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Response of a small felid of conservation concern to habitat fragmentation

Mira M. Fleschutz^{1,6} · Nicolás Gálvez^{2,3,4} · Guy Pe'er⁵ ·
Zoe G. Davies⁴ · Klaus Henle⁵ · Elke Schüttler^{2,5}

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Abstract Habitat loss and fragmentation are major drivers of biodiversity loss. A key question, particularly relevant to carnivore conservation, is to which extent species are able to survive in human-modified landscapes. Currently, conservationists are concerned about the impact habitat fragmentation may have on the long-term persistence of the forest-dwelling guíña (*Leopardus guigna*), given the increasingly modified landscapes in which they live. Here we evaluate the effect habitat cover, fragmentation and anthropogenic pressure have on the occupancy probability for guíñas in privately-owned forest fragments. We collected camera-trap data from 100 temperate rainforest sites in Chile and used single-season occupancy modeling to evaluate the influence of 13 parameters of landscape structure/anthropogenic pressure and four parameters of detection probability on the occurrence of guíñas. The camera-trap survey data comprised 4168 camera-trap days and 112 independent records of guíñas. Surprisingly, fragmented (defined as having a high perimeter-to-area ratio) and moderately sized habitat patches best predicted site

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✉ Mira M. Fleschutz
mira_fleschutz@hotmail.com

¹ Department of Geography, Johannes Gutenberg-University Mainz, Johann-Joachim-Becher-Weg 21, 55099 Mainz, Germany

² Fauna Australis Wildlife Laboratory, School of Agriculture and Forestry Sciences, Pontificia Universidad Católica de Chile, Avenida Libertador Bernardo O'Higgins 340, Santiago, Región Metropolitana, Chile

³ Department of Natural Sciences, Centre for Local Development (CEDEL), Pontificia Universidad Católica de Chile, Villarrica Campus, O'Higgins 501, Villarrica, Chile

⁴ School of Anthropology and Conservation, Durrell Institute of Conservation and Ecology (DICE), University of Kent, Canterbury, Kent CT2 7NR, UK

⁵ Department of Conservation Biology, UFZ - Helmholtz Centre for Environmental Research GmbH, Permoserstraße 15, 04301 Leipzig, Germany

⁶ Present Address: Fabristraße 23, 89075 Ulm, Germany

occupancy. Occupancy also increased where habitat patches were closer to continuous forest and nearer to buildings. Our results imply that guíñas can benefit from a high degree of edge type habitats in fragmented landscapes, capable of adapting to habitat fragmentation in the proximity to large continuous forest patches. This suggests that guíñas have a broader niche than previously believed. Additionally, the guíña is tolerant of human infrastructure. Further research is required to identify potential ecological traps, long-term source-sink dynamics, and the habitat loss/fragmentation threshold beyond which guíña populations are no longer viable.

Keywords Camera traps · Chilean temperate rainforest · Edge effects · Forest specialist · Habitat loss · *Leopardus guigna* · Occupancy

Introduction

Land conversion alters ecosystem functioning and threatens biodiversity worldwide (Sala et al. 2000; Foley et al. 2005). In particular, habitat loss and fragmentation are key threats to species with larger territories, such as mammalian carnivores (Sunquist and Sunquist 2001; Crooks 2002). Within this taxonomic group, 44 % of the world's felids currently face high extinction risk as a result of native vegetation decline and retaliatory killing by humans (Treves and Karanth 2003; Macdonald et al. 2010). Habitat destruction decreases the carrying capacity of remnant patches via reductions in den site and prey availability (Riley et al. 2003; Loveridge et al. 2010a) which, in turn, may influence the foraging habits and behavior of species, potentially exposing them to further risks. For instance, vehicle collision mortality (Forman and Alexander 1998; Klar et al. 2009), as well as avoidance of anthropogenic barriers such as roads and railways, can limit dispersal, thus diminishing both genetic diversity and population viability (Riley et al. 2006). Such changes in landscape structure (LS) and behavior may also subject carnivores to different dimensions of human-wildlife conflict (Inskip and Zimmermann 2009). For example, edge effects along the borders of a protected area can generate source-sink population dynamics due to poaching and retaliatory killing (Woodroffe and Ginsberg 1998; Loveridge et al. 2010b).

While habitat loss and fragmentation are often considered to be coupled processes, and are known to correlate strongly, the two processes have distinct origins and clearly divergent landscape patterns (Fahrig 2003; Fischer and Lindenmayer 2007). Furthermore, the impact that the two processes may have on species behavior and occurrence can also differ strongly. While, in general, habitat loss leads to negative effects, species responses to fragmentation per se may be positive, neutral or negative and can lead to edge effects (Murcia 1995; Haddad et al. 2015) provoking varying responses in affected species (Ries et al. 2004). It is therefore imperative to understand how species of conservation concern are likely to be influenced by habitat loss and fragmentation (both in combination and as separate processes) across various pertinent spatiotemporal scales (Ewers and Didham 2006) and in consideration of species' traits and life history (Henle et al. 2004). Recent studies on felids have shown that most species living within human-modified landscapes tend to avoid intensively managed agricultural land and human settlements, preferentially occupying areas with greater remnant habitat coverage or closer proximity to large tracts of native forest, dense understory and water resources (Klar et al. 2008; Sunarto et al. 2012). Nonetheless, species that predate on small rodents, poultry or livestock may be attracted to

settlements, and thus display different spatial distribution patterns and associated risks (primarily poaching and retributive killing) (Kolowski and Holekamp 2006). Due to this risk-prone behavior, such species are likely to be particularly sensitive to fragmentation per se. Detailed information is therefore required, at the right spatial scale, to assess the response of such species to habitat loss versus fragmentation.

