NEOTROPICAL CERVIDOLOGY Biology and Medicine of Latin American Deer

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CHAPTER 14

SOUTHERN PUDU Pudu puda (Molina 1782)

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SPECIES SYNONYMY

Capra puda, Molina, 1782: 310. Not Capra Linnaeus, 1758.

Capra puda, Anonymous, 1808.

Ovis Pudu [sic], Gmelin, 1788: 200. Not Ovis Linnaeus, 1758.

Ovis Pudu, Shaw, 1800.

[Aries] pudu, Fischer, 1814.

Antelope: de Blainville, 1816: 76. Not Antilope Pallas, 1766.

Mazama Rafinesque, 1817b: 437. Part, not *Mazama* Rafinesque, 1817a.

Antilocapra pudu, Lesson, 1842.

Cervus pudu. Gay and Gervais, 1846, Type locality Chile.

Cervus humilis Bennett, a synonym. Gay, 1847, Type locality — Chile: from Cauquenes to Chiloe; Indian name, pudu or puudu.

Coassus [(*Pudu*)] Pudu Gray, 1850, Type Locality Chile: Concepción; Chiloé.

Pudu pudu, Sclater, 1870, Type Locality Chile: Valdivia. *Pudu puda*. Flower, 1929, *Type*.—None in existence; name based on native accounts of the animal (Hershkovitz 1982).

Mazama pudu, Vanoli, 1967, Type locality Chile: Osorno-Llanquihue.

M[*azama (Pudu)*]. *pudu*, Haltenorth, 1963. *Type* locality.—Southern provinces of Chile (Hershkovitz 1982).

COMMON NAMES

Spanish: pudú, pudú del sur, venado, venadito, ciervo enano, corzuela (Hershkovitz 1982; Neumann 1992).

English: pudu deer, southern pudu, dwarf deer, pygmy deer, Chilean pudu (Hershkovitz 1982; Schürer and Sliwa 2003).

German: Pudu Hirsch, Zwerghirsch (Hick 1969a; Krieg 1925).

Indigenous (Mapuche): pudu, ruco, puüdu, puyú (Krieg 1925; Neumann 1992).

SUBSPECIES

No subspecies have been recognized, nor are there any known molecular genetic studies on the species. The distinctiveness of mainland populations versus those of Chiloé Island should be examined. The main reason for this is that, contrary to what would be expected according to the island rule (Lomolino 1985), individuals from Chiloé island are larger than those from the mainland (Jiménez, in litt.)

MORPHOLOGICAL DESCRIPTION

Hershkovitz (1982) describes the southern pudu as having short and thick legs, low slung body, and rump little or not raised above withers (Fig. 1). Ears are rounded and comparatively small, tail length is less than 8% of head and body length and is hidden by rump hairs. The neck is broad and short; rostrum and muzzle are short through the reduction of premaxilar and nasal bones (Delupi and Bianchini 1992). Spike-like antlers are present only in males, usually measuring less than 10 cm in length, (in a male caught in Chiloé the antlers measured 9.8 cm; Jiménez 1995) and directed backwards (Hershkovitz 1982). Pudus weight less than 15 kg and the height at the shoulders is 30-40 cm (Eldridge et al. 1987; Neumann 1992). Females are about 1 kg lighter (i.e. smaller) than males (Neumann 1992). The few data available on weights indicates that individuals from Chiloé are larger than those from the mainland (Jiménez, in litt.; Osgood 1943; Table 1), perhaps representing divergent phylogenetic lines. This possibility deserves closer examination.



Figure 1 - Adult wild male pudus in Chiloé. Full photo taken in Lliuco January 2005 and insert taken in Tepuhueico April 2003 (J. E. Jiménez).

Dorsal fur is coarse and the basal portions of hairs are pithy and brittle. Hairs are generally long and characteristically hollow, which provides good insulation and buoyancy when in the water (Jiménez, in litt.). In the wild, where pudus are present, the long hairs are readily found attached to the velcro-like seeds of *Uncinia tenuis* (Jiménez 1995).

Frontal glands are not evident in females. Preorbital glands –which are literally absent in *P. mephistofiles*- are large with a wide opening and a deep lachrymal fossa that open when the animal is frightened. Interdigital glands, forming a pocket and are considered the most primitive type of hoof glands in the Cervidae (Pocock 1923). Tarsal and metatarsal glands are not evident in skins (Hershkovitz 1982).

Coloration changes from rufescent and cinnamon rufous during the warm season, to dark brown in winter (Frädrich 1975; Jiménez, in litt.; Osgood 1943). Redford and Eisenberg (1992) describe the color as rich reddish brown agouti with darker head. Rump is darker (Gay 1847), sides, legs, and feet are paler, nearly clear cinnamon rufous hazel (Osgood 1943). Three complete albino individuals are known, all coming from Chiloé Island (Jiménez, in litt.; Neumann 1992). Fawns are darker than the adults and have three rows of white (Hick 1969a) or yellowish spots on each side running from the shoulders to the base of the tail. These disappear by the third month of age (Frädrich 1975; Hick 1969b; Reyes et al. 1988; Vanoli 1967; Fig. 2).



