First records on habitat use of semi-feral cattle in southern forests: topography reveals more than vegetation

Nicolás Seoane

While the presence of cattle in forests is quite common, how they use this habitat is often overlooked. When this is examined, most studies focus on measurements of the vegetation variables influencing habitat selection. This current report provides a suitable model to study habitat use by livestock in forested areas by means of GPS tracking on selected individuals. The model was applied to data from semi-feral cattle in order to obtain the first description of their habitat use in southern forests. Furthermore, the model accounted for individual variability, and hinted at population patterns of habitat use. The positions of 15 individual cows with GPS collars were recorded covering twelve months in a *Nothofagus* (southern beech) forest in Patagonia (Argentina). By projecting these GPS location data into a geographical information system (GIS), a resource selection probability function (RSPF) that considers topographic and vegetation variables was built. The habitat selection by semi-feral cattle in southern beech forests showed a large interindividual variability, but also some similar characteristics which enable a proper description of habitat-use patterns. It was found that habitat selection by cattle was mainly affected by topographic variables such as altitude and the combination of slope and aspect. In both cases the variables were selected below average relative to availability, suggesting a preferred habitat range. Livestock also tended to avoid areas of closed shrublands and showed a slight preference for meadows. Cattle give significant importance to topographic variables to define their habitat selection in this type of mountainous forests. This might be because of an ecological adaptation to the major features of these types of forests due to ferality. Furthermore, these results are the basis for management applications such as predictive maps of use by semi-feral livestock in forested landscapes.

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4 Nicolás Seoane

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6 Laboratorio Ecotono, Universidad Nacional del Comahue, CONICET, Quintral 1250, (8400)

7 Bariloche, Argentina. (Email: nicosaon80@gmail.com) Tel. +54 (02944) 423374

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22 *Abstract*

23 While the presence of cattle in forests is quite common, how they use this habitat is often

overlooked. When this is examined, most studies focus on measurements of the vegetation

variables influencing habitat selection. This current report provides a suitable model to study

habitat use by livestock in forested areas by means of GPS tracking on selected individuals. The

model was applied to data from semi-feral cattle in order to obtain the first description of their

habitat use in southern forests. Furthermore, the model accounted for individual variability, and

hinted at population patterns of habitat use. The positions of 15 individual cows with GPS collars

were recorded covering twelve months in a *Nothofagus* (southern beech) forest in Patagonia

(Argentina). By projecting these GPS location data into a geographical information system

(GIS), a resource selection probability function (RSPF) that considers topographic and

vegetation variables was built. The habitat selection by semi-feral cattle in southern beech forests

showed a large interindividual variability, but also some similar characteristics which enable a

proper description of habitat-use patterns. It was found that habitat selection by cattle was mainly

affected by topographic variables such as altitude and the combination of slope and aspect. In

both cases the variables were selected below average relative to availability, suggesting a

preferred habitat range. Livestock also tended to avoid areas of closed shrublands and showed a

slight preference for meadows. Cattle give significant importance to topographic variables to

define their habitat selection in this type of mountainous forests. This might be because of an

ecological adaptation to the major features of these types of forests due to ferality. Furthermore,

these results are the basis for management applications such as predictive maps of use by semi-

feral livestock in forested landscapes.

47 *Nothofagus* forests; beef cattle; semi feral cattle; resource selection probability functions (RSPF);

48 GPS tracking; habitat distribution modeling.

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64 **1. Introduction**

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66 Cattle (*Bos taurus*) are an important species for forest dynamics globally, and the originally

67 domesticated animals have transgressed to become semi-feral to feral in many areas (Decker et

68 al. 2015, Berteaux and Micol 1992, Hernandez et al. 1999, Baker 1990, Lazo 1994, Rotherham

69 2013). Livestock can affect the diversity and structure of plant communities (Coughenour 1991,

70 Cingolani et al. 2008) mainly through diet selection (Rook et al. 2004), but also due to indirect

71 actions such as changing the distribution of nutrients and compacting the soil by trampling

72 (Milchunas et al. 1998, Cingolani et al. 2008). Thus, it is possibly one of the main ecosystem

73 engineers in forested areas, as has already been demonstrated in grasslands (Jones et al. 1997).

74 Although the impacts of cattle are often studied, their habitat use, which would allow a more

75 comprehensive understanding of the livestock-forest ecological system, has generally been

76 overlooked.

77   Southern beech forests (i.e., *Nothofagus* forests) in Patagonia have been used to raise

78 cattle since the late 19th century. The traditional management involves extensive cattle ranching

79 in the forest. But occasionally and for different reasons, some animals escape the herd,

80 establishing feral populations (Atkinson 2001, Veblen et al. 1996). Although feral cattle can be

81 found in many areas of the *Nothofagus* forests in Patagonia (Novillo and Ojeda 2008) and New

82 Zealand (Howard 1966, Veblen and Stewart 1982), no studies have been performed on their

83 behavior or habitat selection in these southern forests. Additionally, many levels of ferality

84 already exist depending on contact with human settlements, hunting pressure, isolation time, etc.

85   The proportion of time an animal spends in a location to meet their biological demands

86 defines its habitat use (Beyer et al. 2010). As resources are often heterogeneously distributed,

87 individuals need to explore multiple environments to satisfy their needs (Law and Dickman

88 1998). Therefore, the selection of habitats is a key feature of behavior and population dynamics

89 (Morris 1987). This is especially relevant for large herbivores, because their distribution on the

90 landscape can decisively influence the productivity and biodiversity of fields and pastures

91 (Bailey and Provenza 2008).

92   There are multiple relationships between livestock and their environment but one of the

93   major ones is the change in the heterogeneity of vegetation produced by foraging (Adler et al.

94   2001). In the case of forests, despite having high heterogeneity and prevalent presence of cattle,

95   there is no systematic review of the resulting ecological processes due to the introduction of this

96   herbivore worldwide. Furthermore, it is common to have little or no information about the

97   activity patterns of semi-wild cattle in general and due to a large inter-individual variability, it

98   appears impractical to calculate the utilization on a particular mountain range (Cook 1966).