Felids are elusive, making them a challenge to research and restricting our knowledge of their habitat requirements and preferences. Non-invasive survey methods, like camera trapping, allow species population dynamics and occurrence to be assessed over large spatial areas (O'Connell and Bailey 2010). Additionally, occupancy modeling statistical techniques can be used to overcome issues associated with low detection probability (MacKenzie et al. 2006). Indeed, estimated site occupancy is an especially useful metric for interpreting wide-ranging and territorial species surveys, where abundances might not be reliable or cannot be calculated due to data scarcity (MacKenzie et al. 2002; O'Connell et al. 2006).

The guña *Leopardus guigna* (Molina, 1782) is one such elusive species and is the smallest felid of the Neotropics (<2 kg; Nowell and Jackson 1996). Its geographical distribution is limited to a narrow belt of habitat in central and southern Chile and Argentina (Napolitano et al. 2015). This forest specialist is closely associated with the Chilean temperate rainforest, declared a biodiversity hotspot (Myers et al. 2000). Since 1996, the guña has been listed as 'Vulnerable' by the IUCN (decreasing population), primarily due to habitat loss and retribution killing following poultry depredation (Napolitano et al. 2015). Only a few studies have been published on this cryptic felid. They suggest that the guña is a forest specialist with preference for native primary forests (Nowell and Jackson 1996; Acosta-Jamett and Simonetti 2004), but that it can also tolerate other habitats like secondary or thicket forest and scrubland (Acosta-Jamett and Simonetti 2004; Freer 2004). In fragmented landscapes, authors have emphasized the important role corridors and small habitat fragments play in maintaining landscape connectivity (Sanderson et al. 2002; Gálvez et al. 2013). However, the response of guñas to fragmentation remains inadequately studied and poorly understood.

In Chile, the National Park system is heavily biased towards high elevation land in the Andes (>800 m asl), leading to insufficient protection of lowland habitats and, consequently, the native carnivore species that reside in such areas (Simonetti and Mella 1997). Conservation in lowland areas therefore requires collaboration with private landowners (Simonetti and Acosta 2002; Kinnaird and O'Brien 2012) to limit deforestation, improve land/livestock management and curtail retribution killing (e.g. Silva-Rodríguez et al. 2007; Herrmann et al. 2013). Identification of the key parameters that influence the occurrence of this endangered felid will help conservationists to develop more effective interventions for the guña, as well as providing valuable lessons germane to other forest-dwelling carnivores inhabiting fragmented landscapes.

The aim of this paper is to further our understanding of guña responses to habitat fragmentation and anthropogenic pressures within human-modified landscapes. We selected potential predictor variables for our candidate models of occupancy (ψ) and detection probability (p) guided by premises based on landscape structure (LS) and anthropogenic pressure (AP). Candidate models were structured to evaluate previous knowledge that suggests that guñas are forest specialists, require sources of water and can tolerate habitat fragmentation and AP to some extent. Moreover, to differentiate between effects of fragmentation per se and habitat loss on the site occupancy of this species, we examine a suite of new fragmentation parameters. We use landscape scale sample units (buffers), which take into consideration both remnant habitat patch variables and the

surrounding matrix, to improve our understanding of the species' needs along environmental gradients and scales.

Methods

Study area

The study area is located in the pre-Andean zone in the Araucanía district of Chile (39°10'–39°24'S, 72°06'–71°30'W; Fig. 1) within the UNESCO Biosphere Reserve Araucarias (UNESCO 2010). The southern subspecies of the guña (*L. g. guigna*), which is morphologically different from its northern counterpart (*L. g. tigrillo*), is found across this region (Napolitano et al. 2014). The climate is humid-temperate with an average annual precipitation of 2000 mm (Di Castri and Hajek 1976). The native vegetation is dominated by deciduous southern beech forest (*Nothofagus* spp.) with a distinct understory layer characterized by bamboo thickets (*Chusquea quila*) (Luebert and Pliscoff 2006). Since humans colonised the region in the 20th century, the area of native forest has diminished considerably as a result of exploitation and agriculture (Bustamante and Castor 1998); only 37 % of the original cover remains in the lowlands of the study area (<600 m asl) (Fig. 1). The narrow valleys consist of a matrix of extensively used pasture and remnant forest habitat patches of varying sizes and shapes, exposed to different stages of forest degradation (Jaña-Prado et al. 2007; Rojas et al. 2011). To fulfill the objectives of this study, we restricted our survey area to private properties outside protected areas at elevations below 600 m asl.

