



Original investigation

## Habitat use and sensitivity to fragmentation in America's smallest wildcat

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### ABSTRACT

Fragmentation and human-wildlife conflicts represent severe threats to wildcats such as the kodkod cat (*Leopardus guigna*), endemic to the heavily impacted Chilean temperate rainforest. Here we assess to which extent this vulnerable forest specialist is able to use altered habitat (agricultural matrix, forest edge, human presence) by studying its home ranges, habitat use, and patch selection in privately owned rainforest remnants. We radio-tracked five individuals over 33–376 days. Mean 95% kernel home ranges were 623 ha, with a mean 50% core area of 191 ha. Ecological-niche and Mahalanobis distance factor analysis confirmed forest-dependency and revealed that the individuals made intensive use of forest edges, close to water. They did not avoid houses. Generalized linear mixed models showed that the monitored kodkods selected elongated woodland patches. We conclude that the kodkods compensated the non-forest space by maintaining larger home ranges and making efficient use of forest edges probably due to higher prey availability. Future studies should identify ecological traps, and describe connectivity and source-sink dynamics in the agricultural matrix to develop long-term conservation efforts for the smallest cat of the Americas.

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### Introduction

The response by predators to fragmentation of their habitat deserves special interest as they have a crucial role in ecosystem functioning. Mammalian carnivores are sensitive to landscape change due to their large ranges, low numbers, slow population growth rates, and direct persecution by humans (Cardillo et al., 2005; Crooks et al., 2011). Among felids, 44% of the species fall into the top categories of threat of the IUCN Red List (critically endangered, endangered, and vulnerable; Macdonald et al., 2010). They face particular challenges in anthropogenically modified landscapes, even within protected areas (Woodroffe and Ginsberg, 1998). Habitat loss and fragmentation lead to an increase in wild-

cat mortality due to vehicle collisions (e.g. European wildcat *Felis silvestris*, Klar et al., 2009), loss of prey for food specialists (Iberian lynx *Lynx pardinus*, Ferreras et al., 2010), loss of territory due to the preference for undisturbed habitat (jaguars *Panthera onca*, Colchero et al., 2010) or retaliatory persecution following livestock predation (75% of felids, Inskip and Zimmermann, 2009). While conservation efforts have targeted large and charismatic felids, smaller, more cryptic species have received comparatively little attention. Half of the smaller cat species (8 of 16 species < 10 kg) are classified as vulnerable or endangered by IUCN; among those, six are associated with different degrees with forest habitat (Macdonald et al., 2010).

The 2-kg guiña or kodkod cat (*Leopardus guigna*) is the smallest wildcat of the Americas and one of the rarest and least known cats of the world (Nowell and Jackson, 1996). Kodkods are strongly associated with the heavily fragmented temperate rainforests of Chile and Argentina (Wilson et al., 2005) where they have the most restricted distribution range known for any New World felid (30–48°S, Quintana et al., 2009). The species is considered vulnerable on the IUCN Red List due to habitat destruction and human persecution as a response to poultry depredation (Napolitano et al., 2015).

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According to Dunstone et al. (2002), kodkods are forest specialists, including in human dominated landscapes where they favor large tracts of dense native forest over small fragments (Acosta-Jamett and Simonetti, 2004; Sanderson et al., 2002) or pine plantations (Zúñiga et al., 2009). More recent studies showed that kodkods are able to occupy native forest patches as small as 20–40 ha (Gálvez et al., 2013), plantations with well-developed undergrowth vegetation (Simonetti et al., 2013) and even edge type and moderately sized forest patches (Fleschutz et al., 2016). This indicates a higher tolerance to altered habitats than was suggested earlier.

We predict that the survival of kodkods in anthropogenic landscapes is related to its ability to relax its forest-dwelling behavior and/or make intensive use of the remaining forest, for example through hunting at prey-rich forest edges (e.g. leopard cats *Prionailurus bengalensis*, Azlan and Sharma, 2006; European wildcat, Klar et al., 2008). Exclusive forest-dependent behavior in modified habitats can drive felids to a critically endangered status as has occurred with Sumatran tigers (*Panthera tigris sumatrae*, Sunarto et al., 2012). Tolerance to human presence should facilitate felids' movement in impacted habitats (e.g. jaguars, Foster et al., 2010). Sunde et al. (1998) showed that resting Eurasian lynxes (IUCN status: least concern) tolerated short distances (50 m) towards intruding people. Recent camera-trapping revealed that kodkod occupancy increased near buildings (Fleschutz et al., 2016). Yet, a higher permeability of the landscape through tolerance to human disturbance might be at the cost of greater probability of contact and conflict with humans (Silva-Rodríguez et al., 2007).