99   Some studies that have been conducted in different forests account for diet selection along

100   seasons (Marquardt et al. 2010) or in relation to anthropogenic changes, usually due to forest

101   management practices (Roath and Krueger 1982, Kaufmann et al. 2013). In these studies,

102   vegetation type and topography were the most common variables to explain habitat selection by

103   cattle in forests.

104   A variety of technological and statistical tools can be applied to study habitat use. Among

105   the first, radiotelemetry and GPS devices allow for accurate and frequent data collection on

106   animal location, which facilitates the development of mechanistic models of habitat use and

107   movement (Beyer et al. 2010). Therefore, their use is widespread (Johnson et al. 2004, Ungar et

108   al. 2005, Cagnacci et al. 2010, Peinetti et al. 2011). In addition to these data collection methods,

109   habitat use can be modeled by resource selection functions (RSF) and resource selection

110   probability functions (RSPF) that estimate the probability that a given location has been used by

111   an animal (Boyce and McDonald 1999, Beyer et al. 2010). Thus, the RSFs provide a framework

112   for developing an ecological theory of habitat use and allow linking landscape ecology and

113   population biology (Boyce and McDonald 1999, Boyce 2006). One way to build a RSPF with

114   GPS data is to model the intensity of use in sampling units, relating the relative frequency of

115   records per unit to the environmental features of such sampling units (Nielson and Sawyer 2013).

116   The objective of this study was to evaluate the habitat use of semi-feral cattle in southern

117   beech forests as no current data or a common methodology exists for this purpose. Furthermore,

118   the use of vegetation variables is usual in studies on habitat use by cattle, but the role of

119   topography could be of importance especially in mountainous areas, yet it is often overlooked.

120   Specifically, this study address the following questions: (i) What is the habitat use of semi-feral

121   cattle in *Nothofagus* forests?; and (ii) Are the vegetation variables of the landscape more

122   important than topography for habitat use by cattle?. These research questions were addressed by

123   using a utilization distribution approach and the construction of a resource selection probability

124   function (RSPF) which included topographic and vegetation variables.

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127   **2. Methods**

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129   *2.1. Study Area*

130   The study was carried out in the Llodconto Valley, Northwest Patagonia (Rio Negro, Argentina).

131   The valley is within the Nahuel Huapí National Park, between 41º21' and 41º27' south latitude,

132   and 71º31' and 71º41' west longitude, at an elevation ranging from 920 to 2000 m.a.s.l.. It is a

133   mountainous area with cold-temperate to moist-cold climate with prevailing westerly winds. The

134   summers are dry and winters rainy, with a mean monthly temperature ranging from 2.4ºC in July

135   to 12.9ºC in January. The area is part of the Andean-Patagonian forest and includes a wide

136   variety of habitats such as forests, shrublands, meadows, burned forest, riparian and high

137   mountain areas. The dominant species is *Nothofagus antarctica* which is one of the main

138   components of both forests and shrublands. Other species such as the *Nothofagus pumilio* tree,

139   the *Schinus patagonicus* shrub, and the *Chusquea coleou* bamboo are also abundant. The major

140   features of plant communities in the area are listed in Table 1. An uncertain number of free-

141   ranging cattle inhabit the valley and are traditionally and minimally managed by local people

142   only during the summer months.

143

144   *2.2. Data collection and explanatory variables*

145   In order to capture the animals, an enclosure located at the center of the valley was used to herd

146   the animals into. Sixteen female adults caught between 2012 and 2014 were fitted with custom-

147   made GPS collars (GPS Module ZX4120 and Amicus GPS Shiled Antenna, © Crownhill

148   Associates Ltd.). These GPS collars store data on board and therefore, recapture was necessary

149   to recover the data. Each collar was set to record location every ten minutes and these records

150   were later screened by hour in order to standardize the records and eliminate the unacquired data.

151   The individuals were adult cows in a good physiological state (body condition between 3 and 4)

152   and descendants of the Hereford breed originally introduced in these forests. All capture and

153   handling methods used in this study met the standards of animal welfare practices recommended

154   for scientific research (Rollin and Kessel 1998, Gannon and Sikes 2007). All research was

155   approved by the proper authorities of the protected area (Nahuel Huapi National Park,

156   Argentina).

157

158   **Table 1**

159   Plant communities used as vegetation variables in a resource selection probability function

160   (RSPF) to estimate habitat use by semi-feral cattle in Llodconto Valley (Parque Nacional Nahuel

161   Huapi, Argentina).

Habitat type	% of study area	Main species	General description
forests	34	*Nothofagus pumilio*, *Nothofagus antarctica*, *Chusquea culeou*	It includes two different forests, a *Nothofagus pumilio* forest in the hillsides above 1100 m.a.s.l. and a *Nothofagus antarctica* forest at the bottom of the valley. The first is tallest and without a secondary strata of trees. Both have low forage cover and a shrub stratum.
shrubland	39	*Schinus patagonicus*, *Nothofagus antarctica*, *Diostea juncea*	Thick and short vegetation generally occurring in hillsides.
burned areas	8.5	*Berberis microphylla*, *Ribes magellanicum*, *Trifolium repens*	These are typically open areas with several sprouting plants and a high coverage of fallen burned trunks.
meadows	3	*Bromus sp.*, *Poa sp.*, *Juncus sp.*	Small to medium size wet prairies occurring in a forest matrix but also in high Andean areas.
open areas	5	*Baccharis magellanica*, *Acaena*	A variety of habitats with low vegetation cover (< 25%). Riparian areas and some

		spp.	disturbed terrains (e.g. by trampling) are represented here.
high Andean vegetation	10.5	*Gaultheria spp.*, *Empetrum rubrum*, *Senecio spp.*, *Nassauvia spp.*	This area occurs above the *Nothogafus pumilio* community with the timberline at 1700 m.a.s.l. It consists of short vegetation with low cover and highly adapted to extreme conditions.