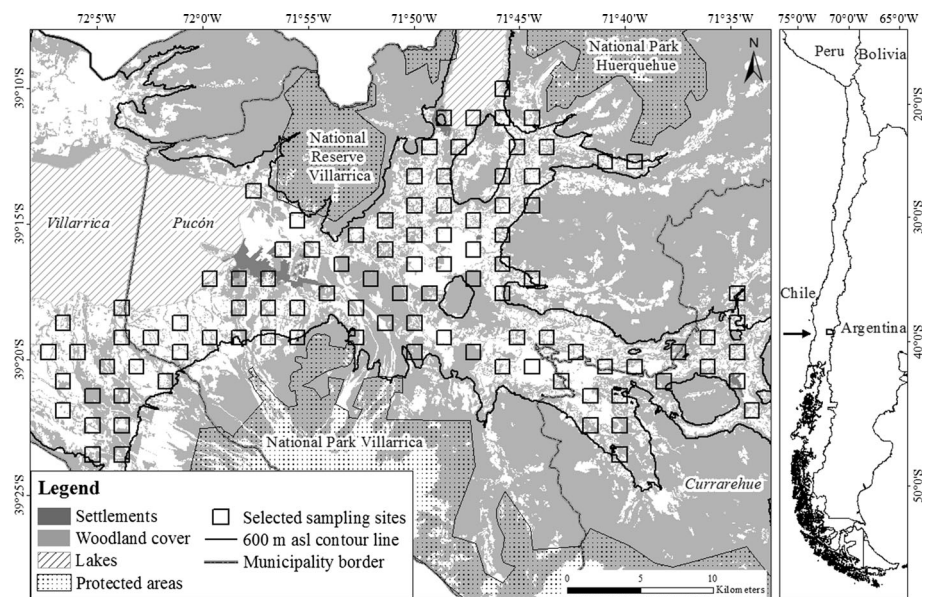


Fig. 1 Study area and sampling sites within the municipalities of Pucón, Villarrica and Curarrehue. White areas within the municipality boundaries represent non-forested land (e.g. pastures, plantations, snow and old lava streams)

Sampling design and data collection

For carnivores in general, and the guiña in particular, camera trap detection probabilities are often at the limit of their reliability ($p < 0.15$, Linkie et al. 2007; Gálvez et al. 2013). We therefore employed a simulation framework for occupancy studies (Guillera-Arroita et al. 2010) to inform survey effort allocation, in terms of number of sites and sampling occasions necessary to ensure the statistical precision of parameters. Occupancy and detection probability parameter estimates for the guiña were taken from Gálvez et al. (2013); in the simulations we used $\psi = 0.48$ and five values for detection ($p = 0.13, 0.20, 0.25, 0.30, 0.40$), setting the precision of both parameters at $SE = 0.075$ and 10,000 iterations. The framework indicated that a sampling effort of between 80 and 180 sites and 5–15 sampling occasions were required across a single-season.

Table 1 Summary of all potential predictor variables for occupancy (ψ) and detection probability (p)

Predictor variables	Abbreviation	Variable description
ψ, p		
Landscape structure (<i>LS</i>)		
Percent of woodland cover	Woodland cover	Percent of woodland (habitat) cover
Mean patch area ^a	PatchArea	Mean patch area of the habitat cover class
Landscape shape index	Fragmentation	Perimeter-to-area ratio of the habitat cover class
Number of patches ^a	NumPatch	Number of patches of the habitat cover class
Patch cohesion ^a	PatchCohesion	Physical connectedness of habitat cover by measuring it's aggregation of patches
Density of hydrology	DensHydro	Total length of rivers, streams and creeks
Distance to water	DistWater	Distance to next river, stream, creek or lake
Distance to meadow	DistMeadow	Distance to the next habitat edge bordering meadow
Distance to continuous habitat ^b	DistContinuousforest	Distance to continuous habitat (habitat cover >200 ha)
Anthropogenic pressure (<i>AP</i>)		
Density of roads	DensRoad	Total road length, independent of road type or cover
Distance to roads	DistRoad	Distance to next paved-, gravel-, or dirt road
Density of buildings	DensBuild	Number of buildings (inhabited and uninhabited)
Distance to buildings	DistBuild	Distance to the next building (inhabited and uninhabited)
p		
Bamboo presence	Bamboo	Amount of bamboo present at a site (four categorical classes)
Density of understory	Understory	Increasing shrub density (four categorical classes)
Rotation	Rotation	4 consecutively sampled subregions
Julian Date	JulianDate	Time specific variable (start date 01.01.2012)

^a Variables that were excluded in the modeling analysis due to strong correlations (r or $\rho > 0.71$);

^b Distance to continuous forest was set to zero (distance = 0) if the detection device was located within a continuous habitat

To maximize precision and detection probability within our logistical constraints, we randomly chose a total of 100 independent sites (Fig. 1) from across a grid of 100 ha cells (1 km²) covering the study area. To ensure site independence, neighboring cells could not be selected. This yielded 400 ha sample units (i.e. the selected site, plus half of each neighboring cell buffer), which are equivalent to the average home range documented for the species in the study area (MCP 95 % = 270 ± 137 ha, Schüttler et al. unpublished data).

Sites were monitored within a 90 day closed season from February to May 2012 with four subsequent rotations of 25 sites. Ninety days was considered as a closed season because the number of individuals in occupied sites should not vary across this period as juveniles disperse later in the year. Each site was monitored for at least 20 days using two camera traps (Bushnell Outdoor Products, Overland Park, KS, USA) and two hair snares (wooden rub stations, Hupe and Simon 2007). The 20 days ensured that an adult guiña could travel across the entire home range (Schüttler et al. unpublished data). Camera traps were fixed to trees 20 cm above ground to produce horizontal captures of the species (Kays and Slauson 2011). To improve detection probability, we placed Hawbakkers Wildcat Lure #2 as well as catnip leaves and spray (*Napeta cataria*) in front of each camera trap and on every hair snare. The camera traps and lures were checked twice (every 5–10 days) while they were deployed in the field. The detection histories of both cameras at each site were pooled and reduced from 20 to 11 sampling occasions by collapsing data into 2-day blocks (Gálvez et al. 2013).

At each site, we categorically estimated bamboo presence and understory density within visible distance around the cameras, and then pooled the values for each site. Coordinates of all detection devices were recorded with Garmin® eTrex HC GPS units. Collected hair samples were identified using light microscopy to classify the cuticular and medullar pattern of guard hairs (following the protocol of González-Esteban et al. 2006).