Here we study habitat use and sensitivity of kodkods to fragmentation, adding to the small body of literature of fragmentation effects for carnivores in southern hemisphere temperate rainforests. Our aim is to quantify kodkod home ranges, describe habitat preferences in the fragmented landscape, and patch selection in forest remnants in the Andean foothills using radio-telemetry. Our predictions were that (1) cats would show aversion to the agricultural matrix (Dunstone et al., 2002; Sanderson et al., 2002), (2) as rodent consumers (Delibes-Mateos et al., 2014; Freer, 2004) they would make efficient use of the forest edge, and (3) human infrastructure would not be avoided (e.g. male kodkods, Sanderson et al., 2002; Fleschutz et al., 2016). We close the paper with recommendations of habitat preferences for kodkod conservation.

## Material and methods

### Study area

The study was conducted in the Chilean Araucanía region at the northern limit of the South American temperate rainforest. We worked in lowland forest (<550 m.a.s.l.) at the pre-Andean foothills of the Lake Villarrica catchment (39°16'S, 71°50'W, Fig. 1). The size of the study area was 133 km<sup>2</sup> with a 52% of remaining forest cover. The protected areas are all situated >800 m.a.s.l. The region has a temperate Mediterranean climate with an annual average temperature of 10 °C and a mean annual precipitation of 2500 mm (DMC, 2001). Lowland vegetation comprises deciduous forests dominated by *Nothofagus obliqua*, *Laurelia sempervirens*, *Aextoxicon punctatum*, *Podocarpus saligna*, and *Eucryphia cordifolia*; the understory is often mixed with bamboo *Chusquea quila* (Luebert and Plissock, 2006). Since colonization during the 20th century, the lowland forest areas have been fragmented and internally degraded through logging, cattle grazing, and fires (Rojas et al., 2011).

### Animal trapping and tracking

We trapped kodkods in forest remnants on private land, based on local information about recent sightings and camera-trap sur-

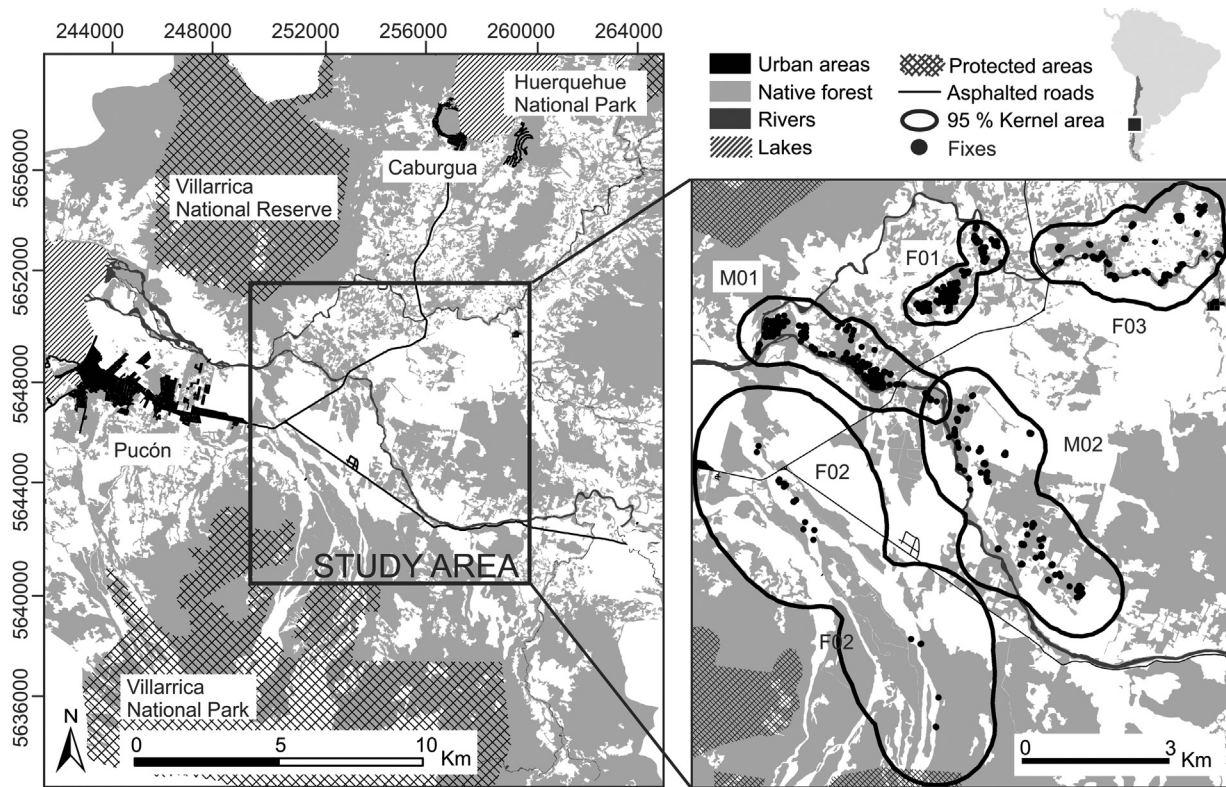
veys (capture period 09/2010–02/2012). All sampling procedures and animal manipulations were approved by the Chilean Agriculture and Livestock Service of the Ministry of Agriculture (trapping permit No. 3729). We used custom-built wooden and Tomahawk traps baited with chicken and a menu of attractants (valerian, catnip, Hawbaker's wildcat lure No. 2, sound attractants imitating mice and birds). The traps were preferably placed on animal trails near creeks, rivers, or wetland and checked once a day at dawn. Captured animals were anesthetized with Ketamine + Xylazine (reversed by Yohimbine) or Medetomidine + Ketamine (reversed by Atipamezole) by a team of veterinarians. During anesthesia the cats were tagged with radio-collars with activity sensors and mortality switches (45 g, Wagener Telemetrieanlagen, Germany). Individuals were classified as juveniles or adults by their body mass, tooth wear, and reproductive condition. When possible, we took samples of feces, hair, and blood for further analysis, such as population genetics (Napolitano et al., 2014).

