Variation in reproduction of a temperate deer, the southern pudu (*Pudu puda*)

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Abstract. Pudu (*Pudu puda*), occurring in the southern cone of Latin America, has been classified as vulnerable by the International Union for Conservation of Nature (IUCN), yet little is known about this animal in the wild, with most knowledge on the breeding behaviour coming from captive animals. For this second-smallest deer in the world, delayed implantation has been suggested to explain the two peaks in the annual cycle of male sexual hormones on the basis of the accepted tenet that the breeding period occurs only once a year, between March and June. However, in the present study, birth dates from fawns born at the Los Canelos semi-captive breeding centre in Chile and male courting behaviour revealed the possibility of two rutting periods: autumn and spring. To our knowledge, this is the first time that late-fall births (May through early June for 17% of fawns in the study population) have been recorded for the southern pudu; two of these four births were conceived by females in the wild. From zoo and captive-animal birth records (*n* = 97), only three fawns were born in the fall. For all births combined (*n* = 121), 77% occurred in spring. The roe deer (*Capreolus capreolus*) and Pere David deer (*Elaphurus davidianus*) have been considered the only two temperate cervids in which sexual activity is initiated by increasing daylength and which breed in early summer. Yet, the present results indicate a similar response from the southern pudu when under a wild or semi-captive environment, with breeding taking place in spring. These results suggest that this species may either have two reproductive periods per year or retains the capacity to be a breeder for a much more extended period of time than documented by earlier studies. Pudu, like other temperate deer, is responsive to photoperiod for timing its breeding period, but may further optimise its production of offspring by also responding to other environmental cues such as seasonal variation in food supply when climatic conditions are favourable.

Additional keywords: aseasonal reproduction, austral, parturition, subtropical breeding, Valdivian rainforest.

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Introduction

The southern pudu (*Pudu puda*) occurs only in southern Chile and south-western Argentina (Fig. 1). The species' distributional range continues to diminish in size due to anthropogenic impacts, with populations today mainly found in the temperate rainforests along the southern Andes. In southern Chile, the species also inhabits the coastal mountain range and scattered forest patches in the valleys (Hershkovitz 1982; Jimenez 2010). Although classified as vulnerable by the IUCN (2008) and being a unique species in that it is ranked as the second

smallest deer in the world (Hershkovitz 1982; Whitehead 1993; Geist 1998), weighing in at <15 kg (Hershkovitz 1982) (cf. 9–10 kg in Whitehead 1993; 6.4–13.4 kg in Geist 1998), little has been published on the biology of this species. Even less is known about the only other species to share its genus, the smaller northern pudu (*P. mephistophiles*), from which it is separated by ~3200 km (Whitehead 1993). The cryptic behaviour of southern pudu in the wild makes it a particularly difficult animal to study in its habitat of dense vegetation along its altitudinal range from sea level to 1700 m above sea level (masl). The individuals are often

Fig. 1. Southern pudu male (*Pudu puda*) in August (winter, photo by J. M. Smith-Flueck).

solitary or in small family groups, coming out to feed at the forest edge in undisturbed areas (Jimenez 2010). Given their elusive nature in the wild, most information on the southern pudu has been acquired through studies on physiology and behaviour of captive animals, and predominately on investigating hormonal profiles in males (reviewed in Bubenik *et al.* 2000). A Web of Science search of original studies published on southern pudu since 1923 revealed 35 hits, of which 91% were of captive populations.

Gestation period in captivity has been recorded to last from 197 to 223 days (Vanoli 1967, cited in Jimenez 2010; Hershkovitz 1982; Reyes *et al.* 1988). Normally, females have one fawn but twins also occur (Hershkovitz 1982; Whitehead 1993). For captive breeding populations, the data have indicated that a monomodal breeding pattern exists in pudu, with the breeding season generally assumed to be between April and June (MacNamara and Eldridge 1987; Whitehead 1993) and for one captive population (Concepción, Chile) between March and April (Reyes *et al.* 1988). Recorded births from captive females have indicated one birthing period between October and February in the southern hemisphere (MacNamara and Eldridge 1987; Reyes *et al.* 1988), with the fawning period shifted by 6 months in northern hemisphere zoos, falling between April and August, with a peak in May (Hershkovitz 1982; Blanvillain *et al.* 1997); individuals translocated to the northern hemisphere synchronise quickly to the local photoperiod. Females remained receptive for ~48 h, during which time they could be bred by multiple males (Reyes *et al.* 1988).