Figure 2 - Half grown pudu fawn in Chiloé (Lliuco January 2005; J. E. Jiménez).

As a curiosity, the southern pudu is listed in the book of Guiness records as the world's smallest true deer and although it is claimed by several authors to be the smallest deer (MacNamara 1983; Miller et al. 1983; Osgood 1943; Spotorno and Fernández-Donoso 1975), the northern pudu is smaller in size (Hershkovitz 1982). Several studies on the anatomy of pudus were conducted at Universidad Austral de Chile.

CYTOGENETIC DESCRIPTION

A male kariotype was first described by Koulischer et al. (1972). Spotorno and Fernández-Donoso (1975)

reported on the female chromosomes. Later Petit and de Meurichy (1989) studied the female kariotype with banding techniques. More recently Schreiber and Dmoch (1994) studied the kariotype of 1 female and 3 males. The four studies concur that the pudu's 2n chromosome number is 70 and FN is 74. Thirty three pairs of autosomes are acrocentric and 1 pair is medium-size metacentric. The X chromosome is the largest and the Y the smallest; both are submetacentric (Fig. 3). Chromosomes are identical as in other Odocoiline (Koulischer et al. 1972; Spotorno and Fernández-Donoso 1975) and the largest acrocentric pair of autosomes has conspicuous satellite appendages (Schreiber and Dmoch 1994).

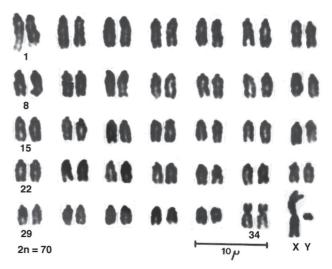


Figure 3 - Pudu male chromosomes (after Spotorno and Fernández-Donoso 1975).

DISTRIBUTION

During the first half of the past century Osgood (1943) described the pudu as being fairly common in the provinces from Arauco to Llanquihue and to be numerous at Lake Todos Los Santos, where currently it is seldom seen (Jiménez, in litt.). Osgood (1943) also described pudus as shy and uncommon in Chiloé, which is opposite to the current situation; up to 8 animals can be observed in one day and tracks are found in many areas of the island, but they still remain shy given the risks they face. Thus, it appears that the fragmentation of the landscape –as on Chiloé- may have favored the pudu as a species that forages along edges and openings close to the forest (Jiménez 1995), rather than exploiting continuous tracts of pristine forests, as is commonly and repeatedly believed, but never been documented as of yet.

The pudu is restricted to the southern temperate rainforests of Chile and adjacent Argentina (Fig. 4). According to Gay (1847) it ranged from Cauquenes province south to Chiloé, in Chile. Osgood (1943) described it up to Isla Riesco (50°S) almost to the Strait of Magellan in the south. Hershkovitz (1982) –based on secondary references- claims its distribution is from Maule to the vicinity of the Strait of Magellan in Chile and from southwestern Neuquén to southwestern Chubut in Argentina (see also Ramilo 1992, and Meier and Merino 2007). The southern distribution in Chile is not substantiated with records, and seems to be unlikely. The most current and accurate distribution seems to be that reported by Glade (1985), as being found in Chile between 35°10' (Río Mataquito and Lontué) and 46°45'S (Lake Buenos Aires, Peninsula Esmeralda and Laguna San Rafael -Fig. 4). However, recent observations confirm its presence near the town of Tortel (Jiménez, in litt.). It is abundant on Chiloé Island (Glade 1985; Jiménez 1995; Miller et al. 1983) and although Reiche (1903 in Osgood 1943) considered it extirpated from Mocha Island, MacNamara and Eldridge (1987) claim that it still occurs there, but there is no recent evidence. There is evidence that pudu may have ranged north up to Santiago (Saavedra and Simonetti 1991; see also Hershkovitz 1982) in the recent past. Pudus are found at elevations from sea level up to 1,700 m in the Andes (Miller et al. 1973). Due to human destruction of ca. 90% of the temperate rainforests (MacNamara 1983) and persecution, the pudu range has been reduced, but it is still found along the Andean and coastal mountain ranges, mainly on the southern part (Wetterberg 1972). The valley populations are scattered and isolated in the few forest patches left, which are highly vulnerable to human related pressures (Bello 2003; Jiménez, in litt.).

KNOWN POPULATIONS

Pudus are often cited as the largest native herbivore found in most national parks in southern Chile, but there are no systematic records of pudu presence/absence from these areas. Recent records for the species in their northern distribution are scarce and anecdotic. Pudus run over by cars and remains in the feces of pumas and foxes are found in Nahuelbuta, Vicente Pérez Rosales, and Chiloé National Parks (Jiménez et al. 1991; Jiménez 1995; Rau and Jiménez 2002a; see also Rau et al. 1992; Rau and Jiménez 2002b; Wetterberg 1972). Additionally, reliable information from rangers and local residents report the pudu as occurring in the National Reserves Altos de Lircay and Los Huemules de Niblinto, and the National Parks Tolhuaca, Conguillío, Puyehue, and Queulat along the Andes. In Argentina it is found in the National Parks Lanín, Nahuel Huapi, Lago Puelo and Los Alerces (Ramilo 1992; Meier and Merino 2007). Based on interviews of local residents and signs found in the field, Bello (2003) compiled fresh evidence of pudus still living in several patches of native, but disturbed forests in the lowland areas close to Valdivia.