We obtained telemetry locations on foot using a 3-element Yagi antenna and receiver (Sika, Biotrack, UK and R-1000, Communication Specialists, USA). Each individual was located at least 15 days per month for the first three months and thereafter at least eight days per month (telemetry period 09/2010–05/2012). We followed a schedule that aimed to equally cover different times throughout the 24 h and added more intensive sessions up to four hours during the nights (32% of locations). Each individual's fixes were systematically taken at 15 min intervals by triangulation based on three bearings. We assume there was no bias regarding the acquisition of fixes in relation to the landscape. Trails within forest fragments were frequent so as to guarantee tracking also deeper inside the forest. Location errors were minimized by using only azimuths that differed by 60°–120° from the previous one. At each fix, we recorded the cat's activity (active/inactive) and presence of bamboo within approximately 50 m of the animal. We used program LOAS (2012) to process the triangulation data and discarded locations with error ellipse sizes  $\geq 1.5$  ha and bearing errors  $> \pm 50^\circ$  (21 locations or 1.8% of all fixes). This yielded  $n = 1132$  fixes with a mean error ellipse area of  $0.09 \pm 0.01$  ha and a mean bearing error of  $0.81 \pm 0.2^\circ$ .

### Statistical analyses

Home range estimates were produced by fixed kernel probability densities. By visual inspection we chose an Epanechnikov kernel (Silverman, 1986) and the reference smoothing parameter ( $h_{ref}$ ). We calculated 95% and 50% contours; the latter was interpreted as an individual's core area size (Laver and Kelly, 2008). In order to reduce temporal autocorrelation for kernel estimates, we used independent fixes only which we defined as fixes separated by at least 6 h ( $n = 11–114$ , assumed time to biological independence). Additionally, we computed the 95% minimum convex polygon areas (MCP) using all fixes ( $n = 37–456$ ). Home ranges were estimated with package "adehabitatHR" (Calenge, 2006) and site fidelity following Spencer et al. (1990) with package "rhr" (Signer and Balkenhol, 2015) from the R Environment (R Development Core Team, 2013).

To explore the kodkod's habitat preferences within the fragmented landscape, we focused on 11 environmental variables (Table 1). We contrasted the distribution of the locations (used space) versus the distribution of the pixels of the ecological space (available) defined as the minimum bounding rectangle around the 95% kernel areas of all individuals (133 km<sup>2</sup>, Fig. 1). For this, we used a statistical approach based on multivariate ordination (Calenge and Basille, 2008). In contrast to more traditional ways of analyzing habitat use (e.g. Aebischer et al., 1993), we chose this method because it is exploratory (we only had five individuals) and allows ecological niches to be quantified and visualized in a



**Fig. 1.** Study area within the district of Pucón in the Araucanía region of southern Chile. The area is defined by a rectangle around the 95% kernel areas of the home ranges of two males (M) and three females (F).

**Table 1**

Environmental variables and fragmentation parameters tested for kodkod preference in a fragmented temperate rainforest in southern Chile. The distances were measured from each pixel of the study area to the edges of the point, line or polygon features of a variable class. For polygon features, negative distances were assigned to pixels inside the variable class, positive distances were outside.