162

163   Topographic mapping and spatial statistical analysis were conducted using Quantum

164   GIS™ software (QGIS™) version 1.8.0 using a digital elevation model (ASTER GDEM) as the

165   data source. Animal locations were overlayed on the digital elevation model and a minimum

166   convex polygon (MCP) with a 200 meter buffer was used around the complete set of GPS

167   positions to define our study area. One thousand sampling units of 100 meters radii each (i.e.,

168   sampling unit area= 0.03km^2) were allocated randomly inside this area.

169   Habitat types were assigned for each sampling unit based on floristic composition,

170   identifying the following vegetation types: forests, shrubland, burned areas, meadows, open

171   areas (vegetation cover <25%) and high Andean vegetation (Table 1). These plant communities

172   are easily distinguishable in high resolution satellite imagery and therefore, the habitats were

173   delineated in the GIS by means of a visual classification on a Google Earth image (© Google

174   Inc). All continuous variables were standardized in order to allow comparison between them.

175   Corresponding values for elevation, slope, aspect, hillshade and ruggedness were extracted from

176   the GIS database for each sampling unit. All these were used as predictor variables in the habitat

177   use model. An additional variable called "NWness" was created to take into account hillside

178   exposure. The rationale for this is based on strong west winds and large thermal amplitudes due

179   to sunlight exposure in north facing sites that shape the rigorous weather in these zones. NWness

180   was calculated as the cosine of the hillside aspect minus 310 degrees. Thus, this variable

181   accounts for the exposure of the slope with a value ranging from 1 (maximum exposure) to -1

182   (minimum exposure).

183   In order to avoid multicollinearity between predictors, highly correlated variables (r >

184   0.6) were not used together in the same model. Squared elevation and slope were included in the

185   models for the purpose of evaluating preferred ranges of use by animals. In order to account for a

186   strong regional climatic pattern, the interaction between slope and NWness was also considered

187   since steep and northwest exposed slopes are generally arid, with short vegetation and low

188   coverage.

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190   *2.3. Data analysis*

191   There are several ways to model habitat use. The most widely used include the GLMs and

192   related models (Guisan and Zimmermann 2000), but multivariate approaches (Clark et al. 1993,

193   Burke et al. 2013), GIS-based habitat suitability models (Osborne et al. 2001, Store and Jokimäki

194   2003), individual based models (Railsback and Harvey 2002), artificial neural networks

195   approaches (Özesmi and Özesmi 1999), and maximum entropy modeling (Baldwin 2009) also

196   exist. Here I applied a utilization distribution approach described by Nielson and Sawyer (2013)

197   to develop the RSPF because it accounts for intensity of use among habitats and is unbiased in

198   the face of temporally correlated animal location data.

199   The utilization distribution approach allows the modeling of habitat use by using the

200   relative frequency of positions within each sampling unit as an empirical estimator of the use

201 distribution (Millspaugh et al. 2006). This relative frequency of positions was used as a response

202 variable in a generalized linear model (GLM) with negative binomial distribution that accounts

203 for over-dispersed count data. In order to relate the observed counts in a sampling unit with the

204 total number of positions recorded for each animal, an *offset* term was included, thus allowing

205 for estimating the probability of use by individual *E(μ[i]/total*, references below).

206 Thus, the RSPF was set as follows:

207 $y_i \sim \text{NegativeBinomial}(\mu_i, \theta)$

208 $\ln(\mu_i) = \ln(\text{total}) + \beta_0 + \beta_1.\text{elevation}_i + \beta_2.\text{slope}_i + \beta_3.\text{ruggedness}_i + \beta_4.\text{NWness}_i + \beta_5.\text{forest}_i$

209 where*:*

210 y_i = number of observations at the *i*-th sampling unit; μ = relative frequency in each sampling

211 unit by animal; θ = overdispersion parameter; *total* = number of recorded positions in the whole

212 study area by animal; *i* = sampling unit with associated habitat covariates.

213 Several models exploring different combinations of predictor variables were fitted for

214 each animal and compared using the Akaike information criterion (AIC). The overdispersion

215 parameter of the negative binomial distribution was estimated simultaneously with the models

216 using the *glm.nb* function in R (Venables and Ripley 2002, R Core Team 2013 version 3.0.2). A

217 set of ecologically plausible models was chosen to work with all animals based on a stepwise

218 regression. The package *glmulti* (Calcagno and Mazancourt 2010) was used as a tool for quickly

219 identifying the best models for each animal. The deviance (Guisan et al. 2000) was used as a

220 goodness of fit indicator.

221 A population-level model was then developed considering each animal as an

222 experimental unit, which reflects the individual nature of resource selection (Marzluff et al.

223 2004, Millspaugh et al. 2006). A single set of covariates was selected considering the

224 comparison among models and the biological relevance of the variables. The estimated

225 coefficients, variance and confidence intervals were calculated for each parameter of this general

226 proposed model.

227 The coefficients of the population model were calculated according to:

228 $\hat{\beta}_k = \frac{1}{n}\sum \hat{\beta}_{kj}$

229 where $\hat{\beta}_k$ is the estimated coefficient k for each individual j (j=1,2,3,4) and n is the total number

230 of animals (n=4).

231 The variance of the estimated coefficients for the population model was computed as:

232 $Var(\hat{\beta}_k) = \frac{1}{n-1}\sum_{j=1}^{n}(\hat{\beta}_{ij} - \hat{\beta}_{ij})^2$

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234

235 **3. Results**

236 A total of 26,187 animal locations (an 87% fix rate for the GPS collars) were obtained from 15

237 of the animals. One of the collared animals could not be relocated during the study and therefore

238 was not recaptured. A total time of twelve months was covered by adding up the trajectories for

239 all the individuals.