Although I have seen a few pudus directly in the wild on the mainland, in several areas of Chiloé Island it is still frequent to observe them, and up to 8 individuals can be seen daily in certain rural areas (Jiménez, in litt.), as well as in different settings with varying disturbance levels and landscape types (Jiménez 1995). It appears that aside from being apparently more numerous and larger on Chiloé, pudus are also tamer and easier to observe compared with those on the mainland. The best evidence of their presence are their tracks on soft ground, their feces, which are distinctive from domestic animals, their hairs left on seeds of carda (*Uncinia*), their remains in puma or fox feces, and more uncommon, carcasses in the field and individuals run-over on country roads.

EX SITU POPULATION

Pudus are not kept easily under captive conditions (C. Saucedo, in litt; see also Schürer and Sliwa 2003). However, it is often seen that local people in southern

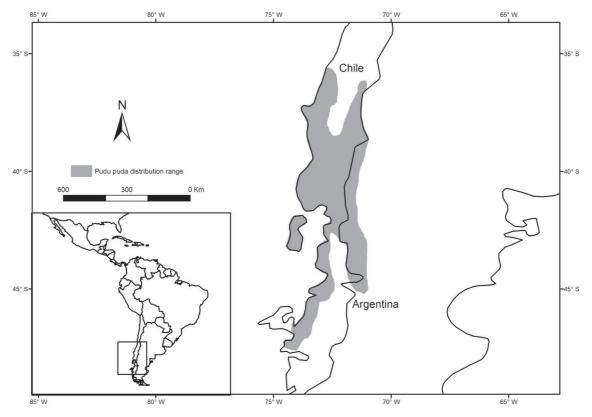


Figure 4 - Current Pudu puda distribution.

Chile keep pudus as pets and that individual animals are traded illegally. There are many reports of animals under captive conditions, some of them attempting to reproduce the species in captivity with the aim of augmenting the wild populations (Bruzone 1984; Reves et al. 1992). A pudu was exhibited for the first time in the Berlin zoo in 1896 (Frädrich 1975). The first record of captive pudus in South America comes from Housse (1953) that reports their presence in a facility in the province of Neuquén, Argentina, which no longer exists. Bruzone (1984) indicates that this facility was located in San Martín de Los Andes and that in 1946 it provided a pair of pudus to the breeding facility where pudus were kept at Isla Victoria in Nahuel Huapi (MacNamara 1983; MacNamara and Eldridge 1987; Ramilo 1992). In Chile more recent facilities that receive pudus to rehabilitate them or to breed them in captivity are at Universidad de Concepción in Chillán (Reyes et al. 2004), Universidad Austral and Forestal Valdivia in Valdivia (E. Silva and C. Verdugo, in litt.), Fauna Andina in Villarrica (F. Vidal, in litt.), and Ensenada (Jiménez, in litt.). Breeding success and survival rates in these facilities are mixed.

Several zoos hold pudus in captivity. According to Hershkovitz (1982) in 1976, 12 pudus existed in captivity; whereas MacNamara (1981) pointed out that in 1981 there were 34 captive pudus. The first reliable systematic records of captive pudus come from the International Studbook which reports that 44 males (m) and 45 females (f) were held captive in 1987 in 11 localities, mostly in Europe (Schürer 1988). Later, Schürer and Sliwa (2003) report that in 2002 there were 65 m and 71 f in 34 zoos, of these 46 m and 52 f were in Europe. More updated information from the AZA cervid taxon advisory group indicates that in 2004 there were 67 m and 67 f in 31 zoos worldwide, mainly in Europe (46 m and 45 f) and in North America (18 m and 20 f) (Fisher 2005). Similar figures for 2005 were 63 m, 74 f in 34 zoos; 43 m, 53 f and 18 m, 20 f, for Europe and North America, respectively; and 2 m in South Africa and 1 in Asia (no studbook records from South America were available). It is encouraging that 15 of the 18 births in 2005 occurred in European zoos (Fisher 2005). Thus, the captive stock in zoos and the number of facilities appeared stable during the last years. In South America, outside of Chile, the only known zoo that has 2 or 3 pudus is the Tamaikén zoo of Buenos Aires. In Chile, according to a report from the Agriculture and Livestock Bureau (SAG, in litt.), there are 295 pudus held in captivity in 18 locations, with various purposes: captive breeding, exhibits and/or rehabilitation. Although there are several places were pudus are held in Chile, their success as breeding centers is questioned as most captive centers appear to augment their stocks from wild caught animals rather than from in situ reproduction (Jiménez, in litt.).

Veterinary protocols for use of anesthetics such as ketamine, medetomidine and butorfanol were evaluated in captive pudus (Fabry et al., in litt). Likewise the use of blowpipes to deliver ketamine, xylacine and hialuronid drugs to pudus were tested (Wrege 1993). Schürer and Sliwa (2003) recommend the use of a combination of medetomidine-ketamine that can be reversed with atipamezol.