Cartographic basis and scales

We used 1:40,000 scale aerial images from 2007 (SAF 2007). Shapefiles (scale 1:10,000, LPT-UCT 2009) provided information on positioning of rivers and lakes, buildings, infrastructure, elevation data and land-use cover. All woody vegetation types that are known to be suitable habitat for the guiña (Nowell and Jackson 1996; Sanderson et al. 2002; Freer 2004) were pooled into a single 'woodland cover' class. Landscape scale metrics (Table 1) were measured within circular buffers centered on the midpoint between the two cameras at each site (see also Boscolo and Metzger 2009; Rhodes et al. 2009). Occupancy patterns, however, may be explained by factors acting at multiple spatial scales (Turner 1989; Šímová and Gdulová 2012). We therefore extracted and compared variables (see below and Table 1) at several spatial extents, using nested buffers of 50, 100, 200 and 300 ha. Prior to modeling, the number of buffers was reduced based on correlations and the Wilcoxon rank sum test. The largest buffer size (300 ha) is equivalent to the average home range area of the guiña in this region (MCP 95 % = 270 ± 137 ha; Schüttler et al. unpublished data). Distance metrics were measured from the camera midpoint per site. Site selection, the preparation of shapefiles and extraction of landscape metrics were all conducted using ArcGIS 10.0 (ESRI 2011) and FRAGSTATS 4.1 (McGarigal et al. 2012).

Candidate models and covariates

Potential predictor variables effecting occupancy (ψ) and detection probability (p) were classified as relating to *LS* or *AP* (Table 1). We fitted p with all variables selected for ψ and

two additional variables to account for sampling specific effects: (1) rotation for each of four consecutively sampled subregions; and, (2) Julian Date as a time-specific variable to test for effects of the ongoing sampling season (Sarmiento et al. 2011). We included two micro-scale variables under the assumptions that guíñas prefer habitats with: (1) bamboo thickets and (2) dense understory for shelter and/or hunting (Nowell and Jackson 1996; Sanderson et al. 2002; Simonetti et al. 2013).

Data preparation

Prior to beginning the occupancy modeling, we explored outliers and redundancy between the different environmental variables and across scales (50/100/200/300 ha buffers). We assessed associations between variables with Pearson's (r) and Spearman's rank (ρ) correlation coefficients. Where two variables were significantly correlated (r or $\rho > |0.7|$), the one with less direct biological meaning for the guíña (mean patch area, number of patches and patch cohesion) was removed from all subsequent analyses. We considered the landscape shape index ('fragmentation') as a measure of fragmentation per se, because of its high correlation with number of patches ($\rho = 0.75$) and only a moderate correlation with percent of woodland cover ($r = -0.51$; Fig. 2). Habitat fragmentation, as measured by the landscape shape index, accounts for an increase in habitat patch edge length (McGarigal and Marks 1995). At the landscape level this implies a higher proportion of edge habitat relative to the core habitat and total fragment area (Ewers and Didham 2006). We applied Wilcoxon rank-sum tests to identify scale effects associated with the predictor variables at each buffer size, regarding binary presence absence data of the guíña, but results were not significant (all $\alpha < 0.05$). The predictor variables were highly correlated between all nested buffer scales (r or $\rho > 0.6$). As such, we only retained the 300 ha landscape scale dataset (i.e., largest buffer size) in the analyses. There was no spatial autocorrelation among sampling sites and presence/absence data of the guíña (Moran's I : 3000 m: $I = -0.03$ ($\alpha = 0.74$); 5000 m: $I = -0.02$ ($\alpha = 0.78$); 10,000 m: $I = -0.02$ ($\alpha = 0.67$)). Variables that were not normally distribution were transformed to z-scores prior to occupancy modeling. All statistical calculations were performed using either R 2.14.1 (R Development Core Team 2008) or SPSS 19 v (IBM 2010).

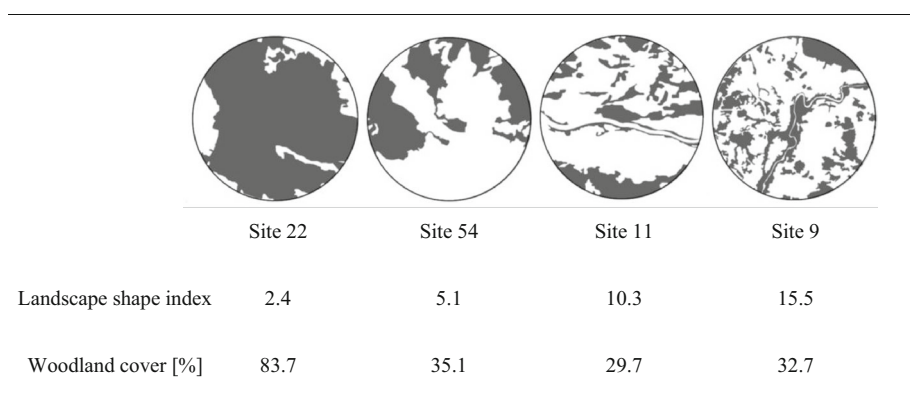


Fig. 2 Four illustrative sampling sites (300 ha) within the survey area, along with their corresponding landscape shape index (a proxy for fragmentation per se) and woodland cover values

Model construction

To estimate site occupancy, we fitted single-species single-season occupancy models with a logistic link structure (MacKenzie et al. 2002, 2006), based on the maximum likelihood method. We used a two-step approach (e.g. Reeves et al. 2010) to determine the best fitting model for ψ and p . First, we ran univariate models with only one predictor variable in separate candidate model sets for p , LS and AP . Second, multivariate models (two- and three-factor models) were constructed by combining each of the best-ranked ($\Delta\text{AICc} < 2$) univariate (and later two-factor) models with each remaining predictor variable for LS , AP and p respectively [e.g. $p(\text{best ranked variable} + \text{combination of remaining covariates})$]. Best ranked univariate models were also included in the multivariate model set. Candidate models for LS and AP were only run with the best predictor variables for p (determined with constant ψ). This approach was considered necessary due to the high number of potentially important predictive variables ($n = 17$ with $n = 100$ histories).