Category	Variable	Variable description
Environmental variables <sup>a</sup>		
Vegetation	dForest	Distance to native (secondary and primary) forest (m)
	dMeadows	Distance to meadows (m)
	dPlantations	Distance to pine plantations (m)
	dScrubland	Distance to scrubland with regrowing trees (m)
Hydrology	dRivers	Distance to major rivers (>20 m width) (m)
	dWetland	Distance to wetland (m)
Infrastructure	dBuildings	Distance to buildings (m), inhabited and uninhabited
	dARoads	Distance to dirt roads (speed limit 50 km/h) (m)
	dDRoads	Distance to asphalted roads (speed limit 100 km/h) (m)
Topography	Elevation	Elevation (m) at 25 m resolution
	Slope	Slope (°)
Fragmentation parameters <sup>b</sup>		
Area-edge	Patch area	Area comprised by a patch (ha)
	Patch perimeter	Perimeter of a patch (m)
	Perimeter-area-ratio	Perimeter to area ratio
Shape	Related circumscribing circle	1 minus the ratio of patch area to the area of the smallest circumscribing circle (0–1, approaches 1 for elongated linear patches)
	Shape index	Perimeter of patch divided by square root of patch area multiplied by a constant of 0.25 ( $\geq 1$ , increases without limit as patch shape becomes more irregular)
Core	Core area	Area within the patch beyond a specified depth of edge distance (50 m) from patch perimeter (ha)
	Core area index	Percentage of patch that is comprised of core area (%)
Isolation	Euclidean-nearest-neighbor distance	Shortest edge-to-edge distance to the nearest neighboring patch (m) using Euclidean geometry

<sup>a</sup> The environmental variables were tested with Ecological-niche and Mahalanobis distance factor analysis.

<sup>b</sup> The fragmentation parameters were tested with generalized linear mixed models.

multidimensional space without seeking for statistical inference. Environmental variables that were categorical were transformed into Signed Distance Maps after conversion into raster format (5 m resolution). We calculated Euclidean distances from each pixel of the study area to the edges of the point, line or polygon features of a variable class. For polygon features, negative distances were assigned to pixels inside the variable class, positive distances were outside. First, we visualized the smoothed kernel density distributions of available and used resource units with the standard deviation of the kernel as the bandwidth (Silverman, 1986). Then, we performed a principal component analysis (PCA) on the environmental variables followed by an ecological-niche factor analysis (ENFA, Hirzel et al., 2002) and computed a habitat suitability map based on a Mahalanobis distance factor analysis (MADIFA, Calenge et al., 2008). ENFA and MADIFA were applied on the PCA results of the environmental variables and using all fixes ( $n=1132$ ) as these tools are less sensitive to temporal autocorrelation between the relocations. The distances of environmental variables were measured with program ArcGIS (ESRI, 2014). The analyses were conducted with R-package “adehabitatHS” (Calenge, 2006).

After confirming preference of forest over other habitat types, we tested forest patch selection of kodkods with generalized linear mixed models (GLMMs) with logistic link and binomial error structure using eight fragmentation parameters (Table 1). The binary response variable were the cats' independent fixes ( $n=294$ ) within forests only ( $n=240$ ) and random locations ( $n=294$  over 95% kernel area of all individuals) within forest only ( $n=141$ ). The cats' and random locations were then set in relation to the fragmentation proxies described in Table 1. As the number of locations varied for the five individuals we accounted for pseudo-replication by including a random-effect for individuals in the models. For the random points, we assigned the individuals randomly, and proportional to the true data. Prior to analysis, we explored the data following Zuur et al. (2010). Collinearity between covariates was assessed with Spearman correlation coefficients (excluding covariates with coefficients  $>0.7$ ) and variance inflation factors (VIF, accepted threshold  $<3$ ). The covariates were z-transformed because they were measured in different units. The models were parameterized with all possible covariate combinations. For model ranking, we used Akaike's Information Criterion (AIC) and selected the best model using Akaike weights. We evaluated the final model by visually inspecting the residuals with respect to homogeneity, normality, and independence (Zuur et al., 2009). Wilcoxon Rank Sum Tests were used to explore the directions of the response variable for the significant model predictors. The fragmentation parameters were extracted from program FRAGSTATS (McGarigal et al., 2012). For statistical modelling we used R-package “lme4” (Bates and Maechler, 2009), the VIF function was assessed from Zuur et al. (2009).

## Results

We captured five kodkods (2 males, 3 females) after  $N=3323$  trap nights during 18 months of trapping. Four of the radio-tagged cats were monitored for at least three months (Table 2), but we lost track of our fifth individual, one juvenile female (F02), after one month while she was dispersing over seven km from the point of capture, towards continuous forest with limited trails and roads.

### Home ranges

Kodkod home ranges (95% kernel) ranged between 178 and 2460 ha and were 3–4 times larger than the respective core areas (50% kernel, range 46–589 ha) (Table 2). F02 had one core area, F01, M01 and M02 had two, and F03 had three. The kernel estimates for

F02 have to be treated with caution as kernels were over-smoothed due to the small sample size ( $n=11$ ,  $\geq 30$  observations per animal is recommended by (Seaman et al., 1999)). The adult females F01 and F03 had smaller home ranges (1/2 and 1/6 times) than the adult male. To summarize, kodkods had mean 95% kernel areas of  $623 \pm 400$  ha and 50% core areas of  $191 \pm 132$  ha (without F02). There was only one minimal overlap of the 95% contours of the males M01 and M02 (Fig. 1). The 95% minimum convex polygon method produced smaller values and less variability between the five individuals (mean:  $270 \pm 137$  ha; range: 123–482 ha) than the kernel method (Table 2).