Results from a study on captive females in Europe suggested that the southern pudu is a seasonal polyestrous breeder, with a reproductive cycle cued to a seasonal factor and a cycle length of ~11 days (Blanvillain *et al.* 1997). Given the wide variation of the oestrous cycle length of three mature females (16, 18 and 33 days), Blanvillain *et al.* (1997) proposed that pudu females might respond to seasonal cues with less rigidity than does northern temperate deer. Bubenik *et al.* (2000), however, in comparing the length of gravidity in pudu (average of 203 days, Reyes *et al.* 1988) with that of red deer (average of 232 days) – an animal 10 times heavier than the pudu – considered the pudu's gestation to be enormously long and speculated that this species might exhibit delayed implantation of the embryo, unique only to the roe deer (*Capreolus capreolus*) among artiodactyls (Aitken 1974; Semperé 1990; Lambert *et al.* 2001). To our knowledge, this hypothesis has never been investigated. Here, we provide observations of reproductive behaviour for the first time from a semi-captive population of pudu and from the wild that challenges this hypothesis and suggests yet another strategy unique to a temperate deer.

Materials and methods

The current study population consists of 28 pudu at the semi-captive centre operated by Fauna Andina, Los Canelos (39°16′S), in the central valley near Villarica, Chile, Araucania Region, within the natural distributional range of the species. The climate is mild and humid with average minimum–maximum temperature ranges in summer and winter of 9–26°C and 4–15°C, respectively, with main precipitation as rain between May and July (late autumn and winter, with 517 mm average, and a total annual average precipitation of 1130 mm). The 13-ha enclosure at 330 masl consists of a mixture of native vegetation common to the Valdivian temperate rainforest ecosystem and open patches of grassland pastures (~2.5 ha); *Nothofagus* and *Festuca* species predominate inside and surrounding the enclosure. All animals are free-roaming inside the enclosure. Disturbance and contact is minimal so that animals retain their elusive behaviour and natural fear of man to facilitate their subsequent reintroduction. No one but the caretaker (F. Vidal) and authorised researchers and government inspectors under Vidal's supervision are allowed into the enclosure. Fresh water is available year round from streams that do not come in contact with any domestic animals or livestock before reaching the pudu.

Data were collected on birth dates of pudu born at the Los Canelos Centre (LCC) between 2000 and 2010, either by directly observing the parturition or the neonate within 2–3 days after birth. Surveillance through cameras and direct observations, made on a daily basis throughout the year, was increased during the birthing period. Individual features allowed for reliably distinguishing mothers and their neonates by caretaker, who was the only person that animals were acclimated to. This dataset of a semi-captive population was compared with parturition dates of captive pudu in the northern and southern hemisphere. For the southern hemisphere, these included 22 births at the captive-breeding centre of La Victoria Island (41°05′S) in the Argentine Nahuel Huapi National Park (MacNamara and Eldridge 1987), four births in the province of Neuquén (~40°40′S), Argentina (Schmidt 1944, cited in Hershkovitz 1982), two births in Osorno-Llanquihue (40°34′S) region of Chile (Vanoli 1967, cited in Hershkovitz 1982), one birth in an unspecified Chilean location (Hick 1967, cited in