We ranked the candidate models according to Akaike's Information Criterion with a bias adjustment for small sample size (AICc) (Johnson and Omland 2004; Burnham and Anderson 2010). We treated all models within 2 ΔAICc units of the most parsimonious as equally plausible and with substantial support, whereas models with $2 < \Delta\text{AICc} < 4$ were defined as receiving moderate support. We selected the best model using Akaike weights (w). In the multivariate model sets, the relative importance of each predictor was determined by summing the Akaike weights (w) of each model ($\Delta\text{AICc}/\text{QAICc} < 4$) that contained the variable in question (w_+ ; Burnham and Anderson 2010). Model averaged parameter estimates of $\hat{\psi}$ and \hat{p} were derived from all models with $\Delta\text{AICc}/\text{QAICc} < 4$ of the multivariate model set. The precision of estimated parameters ($\hat{\psi}$ or \hat{p}) was obtained via the coefficient of variation (calculated as $\widehat{\text{SE}}/\hat{\psi} \times 100$; MacKenzie et al. 2006; Linkie et al. 2007). Estimated covariate beta coefficients ($\hat{\beta}$) were used to explore the direction of predictor impacts on $\hat{\psi}$ and \hat{p} . We used the goodness of fit test (MacKenzie et al. 2004) to assess global model fit (containing the whole set of LS or AP variables respectively) in each multivariate model set and to account for overdispersion in model selection procedures. Adjustments for overdispersion were made using quasi likelihood QAICc for model ranking. Models with convergence problems were eliminated from model sets. All occupancy modeling was conducted in PRESENCE 5.8 (Hines 2006).

Results

The camera trap survey recorded 112 independent photo sequences of the guiña. Overall, we detected guiñas in 54 % of sites resulting in a naïve occupancy estimate (i.e. not accounting for detection probability) of $\psi_{\text{naïve}} = 0.54$. Hair traps proved to be ineffective for the detection of the guiña, confirming its presence in only one sample unit.

Detection probability

Detection probability p ranged between 0.11 and 0.14 and was best described (i.e. substantial support) by understory density and landscape shape index ($\Delta\text{AICc} < 2$) in both the univariate and multivariate model sets (Table 2). Guiñas were better detected where the understory was more dense ($\beta_1 = 0.36$, $\text{SE} = 0.14$) and habitat fragmentation was greater

Table 2 Summary of model selection ($\Delta AICc$ values <4) for detection probability (\hat{p}) and occupancy ($\hat{\psi}$) estimates in univariate and multivariate models

	AICc	$\Delta AICc$	w_i	K	$\hat{\psi}$ (SE)	\hat{p} (SE)	Precision (%)	
							$\hat{\psi}$	\hat{p}
Univariate models								
$\psi(\cdot), p(\text{Understory})$	637.94	0.00	0.42	3	0.73 (0.08)	0.12 (0.02)	10.96	16.67
$\psi(\cdot), p(\text{Frag})$	639.21	1.27	0.22	3	0.71 (0.07)	0.13 (0.02)	9.86	15.38
$\psi(\cdot), p(\text{JulianDate})$	641.01	3.07	0.09	3	0.73 (0.08)	0.14 (0.02)	10.96	14.29
$\psi(\cdot), p(\text{Woodland})$	641.67	3.73	0.07	3	0.69 (0.07)	0.13 (0.02)	10.14	15.38
Multivariate model set								
$\psi(\cdot), p(\text{Understory} + \text{Frag})$	635.85	0.00	0.24	4	0.74 (0.08)	0.12 (0.02)	10.52	12.62
$\psi(\cdot), p(\text{Understory} + \text{JulianDate})$	636.93	1.08	0.14	4	0.77 (0.09)	0.11 (0.02)	11.52	13.45
$\psi(\cdot), p(\text{Understory})$	637.94	2.09	0.08	3	0.73 (0.08)	0.12 (0.02)	10.97	12.91
$\psi(\cdot), p(\text{Understory} + \text{DistRoad})$	638.32	2.47	0.07	4	0.74 (0.08)	0.12 (0.02)	10.79	12.79
$\psi(\cdot), p(\text{Frag} + \text{Bamboo})$	638.44	2.59	0.06	4	0.72 (0.07)	0.13 (0.02)	10.30	12.45
$\psi(\cdot), p(\text{Frag} + \text{JulianDate})$	638.70	2.85	0.06	4	0.74 (0.08)	0.12 (0.02)	11.02	13.15
$\psi(\cdot), p(\text{Understory} + \text{DensRoad})$	638.78	2.93	0.05	4	0.73 (0.08)	0.12 (0.02)	10.90	12.92
$\psi(\cdot), p(\text{Understory} + \text{Bamboo})$	638.82	2.97	0.05	4	0.73 (0.08)	0.12 (0.02)	10.93	12.97
$\psi(\cdot), p(\text{Understory} + \text{Woodland})$	638.96	3.11	0.05	4	0.72 (0.08)	0.12 (0.02)	10.73	0.13
$\psi(\cdot), p(\text{Frag})$	639.21	3.36	0.04	3	0.71 (0.07)	0.13 (0.02)	10.41	13.05
$\psi(\cdot), p(\text{Understory} + \text{DensHydro})$	639.32	3.47	0.04	4	0.73 (0.08)	0.12 (0.02)	10.95	12.94
$\psi(\cdot), p(\text{Frag} + \text{DistBuild})$	639.42	3.57	0.04	4	0.74 (0.08)	0.12 (0.02)	10.80	12.95
$\psi(\cdot), p(\text{Understory} + \text{DensBuild})$	639.74	3.89	0.03	4	0.73 (0.08)	0.12 (0.02)	10.97	13.00
$\psi(\cdot), p(\text{Frag} + \text{DistRoad})$	639.77	3.92	0.03	4	0.72 (0.07)	0.13 (0.02)	10.26	12.40
		Model average			0.74 (0.08)	0.12 (0.02)		