The 50% kernel core areas of three individuals (F01, M01, M02) contained more than 50% of native forest (range 51–69%), which was significantly more than the 95% kernel areas (2-sample tests for equality of proportions,  $\chi^2=5.62$ ,  $p=0.018$  for F01,  $\chi^2=6.39$ ,  $p=0.011$  for M01,  $\chi^2=11.05$ ,  $p=0.001$  for M02). F03's core area had a high percentage of meadow (61%, forest 33%) and F02's had similar amounts of scrubland (30%), forest (28%) and lava corridors (25%). Finally, three (F01, F03, M01) of four animals (without F02) exhibited site fidelity; for M02 home range analysis should be interpreted with caution (Supplementary material S1).

### The ecological niche

A visual inspection of the kernel density distributions of available and used resource units (Fig. 2, in pixels) highlight a strong selection for forest, with 85% of the kodkods' used pixels within forest patches (distances  $\leq 0$ ) and 52% of available forest. Interestingly, the distributions show a preference for the forest edge: 65% of pixels used by kodkods were detected within 50 m from the forest edge while this zone represented only 22% of the available forest habitat. The cats also remained close to rivers (50% within a 300 m distance to rivers, available 15%) and wetland (50% within a 500 m distance, available 14%). They avoided meadows (93% of the used units were positive distances, available 69%), but stayed close to them (52% within 50 m or less from meadows, available 20%). Plantations and scrubland were also avoided (positive distances), but not human infrastructure, such as buildings (60% of used units within a 200 m distance, available 27%) and dirt roads (59% within a 300 m distance, available 43%). Cats selected habitats at lower elevations (50% below 300 m.a.s.l., available 14%).

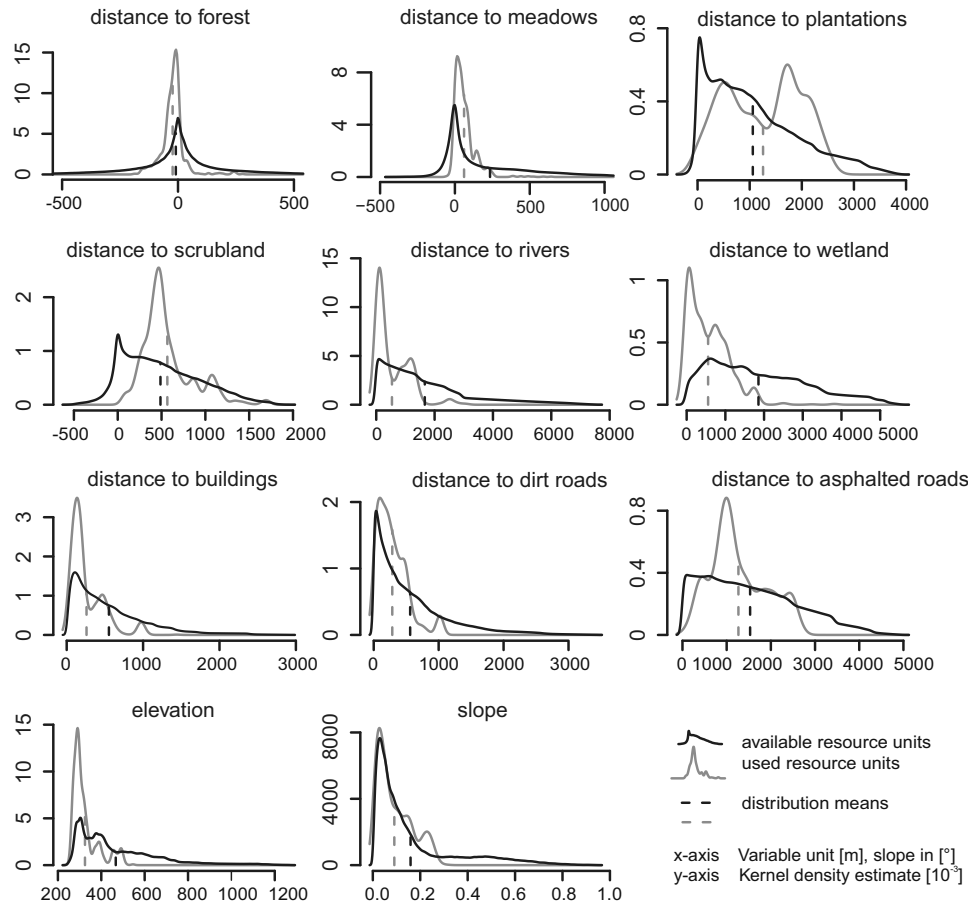
As illustrated by the ENFA (Fig. 3) the centroid of the ecological niche was far from the centroid of available habitat, meaning that used and available distributions differed with respect to their mean (marginality, first axis) and variance (specialization, second axis). The highest absolute coefficients of the marginality axis (value range from  $-1$  to  $1$ ) indicate that the five kodkods preferred habitats close to water and did not avoid human houses (negative signs of distance variables mean preference: distance to wetland =  $-0.57$ , to rivers =  $-0.41$ , to buildings =  $-0.33$ ). The cats also selected habitats at lower elevations (elevation =  $-0.42$ ). With regard to the specialization axis, the niche was narrow in comparison to what was available to the species, i.e. the five kodkods strongly preferred forest (distance to forest =  $0.89$ , close to one).