240 Based on the fitted models for each animal, the general trend was that topographic

241 variables were always more important than vegetation. Given the full additive model (not shown)

242 as an example, the more meaningful variables for all animals were elevation, aspect and the

243 interaction between slope and NWness. In all cases, topographic variables had negative

244 coefficients because the animals preferred elevations below the available mean in the landscape

245 and avoided hillsides with northwestern exposure and steep slopes (Figure 1). The vegetation

246 variables showed different tendencies for each individual and in most cases were not significant

247 (p > 0.05). The shrublands had a tendency of being avoided by all animals except by cows 3, 4, 7

248 and 11. The opposite was observed in the case of meadows, which were preferred by most

249 individuals. Burned areas displayed a remarkable variability that does not allow any inference.

250 Forest habitat had low coefficients for all the animals with values near zero, which showed no

251 tendency to be selected, either in favor or against (Appendix A.2: Coefficients for all tested

252 models and animals).

253   By means of a step-by-step selection procedure over all the models, five plausible

254 ecological models were selected for each animal in order to use them as a RSPF for semi-wild

255 cattle (Table 2, Appendix A.1: Description of the models). These models were among the best

256 ten for each animal. It can be seen that all models have as variables elevation, some aspect

257 indicator, its interaction with slope, and in some cases the vegetation types with greater selection:

258 shrubs and meadows. The coefficients of these five models for all the animals are summarized in

259 the Appendix A.

260   The most parsimonious models for each animal were significantly different from the null

261 model (p<0.01) and explained between 31% and 53% of the total deviance for the different

262 individuals. All the animals selected lower elevations than available in the landscape. Most cows

263 also avoided steep slopes and many did the same with steep hillsides with northwest exposure. In

264 addition, there was a tendency to avoid shrubs and prefer wet meadows. The confidence intervals

265 of the mentioned variables for each individual do not include zero in most cases, suggesting good

266 accuracy and inference level.

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268

269 **Figure 1**

270 Mean coefficients and 90% confidence intervals for individual models (black and white) and

271 population-level model D (grey) for habitat use by semi-feral cattle in Llodconto Valley

272 (Argentina). Positive estimates are in black while negatives are in white.
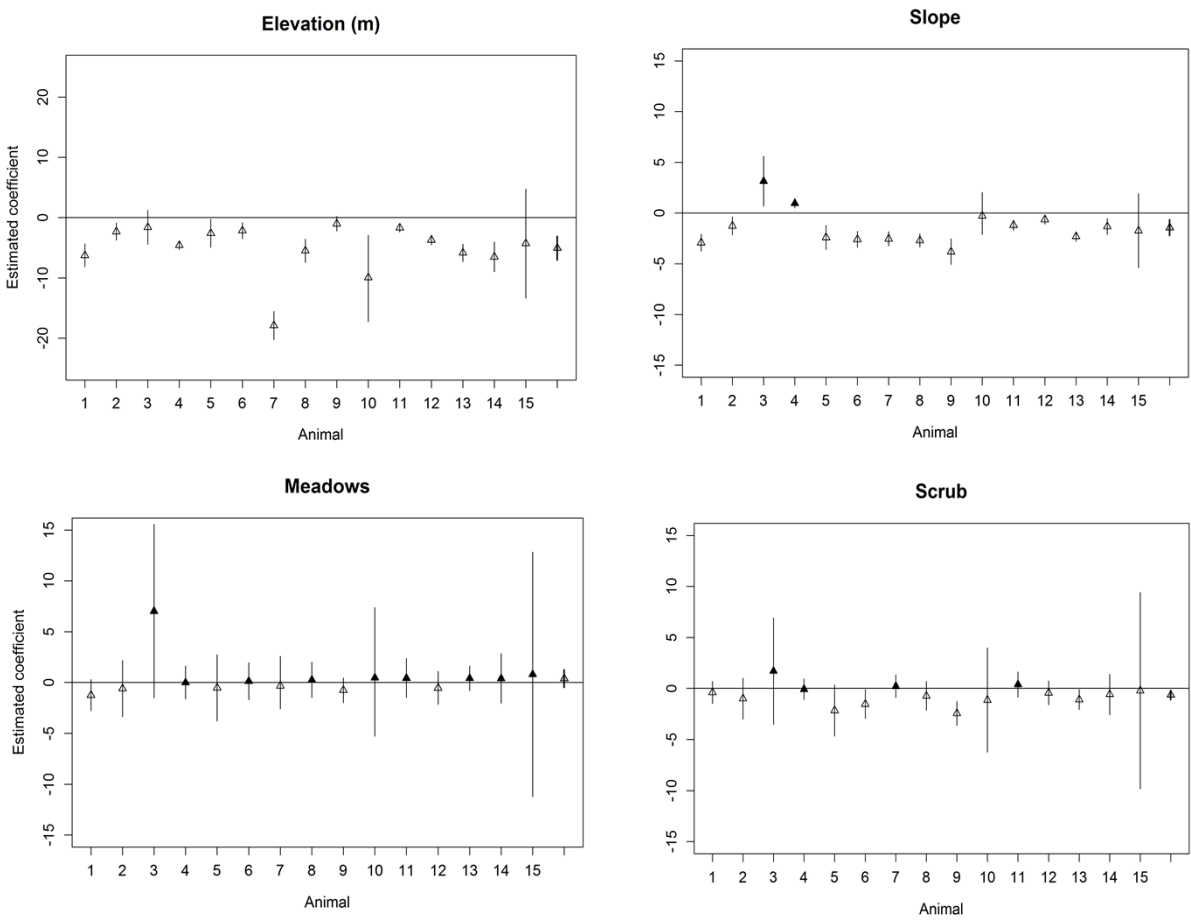
293 **Table 2**

294 Alternative models for free-range cattle habitat use in the study area; the table shows Akaike

295 information criterion value (AIC), number of predictor variables (K) and ranking of models

296 relative to each individual (R).

