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Activity patterns and habitat use of pudu deer (*Pudu puda*) in a mountain forest of south-central Chile

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ABSTRACT

The pudu (*Pudu puda*) is a small, endemic deer, and the only native ungulate found in Chilean and Argentinean temperate forests. Its ecology, including its double role as an herbivore and as a prey, is poorly known. Therefore, it is pressing to gain a better understanding of the pudu given that its habitat is being transformed rapidly by anthropogenic causes. On a coastal mountain range in south-central Chile, we conducted a habitat use study and examined the activity patterns of the pudu using camera traps. The study area was a large native forest patch, surrounded by commercial plantations which would not constitute a habitat for this deer. Using a sampling effort of 7559 camera days, we found that this deer was largely nocturnal with little activity during daytime. The pudu selected *Araucaria* forests, and avoided *Nothofagus* forests. These behaviours suggest that the pudu traded off habitat use patterns and activity time to avoid predation, mainly by puma which is the top predator in the rich local community of carnivores occurring in the latter habitat.

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The pudu (*Pudu puda*) one of the world's smallest deer, inhabits the temperate forests of southern Chile and neighbouring Argentina (Silva-Rodríguez et al. 2016). Its range is restricted and populations are declining in the face of increased threats from human activities such as poaching, habitat loss and fragmentation, predation by exotic carnivores, and potential competition with domestic herbivores (Silva-Rodríguez et al. 2010, 2016). Due to these threats and the fact that it is not well represented in protected areas (Pavez-Fox and Estay 2016), the pudu is considered Near Threatened by the International Union for Conservation of Nature (IUCN) (Silva-Rodríguez et al. 2016). Compounding these problems is the fact that our understanding of the ecology of the pudu is scarce, and thus science-based management actions to conserve it are not available. Expert opinion suggests that urgent studies are badly needed. Limitations to studying this deer include its small size, cryptic coloration and secretive behaviour, and that it has a solitary life and inhabits the dense understory of southern temperate forests (Jiménez 2010).

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Among the few earlier studies that mentioned habitat associations of the pudu to native forest are those of Greer (1965) and Eldridge et al. (1987). To our knowledge, the latest account of habitat use by the species comes from an unpublished report about pudus on Chiloé Island (Jiménez 1995) and in Argentinian forests (Meier and Merino 2007). Given the small amount of native forest left in southern Chile and the alarming rate of its degradation (Miranda et al. 2015), there is an urgent need to understand the ecology of this small deer, the better to manage it – especially considering that vegetation cover is one of the main factors that influences the spatial ecology in deer (Putman 1988), which affects foraging and resting behaviour. However, the choices that deer make are also affected by predation risk, which could be the result of avoiding sites abundant in predators, that results in a 'landcape of fear' for the prey (Brown et al. 1999). Pudus are difficult to study, mainly due to their behaviour of inhabiting a dense forest habitat (Jiménez 2010), where observations are hard to obtain. Therefore, there is a lack of quantitative information on their activity patterns (Eldridge et al. 1987). With the advent of camera trapping techniques to monitor wildlife, this situation is starting to change (Zúñiga and Jiménez 2010). To begin to fill this gap in knowledge, the objective of this work is to document the space use and daily activity patterns of the pudu in a relatively pristine forested ecosystem in southern Chile.

The research was conducted in the 13198 ha Caramávida watershed (37.8383°S, 73.2241° W). This is private land located on the western slope of the Nahuelbuta Mountain Range in south-central Chile, about 18 km north-west of Nahuelbuta National Park (Fontúrbel and Jiménez 2014). This rugged terrain has a temperate-humid climate (Di Castri and Hajek 1976) and ranges in elevation from 778 to 1252 m above sea level. Aside from having extensive patches of relatively well-preserved forests in the higher elevations (Wolodarsky-Franke and Herrera 2011), Caramávida also has large blocks of landscape in different recovery stages due to past intensive livestock use, rigorous agricultural practices and firewood extraction. These impacted lands have often been planted with monocultures of exotic Monterey pine (*Pinus radiata*) and Tasmanian blue gum (*Eucalyptus globulus*) plantations. Given its location, being on the interphase between two geographical regions, the biota of Caramávida is diverse and shows high levels of endemism (Tognelli et al. 2008). Furthermore, Caramávida is considered a high-priority site at the national level for the conservation of its biodiversity (Muñoz et al. 1996).

As part of another study (Zúñiga et al. 2017), between September 2010 and June 2011 (i.e. southern spring through fall), we continuously operated 24 Bushnell Trophy Cam (Bushnell Corporation, Overland Park, KS) camera traps to monitor forest mammals (Kays and Slauson 2008) across the study area. The cameras were laid out along four lines of six cameras each. Camera stations were set up at 1 m from the ground, separated from each other by 500 m and arranged along forest trails in a way that took into account the heterogeneity of the landscape (Wolodarsky-Franke and Herrera 2011).