The Mahalanobis distance factor analysis (MADIFA) allowed us to compute a reduced-rank habitat suitability map (Fig. 4) based on the mean squared Mahalanobis distances between the available distribution and the mean of the niche of the first two axes (together explaining 72% of the eigenvalues). The map highlights lowland forest patches, particularly their edge, as most suitable areas (low Mahalanobis distances). The results of ENFA and MADIFA are complementary as the marginality axis of the ENFA and the first component of the MADIFA were significantly correlated ( $\rho=0.79$ ).

**Table 2**

Home range estimates for five kodkods in a fragmented rainforest ecosystem in southern Chile. Home ranges were computed by fixed kernel density estimators (95% and 50% for core areas) using independent fixes ( $n = 11–114$ , separated by  $> 6$  h) and 95% minimum convex polygons (MCP) using all fixes ( $n = 37–456$  fixes). The kernel estimates for F02 have to be treated with caution as kernels were over-smoothed due to the low sample size ( $n = 11$ ).

ID	Age	Days monitored	All fixes	Independent fixes	95% kernel (ha)	50% kernel (ha)	95% MCP (ha)
F01	adult	216	268	80	178	46	123
F02	juvenile	33	37	11	2460	589	197
F03	adult	87	167	50	639	210	315
M01	juvenile	376	456	114	530	146	231
M02	adult	91	204	39	1146	361	482



**Fig. 2.** Kernel density distributions of available and used resource units. The available resource units are represented by black lines ( $n = 5,343,407$  pixels, 5 m resolution), the used resource units by grey lines ( $n = 931$  pixels). For distance variables, positive values mark the distance to the edge of the habitat, while negative values mark the distance within the habitat to its edge. The distribution means are represented by dotted lines.

### Forest patch selection

Out of 294 independent fixes of all individuals 82% (240 fixes) were located in a total of 16 patches. Each individual occupied 2–4 patches only. The median size of the 16 patches was 102 ha (range 0.36–12,859 ha) while 40% of the locations were located in patches  $< 100$  ha, and 18% in patches  $< 50$  ha. Patches  $< 10$  ha were also used, but only in 3% of the 240 cases. Females ( $n = 113$ ) occupied patches of median area of 63 ha, while males ( $n = 127$ ) occupied patches of median area more than twice that value (162 ha). Only F01 was permanently located in patches  $< 100$  ha (65% of 71 fixes in a 63 ha patch). The 16 patches were rather elongated in shape (median of related circumscribing circle 0.82, range 0.64–0.93), and had a relatively low percentage of core area (median 31%, range 0–80).

Among the 16 candidate regression models, the global model was best supported by the data (Akaike weight = 0.85, Supplemen-

tary material S2). No strong residual patterns were evident when checking the global model for homogeneity and normality, neither when plotting the residuals against each covariate. According to the Wilcoxon Rank Sum Tests (Table 3) between the significant predictor variables of cat and random locations we may conclude that kodkods selected patches with a lower amount of core area and elongated in shape. They occupied less irregularly shaped patches with higher Euclidean-nearest-neighbor distance to the neighbor patches than the random sample.

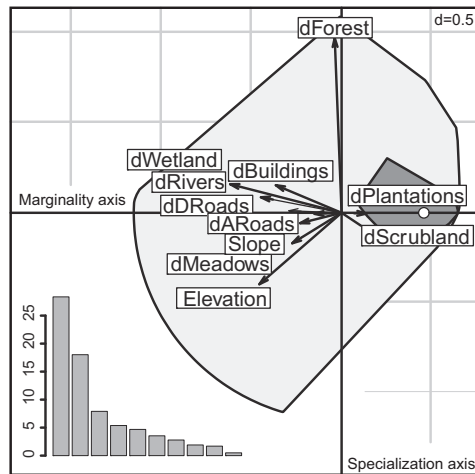
### Discussion

Radio-tracking of kodkods in southern temperate rainforest remnants highlights their ability to establish permanent territories in a fragmented landscape. This indicates that kodkods are more likely to occupy at least moderately fragmented landscapes than previously described, although more individuals are needed

**Table 3**  
Relevant fragmentation parameters for kodkod patch selection. The table includes the estimated beta coefficients and standard errors of the covariates of the best model (global model) of the 16 generalized linear mixed candidate models fitted with logistic links and binomial error distributions (summary in Supplementary material S2). Medians, range, and comparisons between means of the covariates measured at kodkod (n = 240) and random locations (n = 141) are given.