HABITAT

According to several authors the pudu lives in temperate rainforest with thick understory (Greer 1965; Hershkovitz 1982; Krieg 1925; Meier and Merino 2007; Miller et al. 1973; Neumann 1992; Ramilo 1992; Vanoli 1967; Wetterberg 1972). However, the species is also common in disturbed and secondary forest when it is not chased by people and their dogs (Bello 2003; Eldridge et al. 1987; Jiménez 1995; Miller et al. 1983; Fig. 5). Pudus favor especially habitats with dense bamboo (Chusquea spp.) that are used as cover rather than for feeding. Under thick bamboos pudus make runways through which they can move at almost full speed when escaping from threats (Eldridge et al. 1987; Jiménez, in litt.). Pudus use the entangled forest understory mainly for cover. They move to forest edges or more open shrublands for feeding (Figs. 1 and 5), given that there is a higher availability and diversity of soft growing plant tissue (Eldridge et al. 1987; Jiménez 1995). Some authors indicate that the proximity of a river or other water bodies is usually an important component of habitat both as a continuous source of drinking water as well as an escape route from terrestrial predators (Jiménez 1995; Junge 1966; Neumann 1992; Vanoli 1967). On Chiloé pudus are observed in different habitats and under contrasting disturbance and landscape conditions, ranging from heavily disturbed shrubland on the shoulder of the main highway, in forest patches scattered in an agricultural landscape with dairy cows and loose (unrestrained) dogs to coastal and mountain populations under pristine conditions, not always close to water (Jiménez, in litt.). A field study indicated that the relationship between relative abundance of pudus and human disturbance level (with little dog impact) was negative, reflecting perhaps that a more fragmented environment favors pudu by providing more growing plant tissue along edge habitats (Jiménez 1995). Forest gaps were perceived as high quality patches for pudus. In the same study, pudus were found to be more abundant on the lower areas that were also more fragmented.



Figure 5 - Yearling female pudu in Chiloé in typical disturbed environment (El Quilar January 1995; J. E. Jiménez).

SPATIAL USE AND HOME RANGE

As many other aspects of the species' ecology, the spatial use of the environment by pudu has been little studied. Only two studies have documented the movement and habitat use of pudus in the wild, mainly with captive-released animals, in heavily disturbed habitats, restricted under island-type landscapes, and in sympatry with dense populations of exotic deer. Seven pudus were studied at a 1,200-ha Peninsula on Rupanco Lake (Chile). Four of them (3 of which were introduced into the peninsula) had minimum convex polygon home ranges of 16 to 26 ha in size (Eldridge et al. 1987). Although individuals differed in their behavior, on average they used forest and shrubland habitats more than expected by chance. Habitat quality ranged from relatively undisturbed forest to totally altered habitats, which indicated that pudus did not depend on mature forest for all their needs. Some home ranges were used by other non-tracked individuals as tracks indicated that they were following each other. Pudus were territorial and at least one male tracked across seasons was sedentary all year round. During this study, it was also noted that a puma that raised 3 cubs in the peninsula may have removed at least 30 pudus (Courtin et al. 1980).

The other telemetry study followed 10 of a total of 20 released pudus on Isla Victoria, a 3,710-ha island with no predators, in Argentina (Ramilo 1992). Four individuals had home ranges that varied between 2 and 200 ha. At Victoria island, unlike the exotic deer, pudus used the densest parts of the forest and thick shrublands of *Berberis* sp. to feed and for cover. The captive bred animals stayed close to the release point, whereas the 2 wild caught individuals moved extensively, one of them up to 20 km. My direct behavioral observations of wild pudus in Chiloé and data obtained with camera traps and scented stations concur with previous reports that pudus use the edges more than the forest interior and they use a well-known network of trails in thick shrubland (Jiménez 1995).

FEEDING ECOLOGY

The pudu is a browser whose nutrition generally comes from high growing plants as opposed to a grazer that feeds heavily on grasses. Pudus feed on a great diversity of forest-associated species eating the most nutritious and less lignified parts of plants made up of young leaves and sprouts of trees, shrubs and forbs, fruits and flowers. As understory plants, such as saplings and forbs are abundant along edges and in forest openings, it seems that edges and fragmented environments are preferred feeding areas of pudus, rather than forest interior habitat, where there is little nutritious vegetation (Jiménez 1995).

Different researchers have generically described the diet of pudu as composed of herbs, foliage, and shoots (Hershkovitz 1982; Miller et al. 1973; Wetterberg 1972). Specifically, Krieg (1925) indicated that pudus feed on *Fuchsia magellanica* and *Chusquea* sp. and Vanoli (1967) and Neumann (1992) report that they feed on several shrubs species such as *F. magellanica*, *Ugni molinae*, *Berberis buxifolia*, *B. darwinii*, *Crinodendron*

hookerianum, Pernettya pumila, Azara sp., Gunnera tinctoria, Chusquea quila, C. coleu, and Aristotelia chilensis. Pudus also eat the leaves of trees such as Luma apiculata, Amomyrtus luma, Blepharocalyx cruckshanksii, Nothofagus dombeyi, Embothrium coccineum, and Lomatia ferruginea (Neumann 1992).