Occupancy was held constant $\psi(\cdot)$ in all models to fit detection probability. $\Delta AICc$ indicates the distance to the lowest AICc, w_i the model weight, K the number of parameters, SE the standard errors and % the precision of parameters. The covariate abbreviations are given in Table 1

Table 3 Summary of model selection ($\Delta AICc$ values <4) for landscape structure univariate and multivariate model estimates of occupancy (\hat{p}) and detection probability (\hat{p})

Univariate model set	AICc	$\Delta AICc$	w_i	K	\hat{p} (SE)	Precision (%)	
Univariate model set							
ψ models, p (Understory + Frag)							
ψ (Woodland)	632.97	0.00	0.41	5	0.13 (0.04)	5.67	
ψ (Frag)	633.46	0.49	0.32	5	0.14 (0.05)	7.38	
ψ (.)	635.85	2.88	0.10	4	0.11 (0.04)	10.81	
ψ (DistMeadow)	636.46	3.49	0.07	5	0.12 (0.04)	10.53	
Multivariate model set							
		QAICc	$\Delta QAICc$	w_i	K	\hat{p} (SE)	Precision (%)
ψ models, p (Understory + Frag)							
ψ (Woodland)		252.26	0.00	0.17	5	0.13 (0.04)	9.13
ψ (Frag)		252.45	0.19	0.16	5	0.14 (0.05)	11.89
ψ (Frag + DistContinuousforest)		253.69	1.43	0.08	6	0.11 (0.02)	9.30
ψ (Woodland + DistWater)		254.22	1.96	0.06	6	0.11 (0.02)	10.59
ψ (Woodland + DistContinuousforest)		254.30	2.04	0.06	6	0.12 (0.02)	13.75
ψ (Woodland + DensHydro)		254.49	2.23	0.06	6	0.11 (0.02)	10.59
ψ (Woodland + Frag)		254.49	2.23	0.06	6	0.11 (0.02)	16.09
ψ (Woodland + DistMeadows)		254.53	2.27	0.05	6	0.11 (0.02)	11.76
ψ (Frag + DensHydro)		254.61	2.35	0.05	6	0.11 (0.02)	10.11
ψ (Frag + DistMeadows)		254.61	2.35	0.05	6	0.11 (0.02)	8.99
ψ (Frag + DistWater)		254.66	2.40	0.05	6	0.11 (0.02)	12.64
ψ (Frag + DistContinuousforest + DistMead)		255.44	3.18	0.03	7	0.11 (0.02)	6.90
ψ (Frag + DistContinuousforest + Woodland)		255.74	3.48	0.03	7	0.11 (0.02)	17.89
ψ (Frag + DistContinuousforest + DistWater)		255.94	3.68	0.03	7	0.11 (0.02)	10.47
ψ (Frag + DistContinuousforest + DensHydro)		256.05	3.79	0.03	7	0.11 (0.02)	9.20
ψ (Woodland + DistWater + DensHydro)		256.07	3.81	0.03	7	0.11 (0.02)	15.15
			Model average			0.12 (0.03)	

Variables for detection probability were the same in all models: p (density of understory + fragmentation). $\Delta AICc$ indicates the distance to the lowest AICc, w_i the model weight, K the number of parameters, SE the standard errors and % the precision of parameters. Multivariate models were corrected for overdispersion (QAICc). The covariate abbreviations are given in Table 1

($\beta_1 = -0.12$, $SE = 0.05$). Summed model weights in multivariate models ($\Delta AICc < 4$) were 0.76, 0.48 and 0.20 for understory density, landscape shape index and Julian Date respectively. Based on these outcomes, we selected the additive model p (Understory + Fragmentation) as the only model to fit detection probability in occupancy models.

Occupancy

Accounting for detection probability raised the naïve occupancy estimate to 74 % of occupied sites ($\hat{\psi} = 0.74$ without variable effect). Landscape structure ($\hat{\psi} > 0.86$ model average) had a larger impact on $\hat{\psi}$ in candidate model sets compared to AP ($\hat{\psi} > 0.74$).

Landscape structure

The effect of *LS* on occupancy was best described (i.e. $\Delta AICc < 2$) by the landscape shape index and woodland cover (Table 3). Summed weights of top ranked variables in $\Delta AICc < 4$ multivariate models provide further evidence in favor of fragmentation ($w_i = 0.57$) and woodland cover ($w_i = 0.52$), followed by distance to continuous forest ($w_i = 0.26$) and distance to water ($w_i = 0.17$). Distance to meadows and density of hydrology ($w_i = 0.16$) only received moderate support ($\Delta AICc > 2$). Guiñas occupied sites with higher fragmentation (higher perimeter-to-area ratio; $\beta_1 = 0.85$, $SE = 0.56$), less amount of woodland cover ($\beta_1 = -0.08$, $SE = 0.03$), but closer to continuous forest ($\beta_1 = -0.81$, $SE = 0.46$). For all variables the direction of $\hat{\beta}$ was consistent in all models.