Best model covariates	Estimates	Locations (median, range)	Random (median, range)	Wilcoxon W
(Intercept)	1.88 ± 1.23	–	–	–
Core area index	–4.42 ± 0.61***	31.2 (0–79.5)	67.5 (0–88.8)	4113.5***
Shape index	0.91 ± 0.34**	7.7 (1.6–17.7)	10.7 (1.9–17.7)	10,916.5***
Related circumscribing circle	–0.90 ± 0.40*	0.82 (0.64–0.93)	0.67 (0.61–0.96)	26,595.5***
Euclidean-nearest-neighbor distance	–1.10 ± 0.40**	31.6 (10.0–211.9)	11.2 (10.0–581.9)	22,339.5***

Significance levels: \* 0.5, \*\* 0.01, \*\*\* 0.001.



**Fig. 3.** ENFA results displayed by the marginality axis (x-axis) and first specialization axis (y-axis) for n = 1132 fixes. The figure inset shows the barplot of the eigenvalues. Marginality was strong as the dot representing the centroid of the distribution of used units is shifted away from the origin of the axes, the centroid of the distribution of available weights. The polygons correspond to the minimum convex polygons of the distributions of available (light grey area) and used (dark grey area) resource units. The polygon of the used habitat (realized niche) was narrow in its extend on the y-axis meaning that specialization was also high. Direction and length of the arrows are a metric of the contribution of the variables to marginality and specialization.

to extrapolate our results. In the literature, the importance of continuous forest versus small fragments (<40 ha, Acosta-Jamett and Simonetti, 2004; Gálvez et al., 2013) and of corridors between forest tracts (Sanderson et al., 2002) predominated. In this study, although the five individuals did not relax their forest-dwelling behavior (distance to forest = 0.89 on ENFA specialization axis), they made efficient use of the forest edge (most suitable areas following MAD-IFA, Fig. 4), and were tolerant to human presence (60% of used units within 200 m of a building). Our individual-based data are thus in agreement with Fleschutz' et al. (2016) findings of increased occupancy in fragments with high perimeter-to-area ratios and nearer to buildings.

In accordance with prediction 1, clear areas were avoided (only 7% of the used pixels in meadows, while 31% were available), confirming previous studies that the kodkod is a forest-dependent species in landscape mosaics (Gálvez et al., 2013; Sanderson et al., 2002). To cope with the lesser amount of forest, we propose that the monitored kodkods may compensate by amplifying their home ranges. In this study, they had significantly larger kernel home ranges (90% means for n = 4 were 524 ha) than in continuous forest (90% means for n = 6 individuals tracked for 2–4 months were 119 ha in Dunstone et al. (2002); Mann-Whitney U test,  $W = 23$ ,  $p = 0.02$ ). An increase in home range size has been observed in urban bobcats living in areas with high proportions of non-natural habitat or more roads (Poessel et al., 2014; Riley et al., 2003).

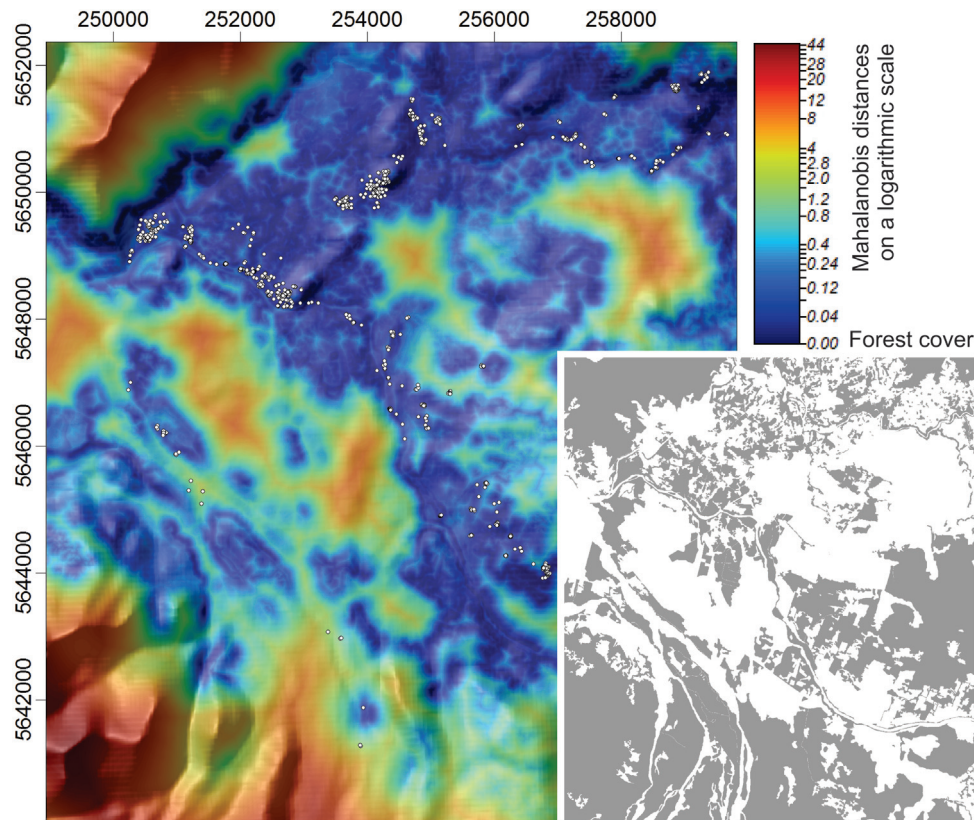
The five kodkods showed affinity for edges (prediction 2). Kernel density distributions revealed that 65% of pixels used by kodkods were within 50 m from the forest edge, Mahalanobis distances were lowest at the ecotones, and GLMMs indicated preference for elongated patches. This could be triggered by a higher prey density (e.g. Fleschutz et al., 2016; Šálek et al., 2010). Rodent abundances were higher in fragmented forest versus continuous forest (e.g. Saavedra and Simonetti, 2005) and seed predation by rodents was higher at the edges of forest remnants in south and central Chile (Díaz et al., 1999; Donoso et al., 2003). Indeed, rodents and small mammals constitute the major prey for this species in the study area (Galuppo-Gaete, 2014) and elsewhere (Delibes-Mateos et al., 2014; Freer, 2004).