To assess habitat use and selection by the pudu, we used Spatial Analyst 2.0 (ArcView 3.2) on digital photos from the national inventory of native forest (CONAF-CONAMA-BIRF 1999). From the images, we could identify the areas having the two main cover classes (Garshelis 2000, p. 1), *Nothofagus* forests (a surface of 10,097 ha) – which included the Coigue-Raulí-Tepa association (*Nothofagetum procera*, sensu Oberdorfer 1960), and Lenga-Araucaria (*Nothofagus pumilio-Araucaria araucana*) forests (3101 ha). We estimated the intensity of habitat use as the relative frequencies of pudu recordings on

cameras located in each of the habitat types (O'Brien et al. 2003). We tested the fit of the pudu records in each habitat type against the availability (in hectares) of each of these using a goodness-of-fit test (Byers et al. 1984; Sokal and Rohlf 1995). We standardised the records to a sampling effort of 100 camera days (Rovero and Marshall 2009).

We evaluated the daily activity patterns of the pudu as the proportion of records obtained during each 1-hr period out of the total daily cycle (which ensures some level of temporal independence), adjusted by day length according to the season. Considering the amount of light intensity, we divided the day into four time periods (Fedriani 1997): dawn, day, dusk and night. We tallied the frequency of independent records of pudu per time period, and we used Levins' index (Levins 1968) to calculate the breadth of its temporal niche, the value of which could fluctuate between 0 and n (in this case, 24 – the total hours of a day). We computed the standard deviation for the obtained value by jackknifing the data (Jaksic and Medel 1987). In addition, we standardised these values in accordance with Colwell and Futuyma (1971). The standardised niche breadth, B_{sta}, ranges between 0 (the narrowest) and 1 (the broadest), depending on the spread of the activity along the time axis. We assumed that detectability was 1 and did not change with season or time of the day.

A total effort of 7559 camera days rendered 78 independent pictures of pudu. These were obtained during the spring (N = 24), summer (N = 23) and fall (N = 31), resulting in a detection rate of 1.03 pudu recordings/camera/100 days. The pudu's activity was largely concentrated during the night (69% on average; Figure 1a). However, it varied according to the season (Figure 1b). Although the main activity was concentrated at night in the tree seasons examined, throughout the day, the activity tended to expand from spring to fall (Figure 2). Levins' index was $\beta = 6.85 \pm 0.87$ for spring, $\beta = 8.96 \pm 0.82$ for summer, $\beta = 11.86 \pm 0.98$ for fall and $\beta = 12.11 \pm 1.10$ for the whole period. The standardised niche was $B_{sta} = 0.25, 0.34, 0.47$ for spring, summer and fall, respectively, and 0.48 for the whole period). During dawn periods the pudu was less active (Figure 3; $\chi^2 = 27.07$, $p < 0.0001$ for spring; $\chi^2 = 16.35$, $p = 0.001$ for summer; $\chi^2 = 11.01$, $p = 0.011$ for fall; all df = 3). This pattern was similar across seasons (Figure 2).

Regarding habitat use, overall the highest proportion of pudu records were obtained in *Araucaria* forests (60.5%) in contrast to *Nothofagus* forest (39.5%), showing therefore that pudu used the habitat in a non-random way. Compared to its availability, pudus preferred the *Araucaria* forest ($\chi^2 = 61.61$; df. = 1; $p < 0.0001$). Eighty percent of the 24 operating cameras – the naïve occupancy – recorded the presence of pudu in the study area.

The activity patterns obtained are in partial agreement with the data of Eldridge et al. (1987) for a telemetry study in the province of Osorno (southern Chile) on a lake peninsula closer to the Andes Mountain Range. These authors found most pudu activity during dawn and dusk, where minimal activity occurred in the daytime, and the highest peaks were at night. On the other hand, our results are also in partial concordance with the observational study of Jiménez (1995), farther south, on Chiloé Island. There, most activity of the observed pudus occurred during the evenings (i.e. dusk). However, in the present study, detections in the morning were rare. In both other sites, forest cover was sparser and patchier than at Caramávida.