	Model	A	B	C	D	E
	Expression	Elevation + elevation^2 + slope + slope^2 + NWness	Model A + shrubland + meadow	Elevation + NWness : slope	Model C + shrubland + meadow	Elevation + slope + forest NWness + shrubland + meadow
	K	5	7	4	6	6
Animal 1	AIC	188.80	190.43	192.69	195.84	199.30
	ΔAIC	0.0	1.6	3.9	7.0	10.5
	R	1	2	3	4	5
Animal 2	AIC	634.30	638.24	629.61	632.89	636.48
	ΔAIC	4.7	8.6	0.0	3.2	6.8
	R	3	5	1	2	4
Animal 3	AIC	499.81	493.15	515.13	505.75	508.27
	ΔAIC	6.7	0.0	21.9	12.5	15.1
	R	2	1	5	3	4

Animal 4	AIC	1869.66	1849.39	1807.97	1807.62	1868.70
	ΔAIC	62.0	41.7	0.3	0.0	61.0
	R	5	3	2	1	4
Animal 5	AIC	630.26	631.87	624.43	625.51	638.97
	ΔAIC	5.8	7.4	0.0	1.0	14.5
	R	3	4	1	2	5
Animal 6	AIC	711.76	711.30	703.59	700.00	711.73
	ΔAIC	11.8	11.3	3.6	0.0	11.7
	R	5	3	2	1	4
Animal 7	AIC	639.96	614.27	629.31	609.62	617.45
	ΔAIC	30.3	4.6	19.7	0.0	7.8
	R	5	2	4	1	3
Animal 8	AIC	758.38	759.02	796.09	795.26	795.48
	ΔAIC	0.0	0.6	37.7	36.8	37.1
	R	1	2	5	3	4
Animal 9	AIC	407.54	481.93	477.80	461.14	416.00
	ΔAIC	0.0	74.3	70.2	53.6	8.5
	R	1	5	4	3	2
Animal	AIC	1025.90	1089.59	1058.49	1066.50	1069.70

10	ΔAIC	0.0	63.6	32.5	40.6	43.8
	R	1	5	2	3	4
Animal 11	AIC	2351.08	2482.34	2282.43	2285.14	2326.21
	ΔAIC	68.6	199.0	0.0	2.7	43.7
	R	4	5	1	2	3
Animal 12	AIC	2052.96	2054.99	2042.84	2046.00	2054.36
	ΔAIC	10.1	12.1	0.0	3.1	11.5
	R	3	5	1	2	4
Animal 13	AIC	953.68	947.65	990.74	984.62	987.96
	ΔAIC	6.0	0.0	43.1	36.9	40.3
	R	2	1	5	3	4
Animal 14	AIC	1601.50	1597.90	1603.50	1599.81	1599.39
	ΔAIC	3.6	0.0	5.6	1.9	1.5
	R	4	1	5	3	2
Animal 15	AIC	1933.01	2042.94	1988.43	1986.27	1982.57
	ΔAIC	49.5	60.3	5.8	3.7	0.0
	R	4	5	3	2	1

297

298

299   Models with the lowest AIC were different for each individual (Table 2). However,

300   model "D" (i.e. including elevation, NWness:slope, shrubland and meadow) is relatively well-

301   ranked for all animals and includes a set of variables that summarize the habitat use patterns

302   observed. Therefore, model "D" was chosen to build the final predictive RSPF with all the

303   individuals. This general proposed model (i.e. model "D", Table 3) shows a common selection

304   for an elevation and slope below the average available, in favor of meadows and against sites

305   with shrub cover. These were the only variables that allow a strong inference, since their

306   confidence intervals excludes zero. Some interesting trends of this population model are

307   noteworthy. Shrublands, for example, reduces the probability of use for a given site and the

308   opposite occurs with meadows (Table 3). Also, a high variability in resource selection could be

309   observed among individuals (Figure 1, Table 2). Some variables (as elevation and slope) were

310   selected with the same tendency while others such as vegetation types and NWness, show high

311   variation between animals (Figure 1, Appendix A.2).

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315   **Table 3**

316   The population model for resource selection by semi-feral cattle with means coefficients

317   (standardized variables), standard errors and 90% percentile confidence intervals.

	Coefficient	SE	90% Confidence intervals	
			Lower limit	Upper limit
Intercept	-12.2613	0.7962	-13.6637	-10.8588
Elevation	-4.4799	0.7412	-5.7854	-3.1743

Slope:Nwness	-0.2509	0.2985	-0.7766	0.2749
Slope	-1.5131	0.4272	-2.2656	-0.7607
NWness	0.3360	0.4007	-0.3698	1.0419
Shrubland	-0.4586	0.1353	-0.6970	-0.2202
Meadow	0.6169	0.3021	0.0848	1.1491

4. Discussion

Using GPS tracking and by means of a utilization distribution approach, a RSPF accounting for topography and vegetation was built for semi-wild cattle in the Andean-Patagonian forest. This study shows that habitat use by livestock in these forests has a large inter-individual variation but also common features that would allow a description of a pattern of use. Topographic variables affected the probability of habitat use by cattle to a greater extent than vegetation types. In the general proposed model, for instance, a change in a single standard deviation unit of elevation (~ 300 meters) resulted in a threefold increased in the probability of use (Table 3) and the squared slope has a similar role in some of the alternative models (Table 2). This suggests that terrain features have a leading role in defining the use of space by livestock, perhaps as an adaptation due to the long history of use and because topography is important in these mountainous forests.