According to prediction 3 (human infrastructure would not be avoided); we found kodkods close to houses (<200 m) and dirt roads (<300 m). Sharing the landscape with humans might not only have disadvantages: more available prey (free-ranging poultry or rodents) could attract kodkods to houses. However, in the vicinity of humans they could also step into an “ecological trap” (Delibes et al., 2001) due to the presence of domestic dogs as predators, and the risks of road kills and retribution killing (Gálvez et al., 2013; Sanderson et al., 2002).

Despite our high trapping effort (3323 trap nights over 18 months) and the variety of attractants used we only captured five individuals of this extremely elusive felid. We emphasize that the low sample size puts limits on the generalizability of our results. However, as individual-based data on this species in fragmented landscapes is extremely scarce (only Sanderson et al., 2002), we think that our data is useful to the emerging picture about this rare species. The recently published patterns of fragment use obtained with camera-trapping (preference of forest edges, certain tolerance of human infrastructure, Fleschutz et al., 2016) were in line with our findings from radio-tracking individuals.

Beyond the study of forest fragments at a patch-level, it is essential to further evaluate landscape-level connectivity among patches (similar to Castro-Bustamante, 2014) to inform conservation decisions on meta-population scales. There is also a need for future studies to investigate population growth rates to determine possible immigration from continuous into fragmented forests (our study area bordered onto two protected areas at higher elevations). Whether or not there are source-sink dynamics (Pulliam, 1988) would help to improve understanding the importance of protected areas, currently seen as insufficient for carnivores and threatened vertebrates (Simonetti and Mella, 1997; Tognelli et al., 2008), for the surrounding landscape.

Our study has implications for kodkod conservation on private lands. When fragment sizes decrease beyond 50 ha, kodkods might get into trouble (see also Gálvez et al., 2013). In only 18% of 240 locations kodkods were located in patches <50 ha, and only one individual permanently occupied patches <100 ha. Wetlands should be conserved and forest not be separated from rivers by “vegetation cleaning” or the construction of roads, as both habitats match the narrow habitat requirements of this species (ENFA results of this study, Fleschutz et al., 2016; Sanderson et al., 2002).



**Fig. 4.** Habitat suitability map for the kodkod in the study area of the Araucanía region of southern Chile. The reduced-rank Mahalanobis distances (with logarithmic scaling and a stretch factor of 1000) were computed using 11 environmental variables for  $n = 1132$  fixes. Suitable areas (low Mahalanobis distance) to unsuitable areas (high Mahalanobis distance) are represented by a color scale from blue to red. White dots represent kodkod locations ( $n = 1132$  for 5 individuals). The hillshading in grey is transparently overlaid by the habitat suitability. Highly suitable dark blue areas are found at the forest ecotones when compared to the native forest cover (in grey, identical map section) to the right. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

As kodkods were significantly more active than inactive in association with bamboo ( $\chi^2 = 15.16$ ,  $p < 0.001$ ,  $n = 1132$ ), this native understory plant may represent good hunting grounds for *Oligoryzomys* (Jaksic and Lima, 2003), one of the most frequently consumed rodent in our study area (kodkod diet in Galuppo-Gaete, 2014).

The above mentioned implications were presented in a stakeholder workshop for “kodkod conservation outside the national parks” with the principal environmental groups from civil society of the region as well as landowners and governmental agencies. This might be one step towards recruiting private landowners for conservation efforts on their lands (Zorondo-Rodríguez et al., 2014), particularly in areas harboring vulnerable felid species.

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### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.mambio.2016.11.013>.

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