Over the year, in general terms, pudu concentrated its activity in a few hours at night. This could be interpreted as a mechanism to reduce predation risk, whereas the expansion of time activity in the fall could reflect a trade-off with food searching, considering that less

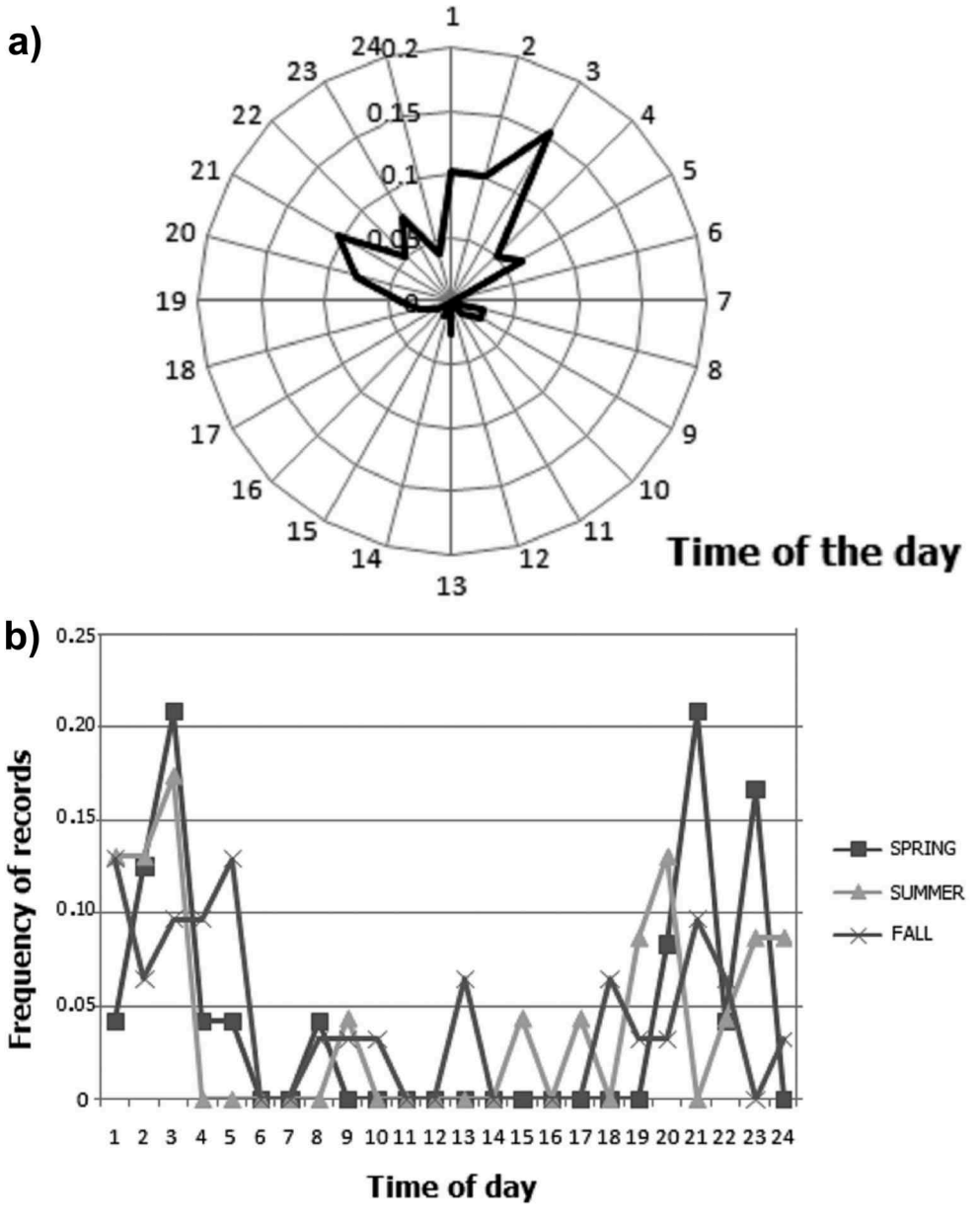

Figure 1. (a) Activity time of the pudu deer in Caramávida, Nahuelbuta Mountain Range, south-central Chile, throughout the entire period of the study. Bold lines indicate the proportions of active behaviour for each hour. (b) Daily activity patterns across seasons.

food is available during this season (Rathcke and Placey 1985). We would expect that pudu in Caramávida would adjust its spatio-temporal ecology as a mechanism to avoid predation, considering the complex assemblage of carnivores, and thus predation pressure (Zúñiga et al. 2017). As the puma (*Puma concolor*), which is the main predator of pudu (Rau and Jiménez 2002; Zúñiga and Muñoz-Pedreros 2014), is abundant and mainly active during the

