, 27
	Fragment size does not influence occurrence	22, 25–26, 28–30
	Fragment size influences occurrence (size threshold variable among studies)	16, 18–19, 21, 23–24, 31–35
Major threats in fragmented landscapes	Dog attacks, roadkills, electrocution and human- or livestock-related infectious diseases	13, 15, 20, 36–45

Sources: [1] Fortes et al. (2015), [2] Cristóbal-Azkarate and Arroyo-Rodríguez (2007), [3] Bicca-Marques (2003), [4] Di Fiore et al. (2011), [5] Bonilla-Sánchez et al. (2012), [6] Chaves and Bicca-Marques (2016), [7] Dias and Rangel-Negrín (2015), [8] Prates and Bicca-Marques (2011), [9] Neville et al. (1988), [10] Bicca-Marques and Calegaro-Marques (1994), [11] Chaves and Bicca-Marques (2013), [12] Chaves and Bicca-Marques (2017), [13] Pozo-Montuy et al. (2013), [14] Bicca-Marques (1992), [15] Pozo-Montuy and Serio-Silva (2007), [16] Boyle and Smith (2010), [17] Estrada and Coates-Estrada (1996), [18] Mandujano et al. (2006), [19] Mandujano & Estrada (2005), [20] Pozo-Montuy et al. (2011), [21] Anzures-Dadda and Manson (2007), [22] Arroyo-Rodríguez et al. (2007), [23] Arroyo-Rodríguez et al. (2008), [24] Cristóbal-Azkarate et al. (2005), [25] Ribeiro and Bicca-Marques (2005), [26] Silva and Bicca-Marques (2013), [27] Zunino et al. (2001), [28] Chiarello (2003), [29] Estrada et al. (2002), [30] Kowalewski and Zunino (1999), [31] Arroyo-Rodríguez and Dias (2010), [32] Benchimol and Peres (2015), [33] Benchimol and Venticinque (2014), [34] Gilbert (2003), [35] Michalski and Peres (2005), [36] Jerusalinsky et al. (2010), [37] Lokschin et al. (2007), [38] Almeida et al. (2012), [39] Almeida, Santos, Cardoso, Silva, et al. (2019), [40] Bicca-Marques et al. (2017), [41] Bicca-Marques and Freitas (2010), [42] Freitas and Bicca-Marques (2011), [43] Holzmann et al. (2010), [44] Possamai et al. (2019), [45] Veiga et al. (2014).

original fauna in these fragmented landscapes (Camaratta, Chaves, & Bicca-Marques, 2017), playing important roles as seed dispersers and promoters of forest regeneration (Bufalo, Galetti, & Culot, 2016; Chaves, Bicca-Marques, & Chapman, 2018).

7 | CONCLUDING REMARKS

In this commentary, our aim was to show that the long-term conservation of howler monkey species is compromised if the need for protection in large tracts of forest is undervalued, particularly given the tolerance of individuals to habitat shrinking. We hope that the reasoning that we presented here stimulates wildlife researchers in general and primatologists, in particular, to continue investigating the factors that modulate the long-term persistence of wild populations in fragmented landscapes. We also hope that our warning helps decision-makers to distinguish between the consequences of the behavioral adaptations at the individual-level from the population- and metapopulation-level processes faced by primates in fragmented landscapes in their conservation assessments.

ACKNOWLEDGMENTS

The authors thank Lisa Gould and Giuseppe Donati for inviting them to contribute to the symposium “Surviving in fragmented landscapes: identifying variables that influence primate population persistence or extirpation in forest fragments” during the XXVII Congress of the International Primatological Society in Nairobi, Kenya, and together with Matthew McLennan to contribute to this special issue. The authors also thank Matthew McLennan and two anonymous reviewers for constructive comments on earlier versions of this paper. The authors thank Stephen D. Nash/IUCN SSC Primate Specialist Group for the permission to use his howler monkey illustration in the graphical abstract. The authors also thank the granting agencies that have supported their field studies, particularly the Brazilian Higher Education Authority (CAPES/Coordenação de Aperfeiçoamento de Pessoal de Nível Superior, PNPD #2755/2010), Brazilian National Research Council (CNPq/Conselho Nacional de Desenvolvimento Científico e Tecnológico, 300439/91-1, 303154/2009-8, 303306/2013-0, 304475/2018-1, 306090/2006-6, 404457/88-6), Rio Grande do Sul Research Foundation (FAPERGS/Fundação de Amparo à Pesquisa do Estado do Rio Grande do Sul, 18/2551-0000243-7, PqG #11/1392-3), World Wildlife Fund-US (6573/1989), and Primate Action Fund/Margot Marsh Biodiversity Foundation/Conservation International, and CNPq and FAPERGS for supporting JCBM participation in the IPS Congress.

This research complies with all ethical and legal guidelines established by the American Society of Primatologists, the appropriate national and institutional standards and guidelines and the Code of Best Practices for Field Primatology of the International Primatological Society and the American Society of Primatologists.

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How to cite this article: Bicca-Marques JC, Chaves ÓM, Hass GP. Howler monkey tolerance to habitat shrinking: Lifetime warranty or death sentence? *Am J Primatol*. 2020;82:e23089. https://doi.org/10.1002/ajp.23089