Detailed observations of feeding pudus and browsed plants in Rupanco Lake indicate that many plants are fed upon, but few are preferred, among them several exotics, such as *Rubus* sp. (Eldridge et al. 1987). The same study showed that pudus feed more on scrublands than in forest or bamboo habitat types. From the higher vegetation stratum pudu fed chiefly on ferns (e.g., *Blechnum*), tree leaves, and shrubs (e.g., *Rhaphitamnus*), being the later the most preferred. Some individuals also fed on vines (*Hydrangea* and *Luzuriaga*) and herbs. They ate 60-80% of all the plant species available, and specific individuals used 25-79% of them.

In the lowest vegetation strata animals fed more on herbs, vines and ferns, whereas mosses and grasses were least preferred (Eldridge et al. 1987). In open habitats pudus foraged on *Plantago*, *Lotus*, and *Dactylus*. Reeds and sedges were avoided.

Fleshy fruits of avellanas (*Gevuina avellana*) and of mirtacea trees are eaten by pudus (Greer 1965; Jiménez 1995; Neumann 1992; Wetterberg 1972). In captivity pudus feed on blackberries, roses, apples (fruits and leaves), strawberries, chestnuts, hazel nuts, acorns, topinambur potatoes, carrots, celery, red and white clover, plantain, pine fungi, and the southern beech fungi *Cittaria* sp. (Junge 1966; Neumann 1992; Vanoli 1967). In Chiloé locals report that wild pudus like to raid their gardens and eat the leaves of apple trees, rose plants, potato shoots, and peas (Jiménez 1995).

Systematic direct observations of wild pudus feeding on browsed vegetation detected on a few sites in Chiloé with different impact levels indicate that they feed intensely and primarily on exotic forbs (i.e., Taraxacum officinale, Lotus uliginosus, and Plantago lanceolata), some ferns, buds, and growing tissues of saplings of most native tree species, avellana fruits, and flowers of Taraxacum sp. and Lotus sp. (Jiménez 1995). Pudu ate seedlings and saplings of Amomyrtus luma, Caldcluvia panniculata, Embothrium coccineum, Eucryphia cordifolia, Myrceugenia planipes, Nothofagus nitida, Pseudopanax laetevirens, and Weinmannia trichosperma. The following vines and epiphytes were taken Asteranthera ovata, Boquila trifoliata, Griselina racemosa, Luzuriaga radicans, Mitraria coccinea, and Sarmienta repens. Shrubs (buds and new leaves) fed upon by pudus were: Baccharis racemosa, Baccharis sp., Chusquea quila, Escallonia sp., Fuchsia magellanica, Gaultheria pillyearifolia, Gunnera tinctoria, Rubus ulmifolius, Senecio otites, and Ugni molinae. Ferns and reeds included in the diet were: Blechnum chilensis, Blechnum pennamarina, Juncus sp. (flowers), and Lophosoria quadripinnata. Pudus fed throughout the day, but more often late in the afternoon, early at night (at night they can be spotted with headlights due to the yellow glow of their eyes) and early in the mornings. When feeding, the animal moves slowly through the vegetation, quickly

taking bits here and there, of many different plant species (Jiménez 1995).

Microhistological analysis of feces remains also showed, as predicted for a herbivore of this small size, that the pudu is a highly selective species (Jiménez, in litt.). This study indicates that in undisturbed sites pudus fed more on trees and shrubs rather than on forbs. The opposite was true in areas that are more fragmented and where forest gaps and edges were more abundant. Interestingly, the exotic and widespread blackberry (*Rubus ulmifolius*) emerged as a highly-preferred species on disturbed sites and the vine *Asteranthera ovata* as preferred at undisturbed sites.

The rectangular crown morphology of the incisors (Traub 1984) and the small size of the arcade (Jiménez, in litt.) indicate that pudus can finely select specific plant structures from what is available, and can thus have a very selective diet (Jiménez 1995; Neumann 1992). Pudus dot not take large quantities of a single species of plant, but little bits of everything (Jiménez 1995; Vanoli 1967). Compared to the highly frugivorous *Mazama americana*, *Cephalophus dorsalis*, and *C. maxwellii*, the digestion efficiency of the pudu was similar to them (Conklin-Brittain and Dierenfeld 1996). This same study estimated that mean transit time of forage was 29.9 hr.