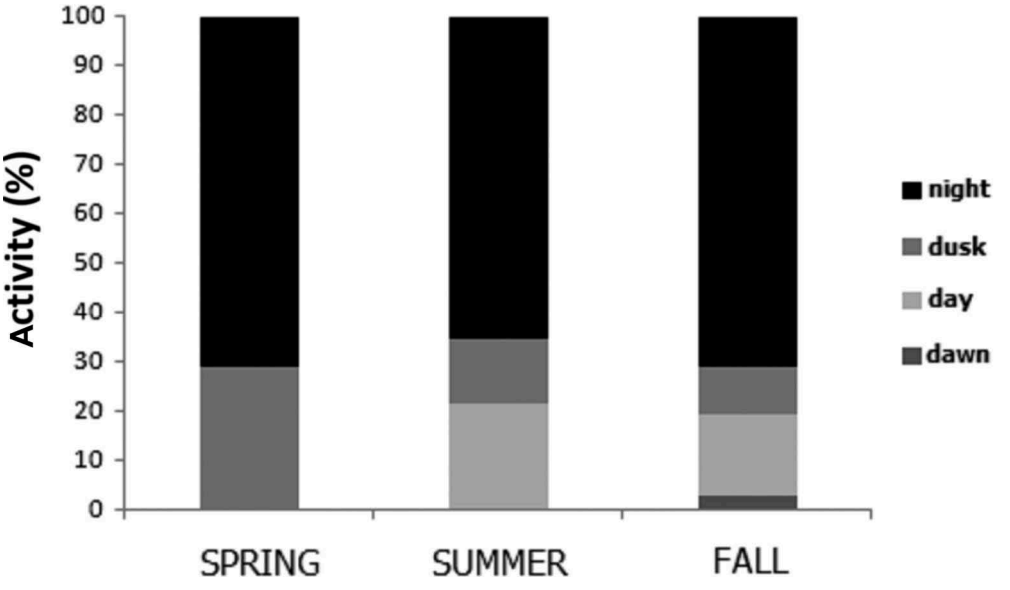

Figure 2. Percentage representation of activity patterns of pudu in Caramávida, Nahuelbuta Mountain Range, according to light availability periods (see text for criteria) during the seasons surveyed.

Figure 3. Picture of a pudu deer, obtained through camera trapping in Caramávida.

day in Caramávida (Zúñiga et al. 2017), the pudu may avoid it by being active at night. This is in line with the more diurnal pudu activity on Chiloé where pumas are absent (Jiménez 1995). However, the pudu would be confronted by the mainly nocturnal culpeo fox (*Lycalopex culpaeus*), another large syntopic predator that seems to avoid pumas and that also preys on medium-sized mammals (Jiménez 1993; Novaro et al. 2009). Likewise, the morphological similarity of culpeo to feral dogs (*Canis lupus familiaris*) suggests that dogs are an important threat to pudu, as has been repeatedly evidenced in southern Chile through frequent attacks (Silva-Rodríguez et al. 2010). Our records show that dogs continuously patrol the local trails all day long, by themselves or in the company of cowboys on horseback, which reinforces the need for pudu to complement its activity pattern with another ecological niche axis to minimise the impacts of predation.

Habitat use of pudu in Caramávida showed a positive selection for *Araucaria* forests. At least three different explanations may account for this pattern to emerge. First, in contrast to *Nothofagus* forests, *Araucaria* forests are more open and have a sparser understory that appears to offer a better mix of forbs and grasses for pudus to feed on. This more closely resembles edge habitat conditions, where Jiménez (1995) documented most pudus in Chiloé, arguing that the broad-leafed old-growth forest floor offers few feeding opportunities to pudus. Second, Jiménez (1995) and Meier and Merino (2007) claimed that pudu abundances are inversely related to people, likely mediated by the density of dogs (Silva-Rodríguez and Sieving 2012). Third, our camera trapping data at Caramávida showed a higher abundance of puma associated with *Nothofagus* forests rather than with *Araucaria* forests, which correlates inversely with our pudu records in these habitat types, a pattern expected for a prey that avoids its predator (Zúñiga et al. 2017).

In sum, the combination of strategies shown by pudu for its activity patterns and habitat use could be explained as a trade-off mechanism, based on predator avoidance – where a minimisation of active time with the main predator is observed – and maximising foraging opportunities between contrasting neighbouring habitats.

A few large tracks of native forests in the Nahuelbuta Mountains remain in good condition, but they are immersed in an ocean of exotic plantations and degraded lands, such as the one found in the Caramávida watershed. To keep the pudu and a functional native community of predators and prey in this unique and diverse ecosystem, the last remains of rainforests need to be protected from destructive influences such as forest loss and conversion, and also from the longstanding practice of country people to allow dogs to roam unleashed and free (Schüttler et al. 2018). Unless these threats are reduced or eliminated from this landscape, there is no prospect for keeping a healthy community that harbours the largest, hard-to-see predators and their prey in this southern temperate forest. This is especially important considering that the small pudu deer is the largest native herbivore in this ecosystem and may play an important role in maintaining the populations of pumas. Additionally, given that these coastal forests are scarcely represented in the national protected-area system in Chile (Pavez-Fox and Estay 2016), and that Caramávida's old-growth forest is close to Nahuelbuta National Park (Wolodarsky-Franke and Herrera 2011), every effort should be made to enhance the connectivity between these last wild patches of forests that sustain a diverse community of vertebrates (Murúa 1996; Zúñiga et al. 2017).

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