Some common features such as the preferred elevation range and the tendency to prefer meadows suggests that it would be possible to describe a population-level home-range for a more comprehensive description of habitat use. In this regard, the squared elevation would play an important role in defining a preferred elevation range, although there seems to be a high

336 variability among individuals. This variability could be modeled by a RSPF with a hierarchical

337 formulation, for example. Cattle tend to slightly avoid shrubland (Table 3). This may be due to a

338 lower proportion of trails in this type of thick vegetation, in contrast to more accessible areas or

339 those that offer better protection from snow, such as forest. Moreover, these paths are almost

340 unusable in the winter because of snow. In this scenario, the availability and network of trails

341 would play an important role in defining the population-level home-range of cattle, and

342 therefore, in determining habitat use. At the same time, the use by livestock has created the paths

343 on the landscape over time, so there is a reciprocal interplay that shows a sort of memory process

344 at the population level.

345   The response variable and statistical procedure used in this study proved to be appropriate

346 and useful as they describe the habitat use of cattle in probabilistic terms. Additionally, this

347 methodology achieves some improvements over earlier approaches on the subject. Sights-based

348 multiple regression models (Cook 1966, Senft et al 1985) were pioneers in disentangling some

349 factors influencing patterns on cattle grazing, but data collection is laborious and it is impossible

350 to apply to feral cattle. The GPS-based logistic regression approach used by Walburger et al

351 (2009) and previous studies, models the habitat use by cattle as a binary response and therefore,

352 it does not allow for modeling the utilization distribution of the animals.

353   Comparing with other studies conducted in forests inhabited by cattle, we find interesting

354 relationships in the applied variables and scales. Studies on seasonal diet selection (Marquardt et

355 al. 2010) in Bolivian forests for example, show that different functional groups of plants are

356 preferred in different seasons. It would be possible to infer species selected by livestock

357 throughout the year in the Andean-patagonian forest if direct observations of consumed plants by

358 cattle were added to this study. Kaufmann et al. (2013) found that in silvopastoral systems cattle

359 prefer places with forest cover, avoiding places with high slope and low biomass, particularly

360 logged sites. A comparison with this study could be made by an analogy between logged and

361 burned areas, both without forest cover. Nevertheless, with the available data we cannot make

362 inferences about the type of selection in burned areas so far (Tables 1-3, Appendix A). However,

363 it may be noted that other studies in burned forests of Patagonia (Blackhall et al. 2008, De Paz

364 and Raffaele 2013) found a relevant influence of cattle on vegetation, making it clear that the

365 cows are foraging in these areas. Roath and Krueger (1982) also used topographic and vegetation

366 variables to study the behavior of cattle in a forested mountainous environment, finding that the

367 type of vegetation and water availability determined the degree of use by livestock. These

368 apparently opposite results are consistent if we consider the differences between the study areas.

369 While Roath and Krueger (1982) worked in a dry, arid vegetation and elevational range of 300

370 meters, Llodconto Valley is an area with high water availability, abundant streams, and altitudes

371 ranging from 800 to 2000 m.a.s.l. This shows that although topography and vegetation variables

372 are widely used in habitat selection studies, their effects depend on the availability on the

373 landscape. Since this effect is well known (Arthur et al. 1996, Beyer et al. 2010), how habitat use

374 by cattle change with different availability of resources in the forest is scarcely addressed.

375 Interestingly, Johnson et al. (2004) conducted a study on resource selection by caribou at two

376 spatial scales, finding that topographic variables such as elevation and slope are more important

377 at a landscape scale, while vegetation variables were more important at the patch scale.

378 Something similar could be occurring in this present study, which is closer to the landscape

379 scale.

380   As mentioned, cattle can increase landscape heterogeneity, especially when the spatial

381 pattern of vegetation is already heterogeneous (Adler et al. 2001) as in the case of the currently

382　studied forests. This has implications for forests dynamics because although there are studies on

383　cattle inhabiting forest (Bartolomé et al. 2011, Kauffmann et al. Rotherham 2013), there still

384　remains a lack of knowledge regarding how forest dynamics are affected by the distribution of

385　wild cattle worldwide. Recently, a study conducted in Patagonia developed a model that

386　proposes distance to meadows as an estimator of forest use by livestock (Quinteros et al. 2012).

387　While meadows are of crucial importance to the Andean-Patagonian forests and Quinteros et al.

388　(2012) make a practical contribution in relation to forest management, their model has a spatial

389　limitation, being restricted to meadows surroundings. Thus, it is not possible to make inferences

390　at a landscape scale and the model fails to consider other relevant variables such as topography,

391　which proved to have greater importance in resource selection by cattle (Tables 2-3, Figure 1).

392　Nonetheless, the approaches are consistent, because as the distance to meadows increases, the

393　intensity of use by livestock decreases (Quinteros et al. 2012), although altitude is generally

394　higher, which is predicted by the model in this current study.

395　　　　There remains a need for tools that enable animal management in agreement with

396　conservation practices of native forests. In Patagonia, for instance, extensive livestock farming

397　has been identified as an activity with potential to be carried out in the forest. Yet, there have

398　been only some pioneer silvopastoral experiences (Fertig and Guitart 2006), and current

399　livestock handling is still scarce (Ormaechea et al. 2009). Effective management depends heavily

400　upon knowledge about the interaction of the animal with its environment. Nonetheless, it is

401　common to have poor information on the activity patterns of semi-wild cattle (Moyo et al. 2012),

402　and a lack of understanding on animal movements and foraging decisions at several scales of diet

403　selection (Rook et al. 2004) still prevail. This current study provides a direct contribution to this

404　knowledge-gap, and direction for future research in these ecological systems. As an example, a

practical application of this approach is the production of maps showing intensity of land use by livestock. Similar maps have been developed for other regions using equivalent methodologies (Nielsen et al. 2003, Sawyer et al. 2009), and therefore offer an ecological-based management tool within protected areas or productive forests.

5. Conclusions

The present study demonstrated that the habitat use by semi-feral cattle in southern beech forests has a large inter-individual variability but also similar characteristics which allow the description of a pattern of use. Particularly, the results indicate that vegetation variables are no more important than topography features. Conversely, habitat selection by cattle in these southern forests is mainly affected by topographic variables such as altitude and the combination of slope and aspect. These results suggest an adaptation by semi-feral cattle to the major features of the landscape of these mountainous forests maybe due to ferality.