REPRODUCTIVE BIOLOGY

Mating occurs in March and April; intercourse is quick (2 to 3 sec) and is repeated frequently during a 48-h receptive period of the doe (Reyes et al. 1988). Gestation in captivity takes 207 and 223 days according to Vanoli (1967), 202 days according to Hick (cited in Schürer 1988), and 197 to 210 days (n = 6 — Reves et al. 1988). Blanvillain et al. (1997) examined the birth records of the studbook and reproductive hormones in the feces of captive pudus. They found that in the southern hemisphere fawns are born between October and February, peaking in November and December (n = 36births) and determined that the females are polyestrous breeders with cycles every 11 days. Records of 13 births by Bruzone (1984) in Argentina showed similar peaks in November and December. MacNamara and Eldridge (1987), Neumann (1992), and Schürer (1988) also found similar timing for birthing and Reyes et al. (1988) added the month of October. Usually 1 fawn is born (Hershkovitz 1982), but Neumann (1992) reported 3 cases of twins. Schürer and Sliwa (2003) documented a sex ratio at birth of 372 males to 389 females and four cases of twin births; whereas Frädrich (1975) documented a sex ratio 1:1 in 22 fawns born. Reyes et al. (1988) described parturition in captivity and Hick (1969a,b) the behavior of a fawn during its first 2 months of life.

Fawns weight 850-1000 g, are 19.5 to 20 cm high and at 2 months reach the size of the adults (Neumann 1992), whereas Reyes et al. (1988) describes newborns weighting 700-1110 g and having a height of 17.5 to 23 cm. According to Schürer and Sliwa (2003), at birth female fawns weight 896 g (n = 28) and males 884 g (n = 27). Fawns loose their spots before three months of age. Young become reproductive at 6 moths of age (Vanoli 1967) and at 15 to 18 months as determined histologically by Reyes et al. (1988). In zoos the minimum age of conception was a female of 4.5 months of age and the maximum recorded was in a female of 6.5 years, with a peak during 12-18 months (n = 144; Schürer and Sliwa 2003). The youngest recorded male mated at an age of 4.7 months and the oldest did it for the first time at 9.5 years. However, most males mate between 2 and 2.5 years (n = 104; Schürer and Sliwa 2003).

Mean and maximum life expectancy of captive females is 4.35 and 17.4 years, respectively (n = 194), whereas for males is 4.44 and 15.8 years, respectively (n = 190 -Schürer and Sliwa 2003). Mortality (pooled sexes) during the first 30 days of life is 26%. The average life time achievement of 121 females was 3.88 fawns. One female produced 14 fawns throughout her 15 years of life and a male sired 28 fawns (Schürer and Sliwa 2003).

In bucks the size of testicles and spermatogenesis show 2 peaks, in spring and in the fall (Reyes et al. 1988). Similarly, Bubenik et al. (1996) found that males have 2 high peaks of testosterone (March and October) and LH (February/March and July-September) along the year as it occurs in the roe deer (Capreolus capreolus) and one peak of cortisol in March (Reyes et al. 1997). These were associated withs the rut, with the mineralization of the antlers and with social dominance (Bubenik et al. 1999; 2002). The rut was also documented by Bruzone (1984) as occurring during April and May, and MacNamara and Eldridge (1987) included June. Young males have their first antlers at 9 months of age according to Vanoli (1967), and at 12 months according to Reyes et al. (1988). Antlers are shed in July (Vanoli 1967; Hick 1969a; MacNamara 1983; MacNamara and Eldridge 1987) and are controlled by variations of androgens (Bubenik et al. 2002). Fabry et al. (2004) obtained sperm with electroeyaculation, with high variability in numbers and quality of sperms among captive males. Samples are stored in a sperm bank in the Santiago zoo.

BEHAVIOR

The pudu conforms well to the syndrome of the small solitary forest ruminants, by sharing many adaptations to forest life with other ruminants and rodents (Eisenberg and McKay 1974). These include being small with little sexual dimorphism, territorial, solitary and dispersed, having spotted fawns, avoiding predation by freezing, and been a cryptic and inconspicuous forest dweller that communicates with scents and that is highly selective for nutritious foods (Jiménez manuscript).

First descriptions that pudus form herds (Gay 1847; see also Wetterberg 1972) are not correct as they are essentially solitary when not in rut (MacNamara and Eldridge 1987; Ramilo 1992, Reyes et al. 1988; Vanoli 1967; see also Courtin et al. 1980). During spring and summer, females are seen with their fawns until they become independent just before eight months of age (Hershkovitz 1982; Jiménez, in litt.). Males and females are territorial and do not accept another individual of the same sex in their territories, defending it with their antlers and hoofs to the point of killing intruders with their antlers (Eldridge et al. 1987). Individuals mark their territories with urine, feces, antler rubs, preorbital glands, and by

scratching the ground with their frontal hooves (Feer 1984; Jiménez 1995; MacNamara and Eldridge 1987; Neumann 1992). The use of latrines is a specialized defecation behavior important in communication among pudus (MacNamara and Eldridge 1987). Observations of a dominance hierarchy, as described in captive animals by Bartoš et al. (1998), Bruzone (1984), Cortés et al. (1988), Feer (1984), and Neumann (1992) may be misleading given the crowded and artificial conditions of captivity. Pudus are also sedentary (Eldridge et al. 1987; Miller et al. 1973; Ramilo 1992) and early descriptions of Molina (cited in Hershkovitz 1982) that they descend from the mountains during winter may not be accurate.