Anthropogenic pressure

In the univariate models, distance to buildings received the highest weight ($w = 0.37$) followed by density of buildings ($w = 0.16$, Table 4). Summed weights of top ranked variables in $\Delta AICc < 4$ multivariate models showed evidence in favor of distance to buildings ($w_i = 0.43$) and density of buildings ($w_i = 0.17$). Both distance and density of roads had similar weights ($w_i = 0.08$ and $w_i = 0.9$ respectively) but received only moderate support ($\Delta AICc > 3$). Guiña site occupancy was higher close to buildings ($\beta_1 = -0.53$, $SE = 0.33$) and where density of buildings was grater ($\beta_1 = 0.42$, $SE = 0.63$), although large standard errors indicate that their effects are uncertain.

Precision of the $\hat{\psi}$ and \hat{p} estimates was good for all top ranked models in all candidate model sets, never exceeding 20 % (Tables 2, 3, 4; Bailey et al. 2004; Linkie et al. 2007). The goodness-of-fit test indicated some degree of overdispersion for the *LS* ($\hat{c} = 2.6$, $\alpha = 0.05$, bootstrap = 10,000) and *AP* ($\hat{c} = 1.9$, $\alpha = 0.09$) multivariate model sets.

Discussion

Our study provides new insights into the response of a vulnerable felid to habitat fragmentation and human pressures. The results show that the guiña is able to tolerate at least moderate levels of habitat loss and fragmentation, and is far more likely to occupy fragmented landscapes than had been documented previously. Indeed, the species occupied a large proportion of sites (>86 %; *LS* model averages) across the human-modified landscape. Nonetheless, we need to be cautious in how these findings are interpreted as occupancy probabilities are not necessarily robust proxies for abundance (Efford and

Table 4 Summary of model selection ($\Delta AICc$ values <4) for anthropogenic pressure, univariate and multivariate model estimates of occupancy ($\hat{\psi}$) and detection probability (\hat{p})

Univariate model set	AICc	$\Delta AICc$	w_i	K	$\hat{\psi}(SE)$	$\hat{p}(SE)$	Precision (%)
ψ models, p (Understory + Frag)							
ψ (DistBuild)	634.68	0.00	0.37	5	0.75 (0.07)	0.13 (0.05)	9.39
ψ (.)	635.43	0.75	0.25	4	0.74 (0.08)	0.11 (0.04)	10.52
ψ (DensBuild)	636.41	1.73	0.16	5	0.73 (0.08)	0.12 (0.04)	10.96
ψ (DensRoads)	636.94	2.26	0.12	5	0.73 (0.08)	0.12 (0.04)	10.96
ψ (DistRoads)	637.43	2.75	0.09	5	0.74 (0.08)	0.11 (0.04)	10.81
Multivariate model set	QAICc	$\Delta QAICc$	w_i	K	$\hat{\psi}(SE)$	$\hat{p}(SE)$	Precision (%)
ψ models, p (Understory + Frag)							
ψ (.)	340.86	0.00	0.40	4	0.74 (0.11)	0.11 (0.05)	14.87
ψ (DistBuild)	341.68	0.82	0.26	5	0.75 (0.10)	0.13 (0.06)	13.26
ψ (DensBuild)	342.59	1.73	0.17	5	0.73 (0.11)	0.12 (0.06)	15.09
ψ (DistBuild + DensRoads)	343.93	3.07	0.09	6	0.76 (0.15)	0.12 (0.03)	19.74
ψ (DistBuild + DistRoad)	344.00	3.14	0.08	6	0.75 (0.15)	0.12 (0.03)	20.00
$c\text{-hat} = 1.9$							
					Model average	0.74 (0.11)	0.12 (0.05)

Variables for detection probability were the same in all models: p (density of understory + fragmentation). $\Delta AICc$ indicates the distance to the lowest AICc, w_i the model weight, K the number of parameters, SE the standard errors and % the precision of parameters. Multivariate models were corrected for overdispersion (QAICc). The covariate abbreviations are given in Table 1

Dawson 2012). Detection probability increased with greater understory density, which one might hypothesis because it is likely to provide the guiña with prey and shelter (e.g. Dunstone et al. 2002; Sanderson et al. 2002). We found that occupancy was impacted by LS rather than the AP evaluated, and was best explained by woodland cover and habitat fragmentation per se. Surprisingly, guiña occupancy was higher in areas characterized by lower habitat cover and greater edge area (i.e. high geometric complexity of fragments), but also closer proximity to continuous forest (>200 ha). In the existing literature, guiñas have been described as using forest fragments as small as 20–40 ha, but with the amount of surrounding native forest playing an important role (Gálvez et al. 2013). While Acosta-Jamett and Simonetti (2004) considered the species to be a forest specialist, we suggest that it is actually forest dependent but with a broader habitat niche than previously assumed.