6. Acknowledgements

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576 **Appendix A: The models and their coefficients for all animals.**

577

578 ##

579 A.1. Description of the models

580 A.2. Coefficients of all tested models and animals

581 ##

582

583 **A.1. Description of the models**

584 *A.1.1. Mathematical description*

585 $y_i \sim \text{NegativeBinomial}(\mu_i, \theta)$

586 $\ln(\mu_i) = \ln(\text{total}) + \beta_0 + \beta_j.\text{variable}_i$

587 where:

588 *y* = number of observations per sampling unit; μ = relative frequency in each sampling unit by animal; θ =

589 overdispersion parameter; *total* = number of recorded positions in whole study area by animal; *i* = sampling unit

590 with associated habitat covariates; *j* = number of variables in each model.

Model	Description of variables involved in each model
A	elevation + sqr.elev + slope + sqr.slope + NWness
B	elevation + sqr.elev + slope + sqr.slope + NWness + shrubland + meadow
C	elevation + slope + NWness * slope
D	elevation + NWness * slope + shrubland + meadow
E	elevation + slope + NWness + forest + shrubland + meadow

591

592

593

594

595

596 *A.1.2. Programming*

597 ```
FIT MODELS FOR EACH ANIMAL X IN THE FORM:
```

598 ```
fit.X = glm(count ~ elevation + NWness*slope + forest + scrub + burned +
```

599 ```
            meadow , family=negative.binomial(W), data= animal X,
```

600 ```
            offset=log(total.locations[animal==X]), init.theta= W)
```

601 ```
Note that W is the overdispersion parameter theta estimated using the
```

602 ```
# glm.nb function on package MASS.
```

603

A.2. Coefficients of all tested models and animals

606

A.2.1. Model A

Variable	AIC	Theta	SE.theta	intercept	elevation	sqr.elev	slope	sqr.slope	NWness
Animal_1	188.802	0.205	0.095	-80.572	-14.585	-69.404	-2.387	-0.139	-0.06
Animal_2	634.3	0.055	0.01	-3.79	-1.907	0.341	-1.325	-0.065	0.894
Animal_3	499.811	0.029	0.006	-3.967	-2.176	-1.113	1.946	1.531	1.508
Animal_4	1869.659	0.053	0.005	-1.603	-4.339	-0.03	1.533	0.909	1.021
Animal_5	630.264	0.051	0.005	-6.21	-2.631	1.395	-1.277	0.548	-0.166
Animal_6	711.756	0.095	0.016	-5.266	-2.521	0.405	-1.217	0.745	0.484
Animal_7	639.958	0.083	0.023	-72.265	-23.277	-36.452	-0.997	-1.642	-1.961
Animal_8	758.382	0.105	0.016	-98.294	-17.797	-88.733	-6.049	-2.25	0.265
Animal_9	407.543	0.127	NaN	-69.257	-39.128	-20.427	-14.234	-4.141	0.697
Animal_10	1025.896	0.12	0.017	-14.022	-3.677	2.465	-2.315	-1.133	-0.303
Animal_11	2351.081	0.1	0.009	-9.118	-2.548	0.838	0.013	0.131	0.659
Animal_12	2052.956	0.13	0.012	-9.635	-2.711	0.244	-1.507	-0.725	1.112
Animal_13	953.682	0.22	0.031	-71.296	-12.501	-61.268	-1.245	0.04	0.158
Animal_14	1601.5	0.273	0.029	-13.57	-3.869	1.616	-2.206	-0.481	-0.004
Animal_15	1933.014	0.193	0.018	-11.887	-3.322	2.194	-1.734	-0.523	-0.117

608

609

A.2.2. Model B

Variable	AIC	Theta	SE.theta	intercept	elevation	sqr.elev	slope	sqr.slope	NWness	scrub	meadow
Animal_1	190.427	0.23	0.109	-88.62	-15.408	-73.465	-2.722	-0.282	-0.045	-0.226	-1.664
Animal_2	638.244	0.055	0.01	-9.8	-1.915	0.312	-1.314	-0.066	0.933	-0.126	-0.162
Animal_3	493.152	0.032	0.007	-9.92	-2.478	-1.646	2.381	1.356	2.254	-0.809	3.392
Animal_4	1849.387	0.059	0.006	-9.329	-3.199	-0.519	1.406	0.942	1.046	1.747	0.08
Animal_5	631.866	0.05	0.005	-12.866	-2.519	1.257	-1.48	0.415	1.123	-0.285	0.783
Animal_6	711.305	0.103	0.017	-11.711	-2.683	0.039	-1.07	0.717	0.527	-0.725	0.679
Animal_7	614.274	0.202	NaN	-80.276	-16.164	-66.916	-2.631	-1.301	-0.967	0.178	-0.297
Animal_8	759.016	0.109	0.017	-97.369	-17.749	-89.163	-6.383	-2.535	0.273	-0.478	0.951
Animal_9	481.928	0.092	NaN	-21.064	-41.487	-21.821	-10.503	-2.797	0.726	-1.272	0.641
Animal_10	1089.588	0.075	0.01	-12.632	-3.959	3.476	-2.906	-1.168	-0.095	0.075	1.196
Animal_11	2482.336	0.113	0.01	-9.81	-3.027	1.651	0.142	0.289	0.066	0.441	-0.284
Animal_12	2054.989	0.131	0.012	-10.422	-2.884	0.844	-1.216	-0.488	0.603	0.59	0.526
Animal_13	947.651	0.237	0.034	-66.969	-11.743	-57.904	-1.115	0.136	0.164	-0.792	0.523
Animal_14	1597.901	0.286	0.031	-13.299	-3.881	1.51	-2.171	-0.514	0.005	-0.498	0.491

Animal_15 2042.943 0.061 0.003 -12.791 -3.303 1.639 -1.559 -0.153 0.201 -0.385 0.541