The pudu social behavior has not been quantified under natural conditions. Cortés et al. (1988) described 7 different types of behavior in captive pudus. Four of them were agonistic behaviors (i.e., crouching, displaying the shoulder, standing, and scratching the ground) and 3 were of general type (i.e., alert, sniffing, and calling the fawn). Neumann (1992) described 19 different types of behavior observed in captive animals. In a more detailed study, MacNamara and Eldridge (1987) compared the behavior of pudus and Mazama americana, indicating that their behaviors resembled those of most cervids, but each of these 2 species had unique patterns. These authors described a rich repertoire of 40 different types of behavior in captive pudus grouped in 3 non-mutually exclusive categories of maintenance, object-oriented contact patterns, and scent marking. In descending order, the most common types of behavior in both genders were defecating, withdrawing, urinating, sniffing, smelling, chasing, and following. As described by other researchers, the sense of smell plays a crucial role in the life of pudus (MacNamara and Eldridge 1987).

Although variability in daily and seasonal activity patterns exist among wild pudus, on average they were active about half of the time, and most of their activity was nocturnal, especially during late afternoon and evening, and early mornings (Eldridge et al. 1987). Individuals were less active during calm and sunny days, than on windy and sunny days. These activity patterns agreed with observations of several wild pudus in Chiloé (Jiménez, in litt.). However, unlike Junge's (1966) claim that pudus are intolerant of heat, a buck was observed for more than 30 minutes feeding during midday under direct sunshine in a calm and hot summer day, before retreating into the forest (Jiménez 1995).

INTER-SPECIFIC RELATIONS

Anecdotal reports consider pumas (*Puma concolor*), foxes (*Pseudalopex* spp.), kod-kods (*Oncifelis guigna*), and owls (*Bubo magellanicus*) as pudu predators (Glade 1985; Hershkovitz 1982; Neumann 1992; Vanoli 1967). Quantitative studies indicate that in some areas pudus made an important part of the puma diet. Courtin et al. (1980) estimated that in less than a year at Rupanco Lake, one puma killed 30 to 40 pudus, whereas Rau et al. (1992) working in southern Chile estimated that in one year a puma would kill 15 pudus, an amount that made up 11 to 49% of the puma diet biomass and that European hares acted as alternative prey. Puma appeared to prey mainly (73%) upon juvenile pudus (Rau et al. 1991). Rau and Jiménez (2002a), comparing the diet of coastal and Andean puma populations in the Lake Region, found that pudu made up 5.9% of coastal puma prey and 22.6% of the diet of the Andean population.

Regarding other predators of pudus, only Darwin's foxes (*Pseudalopex fulvipes*) have been studied. Medel et al. (1990) found that 2% of the prey of foxes in Nahuelbuta National Park were pudus and a longer study reported only 0.2% of pudus as prey of foxes in the same park and 3.9% on Chiloé Island (Jiménez et al. 1991). On Chiloé National Park the pudu made 5.2% of Darwin's fox prey (Rau and Jiménez 2002b), in Piruquina 2.8 to 6.9% of prey were pudu (Jiménez 2000) and in Ahuenco (also on Chiloé Island) the pudu composed 2.7% of its prey and was found in 6.1% of the fox feces (Jiménez 2007). Aside from the above, no other carnivore or raptor was confirmed as a pudu predator.

PARASITOLOGY

The parasitic fauna of the pudu is relatively well known. Most of the studies conducted are based on autopsies of animals killed or caught in the wild or from captive individuals. Sievers (1992) reviewed the parasitology of pudus and describes that eggs of Strongylida sp. are found in fecal samples and that 55 to 100% of the feces had eggs of the pulmonary nematode Muellerius sp. (also found in sheep and goats), which is the most important parasite for the species, along with Capillaria sp. and Eimeria sp. Intestinal parasites of pudus shared with domestic livestock, were Ostertagia ostertagi, Spiculopteragia asymetrica (Díaz et al. 1977), Oesophagostomum, Nematodirus, Trichostrongylus and Cooperia (Sievers 1992). The pudu is one of the hosts of Cysticercus tenuicollis, the larval form of the cestod Taenia hydatigena (Díaz et al. 1977; González-Acuña 2002; Sievers 1992; see also Frädrich 1975 and Neumann 1992). Linguatula serrata were found in pudu lungs and livers (Fernández 1986 in González-Acuña et al. 2004). Dictyocaulus sp. produced a case of bronchopneumonia and Sarcocystis sp. was found in skeletal and heart muscle (Díaz et al. 1977). Neumann (1992) reported that 5 captive individuals died from foot and mouth disease. Junge et al. (2000) describe a poxvirus infection in captive animals and Ortega et al. (in litt.) the first isolation of bovine pestesvirus from a dead wild pudu.

Pudu has several external parasites. González-Acuña et al. (2004) reported the Phthiraptera lice *Bovicola caprae* (common in goats) and the Anoplura *Solenopotes binipilosus* (common in other wild cervids) from 7 pudus and described the acaridae *Ixodes stilesi* and *I. taglei* in pudu (González-Acuña and Guglielmone 2005). In necropsies of pudus, Sievers (1992) has found pudu ticks *Ixodes taglei* (see also Kohls 1969), Hippoboscidae biting flies *Lipoptena pudui*, chewing lice of the family Bovicolidae and biting lice *Linognatus* sp. All these external parasites are unique from pudu.