The capacity of guiñas to use fragmented landscapes may arise due to several factors. First, fragments of various age, size, structure and shape can form a mosaic of qualitatively different habitat across the landscape, thereby supporting greater habitat heterogeneity and structural complexity (Murcia 1995; Jaña-Prado et al. 2007). In turn, the landscape is likely to sustain higher species diversity and may provide additional resources for the guiña (Law and Dickman 1998; Tscharnke et al. 2005). The felid is probably attracted to habitat edges because they provide greater food availability, with small mammal abundances being larger (Kelt 2000; Jaña-Prado et al. 2007; Šálek et al. 2010) and the main prey for the species (Freer 2004; Delibes-Mateos et al. 2014). In the temperate rainforests of Chile, forest edges are often composed of dense and shrubby vegetation with early succession stages of native and exotic species (Díaz et al. 1999; Donoso et al. 2003). Simonetti et al.

(2013) demonstrated that well-developed understory cover is key to maintaining guiña population persistence within plantations. Finally, the fragmented remnant forest patches are probably well connected from the guiñas' perspective across the landscape. The region is characterized by large tracts of forest (>10,000 ha) which are legally protected up in the mountain ranges, but extend down into the narrow agricultural valleys as long slender remnant areas. These remaining natural corridors might serve as connecting elements between intact contiguous forests and habitat fragments within the agricultural matrix (Acosta-Jamett et al. 2003; Gálvez et al. 2013). As a result, 91 % of our sampling sites were less than 1000 m away from corridors connected with continuous forest tracts, equating to the radius of an average guiña home range. Furthermore, substantial areas of woodland cover (>200 ha) persist in the lowland areas, particularly along rivers and streams, forming complex spatial structures with the habitat patches having high edge-to-area ratios. These steep and narrow forested ravines within the agricultural matrix facilitate guiña movement (Sanderson et al. 2002), even in heavily fragmented landscapes (Gálvez et al. unpublished data). Additionally, this type of landscape occurs along the entire gradient of temperate forest of southern Chile and is thus representative of the landscape conditions where the species largely occurs. That said one must consider that fragmentation effects may be masked by environmental variables which were not measured as part of this study, including slope or elevation (e.g. Sunarto et al. 2012; Ewers and Didham 2006). These topographic variables were not considered in this paper as we wished to minimize the number of parameters to enhance model inference.

The high estimated occupancy in fragmented sites should not be interpreted as a habitat preference for the guiña, or as it being beneficial for the population dynamics of the species. Species existing in fragmented landscapes may exhibit higher site occupancy because they are restricted to smaller areas of suitable habitat, resulting in higher activity-density. Considered from a metapopulation-perspective, connectivity between continuous and fragmented forest may result in source-sink dynamics (Pulliam 1988). If this is the case in our study area, vacant territories might be occupied by new individuals originating from the protected areas surrounding the agricultural lands. The potential attraction of guiñas to human-dominated areas may even represent a true ecological trap (Delibes et al. 2001). This is especially true if the benefits of occupying fragmented habitats close to habitat edges or human settlements bear high costs for the guiñas via increased mortality and/or competition (i.e. by interference and or resource use) due to road kills, retribution killings or the presence of foxes, domestic dogs and cats (Gálvez 2010). Such dynamics are known among other predators, leading to direct conflicts with humans (e.g. lions, leopards and bears; Loveridge et al. 2010b; Northrup et al. 2012).

We found guiñas respond positively to anthropogenic pressures, such as proximity to and density of human infrastructure, although the magnitude of the effect was uncertain. These results concur with the positive relationship between detection probability and distance to inhabited houses reported by Gálvez et al. (2013) for the species. Sanderson et al. (2002) also reported that two radio-tracked males were attracted to houses with free ranging poultry, probably due to prey availability in the form of free ranging chickens and/or rodents, caused by agricultural activities and rubbish tipping. Nonetheless, our study indicates that guiña occupancy is primarily influenced by landscape structure rather than by the anthropogenic variables we evaluated.

From a methodological perspective, our study demonstrates the value of non-intensive camera trap surveys of elusive, rare and wide-ranging species that would otherwise need to be assessed/monitored using cost- and time-intensive approaches such as telemetry. However, despite our rigorous sampling, the detection probability was still below $p = 0.15$

which is defined as critical for a given candidate model (MacKenzie et al. 2002). The modeling results must therefore be deciphered with caution as the low detection probability may bias the accuracy of the occupancy estimates (MacKenzie et al. 2002).

While our research indicates that the guiña is more capable of existing in fragmented habitats than previously believed, future research should focus on medium and long-term temporal changes in occupancy to fully understand the population dynamics of the species within agricultural landscapes. Potential sinks or ecological traps should be identified by assessing mortality, reproduction and dispersal capacities of the species in continuous versus fragmented habitats. Areas characterized by very high fragmentation and minimal woodland cover (<20 %) should be included to identify potential thresholds for guiña occupancy, as well as teasing apart the interplay between habitat loss, fragmentation per se and edge effects. Such information is crucial not only for felid conservation, but biodiversity science more broadly (Fahrig 2003; Fischer and Lindenmayer 2007).

From a conservation standpoint, our study should not be perceived as a green light for continued fragmentation of the temperate rainforests of Chile. Our study confirmed that guiñas are not restricted to protected areas or contiguous forests (Sanderson et al. 2002; Gálvez et al. 2013) and, as first shown here, can even benefit from a high availability of edge type habitats in fragmented landscapes. The threatened guiña persists on private land and is therefore highly dependent on management decisions made by landowners. Incentives should be given to landowners for shutting up their poultry at night, which should prevent the species from being drawn into settlements. Moreover, we advocate that forest fragments, and their associated understory, should be retained, especially along creeks and rivers to provide the felid with shelter, food resources and movement conduits within the landscape. These interventions could enhance substantially the long-term viability of the forest-dependent guiña, allowing them to co-exist alongside people in agricultural areas.

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