611

612

A.2.3. Model C

Variable	AIC	Theta	SE.theta	intercept	elevation	slope	NWness	Nwness:slope
Animal_1	192.693	0.15	0.061	-16.662	-6.801	-3.069	-2.678	-2.123
Animal_2	629.612	0.057	0.01	-10.369	-2.501	-1.346	1.486	0.753
Animal_3	515.128	0.023	0.005	-8.73	-2.104	2.309	1.132	0.22
Animal_4	1807.974	0.067	0.007	-9.705	-4.241	0.801	2.539	2.348
Animal_5	624.425	0.071	0.013	-13.407	-3.578	-2.554	1.128	1.294
Animal_6	703.589	0.099	0.016	-13.031	-2.843	-2.795	2.18	1.684
Animal_7	629.306	0.15	NaN	-18.586	-10.914	-0.778	-2.441	-1.001
Animal_8	796.09	0.079	0.012	-16.733	-7.301	-2.665	0.756	0.258
Animal_9	477.798	0.092	NaN	-11.259	-0.743	-3.602	0.519	-0.074
Animal_10	1058.485	0.046	0.006	-9.181	-3.531	-2.217	-0.184	-0.922
Animal_11	2282.429	0.121	0.01	-9.431	-1.944	-1.006	1.556	1.354
Animal_12	2042.842	0.132	0.012	-10.685	-3.956	-0.607	1.458	0.895
Animal_13	990.74	0.159	0.021	-16.869	-7.665	-2.33	1.074	0.681
Animal_14	1603.496	0.268	0.029	-14.283	-6.384	-1.437	-0.137	-0.139
Animal_15	1988.429	0.164	0.016	-9.683	-3.785	-2.931	-0.396	-0.759

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A.2.4. Model D

Variable	AIC	Theta	SE.theta	intercept	elevation	Nwness	slope	scrub	meadow	Nwness:slope
Animal_1	195.837	0.153	0.062	-16.505	-6.805	-2.48	-3.058	-0.247	-1.052	-1.984
Animal_2	632.888	0.058	0.011	-10.109	-2.458	1.693	-1.271	-0.506	-0.141	0.839
Animal_3	505.752	0.027	0.005	-8.998	-1.835	2.004	2.838	-0.876	4.429	-0.637
Animal_4	1807.617	0.069	0.007	-9.922	-4.095	2.215	0.858	0.691	0.845	2.19
Animal_5	625.511	0.074	0.013	-12.954	-3.454	0.987	-2.299	-0.531	0.852	1.27
Animal_6	699.995	0.11	0.019	-12.294	-2.498	2.396	-2.586	-1.02	0.62	1.816
Animal_7	609.615	0.161	NaN	-18.406	-11.093	-2.089	-0.741	-0.62	-0.276	-0.851
Animal_8	795.258	0.081	0.012	-15.334	-6.422	0.932	-2.67	-0.526	0.348	0.387
Animal_9	461.137	0.124	NaN	-10.9	-0.724	0.366	-3.468	-1.268	0.744	-0.285
Animal_10	1066.5	0.045	0.006	-8.814	-3.152	0.175	-2.103	-0.729	0.586	-0.737
Animal_11	2285.14	0.122	0.011	-9.532	-1.896	1.472	-1.023	0.256	0.41	1.321
Animal_12	2045.995	0.132	0.012	-10.775	-3.876	1.316	-0.657	0.291	0.142	0.81
Animal_13	984.623	0.171	0.023	-15.861	-6.802	1.173	-2.318	-0.843	0.597	0.771
Animal_14	1599.805	0.28	0.03	-13.976	-6.28	-0.018	-1.343	-0.516	0.479	-0.016
Animal_15	1986.273	0.167	0.016	-9.539	-3.125	-0.308	-2.858	-0.436	0.67	-0.646

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621 *A.2.5. Model E*

Variable	AIC	Theta	SE.theta	intercept	elevation	slope	NWness	forest	scrub	meadow
Animal_1	199.296	0.145	0.06	-15.361	-6.405	-2.552	-0.02	-0.018	-0.377	-1.299
Animal_2	636.482	0.055	0.01	-9.657	-2.108	-1.269	0.954	-0.073	-0.27	-0.21
Animal_3	508.27	0.025	0.005	-8.771	-2.013	2.504	1.844	-0.231	-0.988	3.115
Animal_4	1868.703	0.054	0.005	-6.473	-3.763	1.646	0.779	-2.681	-0.792	-1.751
Animal_5	638.97	0.06	0.011	-10.164	-3.578	-3.235	-0.047	-0.767	-0.784	0.614
Animal_6	711.728	0.105	0.018	-9.408	-2.396	-2.016	0.497	-0.406	-1.002	0.553
Animal_7	617.449	0.116	NaN	-18.806	-11.227	-0.451	-1.098	0.676	-0.043	-0.259
Animal_8	795.479	0.08	0.012	-13.918	-6.616	-2.632	0.564	0.263	-0.257	0.564
Animal_9	416.001	1.879	NaN	-11.494	-0.746	-3.525	0.762	-0.47	-1.67	0.315
Animal_10	1069.703	0.044	0.006	-10.074	-4.001	-2.007	-0.264	0.975	1.238	1.974
Animal_11	2326.209	0.11	0.009	-5.212	-1.571	-0.807	0.73	-0.632	0.075	0.208
Animal_12	2054.361	0.13	0.012	-7.257	-3.43	-0.732	0.758	-0.187	0.459	0.153
Animal_13	987.956	0.17	0.023	-13.131	-6.412	-2.301	0.382	0.089	-0.7	0.706
Animal_14	1599.39	0.28	0.03	-10.972	-6.408	-1.322	0.004	-0.257	-0.739	0.252
Animal_15	1982.571	0.17	0.016	-10.653	-3.988	-2.812	0.126	1.372	0.617	1.836

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