CONSERVATION STATUS

The pudu is considered as Vulnerable both in Chile (from the VIIth to the Xth Region and Insufficiently Known

in the XIth Region - Glade 1993) and in Argentina (Ramilo 1992). It is listed in Appendix I of CITES and is considered as Vulnerable by the IUCN (VU A2cd+3cd) (Jimenez and Ramilo 2008).

The pudu is generally perceived as a species that is declining mainly due to habitat fragmentation, loss, and conversion into open lands and exotic tree plantations, competition with livestock, been killed directly by people or by their vehicles on roads, and more than anything else by the many feral or unleashed dogs in the countryside that specialize in hunting pudus (Bello 2003; Eldridge et al. 1987; Glade 1985; Hershkovitz 1982; Jiménez 1995; Junge 1966; Krieg 1925; MacNamara 1981; Miller et al. 1973; 1983; Ramilo 1992; Wetterberg 1972). Nonetheless the above and the general agreement that populations are being affected, there is no study that examines any of these threats to pudus in a systematic way. In several places, dogs are unleashed, not well fed by their owners and go out in the forest at any time to hunt pudus. Dogs return to their homes engorged and defecate abundant pudu remains. Camera traps have also confirmed that these dogs used the same trails as pudus (Jiménez 1995). It seems that dogs learn quickly how to hunt pudus and specialized in finding and killing them (Neumann 1992). Dogs are often seen chasing panting pudus for long distances in Chiloé (Jiménez, in litt.) as well as on the mainland (Bello 2003). Further, in some localities, pudu skeletons are often found in the wild, most likely killed by dogs. Pudus are not enduring runners and become exhausted quickly (Junge 1966), if a body of water where they can jump into is not readily available, the chances of a pudu to escape from dogs are slim. To escape from predators, pudus use the tactic of running fast in the thicket for a few meters, emitting a characteristic noise in ca. 5 to 20 panting bursts that is heard as a loud agitated breathing, and then freeze in the understory. In this way they avoid being found by remaining cryptic and motionless. This behavior might work for native predators, but dogs follow the scent and quickly find them (Glade 1985; Jiménez, in litt.). A feral dog management plan (Dellafiore and Maceira 1998) and education campaigns for the responsible tenure of domestic dogs within pudu range is highly desirable to help conservation of the species. Because populations coexist in areas with cattle and sheep, contrary to what is often claimed, competition with livestock does not appear to be a threat to pudus (Jiménez 1995, Meier and Merino 2007).

Pudu populations are still declining and the range of the species has diminished considerably and become more fragmented due to temperate rainforest fragmentation, loss, and conversion into pastures or exotic tree plantation (Eldridge et al. 1987; Hershkovitz 1982; MacNamara 1981; Miller et al. 1973; Schürer 1988). It is generally accepted that over 90% of former pudu habitat in Chile has been lost (MacNamara 1983). Other causes of the decline are poaching for zoos and private collections (Bruzone 1984). There is compelling evidence that during recent decades pudus were heavily poached for the pet trade. Only on Chiloé Island, more than 600 pudus were taken alive from 1983 to 1985 (T. Daube, in litt.; Jiménez 1995). Pudus are also killed as a source of protein by local residents (Bello 2003; Hershkovitz 1982; Jiménez, in litt.; Junge 1966; Miller et al. 1973). Rural people would kill a pudu when they have a chance. On the Pacific shore of Chiloé, fishermen often report that they supplement their diet with pudu meat (Jiménez, in litt.), as is also the case with farmers on the mainland (Bello 2003).

Other important causes of the decline are diseases transmitted from livestock and potential competition by introduced deer (Eldridge et al. 1987; Glade 1985; MacNamara 1981; 1983). Circumstantial evidence supports the last two claims. Eldridge et al. (1987: 361) reports that pudus avoid areas occupied by exotic deer and Díaz et al. (1977) reported at least 5 different endoparasite species in wild pudus, 2 of which are shared with domestic livestock as well as with free-ranging exotic ruminants (see bellow).

Perhaps, one of the main limitations for science-based conservation actions on pudus is the lack of information available from wild populations. The pudu is an extremely difficult species to study in the wild, mainly because of the type of environment where it lives (remote, thick, moist, etc.), their low densities, and secretive and elusive habits. As a result, the literature on the species is almost entirely anecdotal (MacNamara and Eldridge 1987; Miller et al. 1983). To my knowledge there is no information on attempts to quantify pudu populations in the field. The best population estimation is that there are less than 10,000 individuals left in the wild (Fisher 2005; Hershkovitz 1982; MacNamara and Eldridge 1987). During 1995 research was conducted to test three independent methods for estimating pudu relative abundances (camera traps, hair collectors, and scented stations) on Chiloé Island, attempt to capture individuals with snares and traps made up of fishing nets, and describe information on the natural history of the species, evidence left in the wild, feeding behavior, and detailed observations of 6 individuals (Jiménez 1995). Aside from this study, there is no other account on quantitative information of free ranging wild pudus.

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