Hershkovitz 1982) and six births at two breeding centres of the University of Concepción (36°50′S) in Chile (Reyes *et al*. 1988). For the northern hemisphere, birth records included:17 fawns born in western European zoos (Hershkovitz 1982), parturition dates (*n* = 12) of the past 5 years at the North American zoos of Detroit (42°20′N) and Woodland Park (Seattle, 47 36′N), and the United Kingdom's Belfast Zoological Gardens (54°35′N), Bristol Zoo Gardens (51°27′N), Edinburgh Zoo (55°57′N), Hamerton Zoo Park (52°24′N), Marwell Wildlife (51°01′) and Paignton Zoo (50°26′N) that were obtained from the zoos' electronic news briefs. Thirty additional births from studbook data collected from North American and western European zoos between the latitudes of 28°13′N and 55°22′N (Schürer 2009) were also included. Fawns in the studbook that died before 3 months of age were excluded from analysis to avoid including premature births. Comparison of birthdates by month were made among the following three groups: (1) captive deer from northern hemisphere, (2) captive deer from southern hemisphere and (3) semi-captive and wild deer from southern hemisphere, while taking into account that fawning period shifts by 6 months in the zoos of northern hemisphere. From the European zoos, three were conceived in Chile; for the analysis, these were included in the dataset for captive centres in the southern hemisphere. A lone winter birth (January) at Germany's Cologne zoo was not included in the dataset because no history was available regarding this individual's conception site (Hershkovitz 1982). Despite some of the record books being stolen, we have 23 dates from a total of 30 births at the centre to include in the present analysis, plus an observation of a wild fawn in the Huilo Huilo Reserve (39 48′S). For the analysis, we consider the meteorological season of winter to begin 1 June and 1 December for the southern and northern hemispheres, respectively.

On a daily basis at LCC, animals were observed for health condition and any behavioural changes. Whenever opportunities arose to record courtship, copulations and parturition behaviour, *ad libitum* sampling was conducted on those individuals.

Results

A characteristic autumnal rutting period, occurring between 24 March and 20 April was observed at LCC. A second rutting period was observed to take place in the spring, occurring between 17 October and 20 November.

For the entire dataset, the majority of births fell during the three months of spring (77%), mostly falling in the middle month of spring (50%), signifying May and November for the northern and southern hemisphere, respectively (Fig. 2). In the southern hemisphere, birth dates at captive centres in Argentina and Chile (*n* = 38) were between October and February, while birth dates for the 20 semi-captive fawns born in the spring–summer at LCC ranged from 19 October to 17 February (121 days). The spring–summer births at the northern hemisphere zoos, comprising 95% of their births, ranged from 27 April and 9 September (135 days). In the southern hemisphere study population, late-fall births (May and first week of June) were observed in 17% (*n* = 4) of the cases; of the three of these born at LCC, one was conceived in the wild; the fourth was a wild fawn seen in July at the Huilo Huilo Reserve observed from a distance of 10 m (F. Vidal and E. Arias, pers. obs.). A May birth
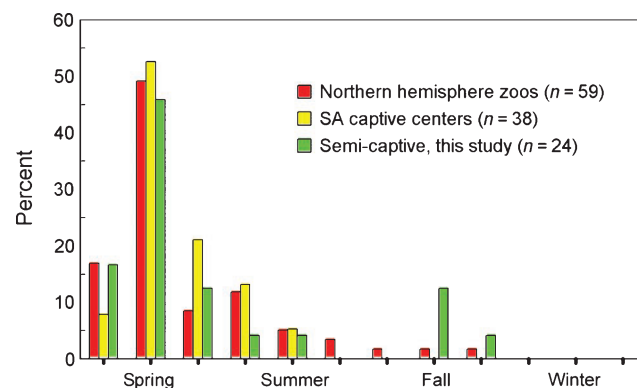

Fig. 2. Birth dates by month for southern pudu fawns born in northern hemisphere zoos, captive-breeding centres in South America, and the Los Canelos semi-captive centre in Chile (LCC). Two of the four fawns born in winter were conceived in the wild, and included one wild fawn observed at Huilo Huilo Reserve, Chile. The *x*-axis, defined by months, begins with April for northern hemisphere dates and October for the south; northern spring is April–June; southern spring is October–December.

date was estimated on the basis of the individual's size and vivid spots, which, for this species, generally begin to fade at 6 weeks of age and disappear by 3 months of age (Reyes *et al*. 1988). Births were completely absent for the 3 months of winter for the entire dataset.

Discussion

Observations of females and their fawns (*n* = 4) during parturition were similar to those of Reyes *et al*. (1988). Lying on her side, the female gives birth to a fawn with the eyes already open. The mother stands up almost immediately after her newborn is dropped and begins cleaning it intensively. Suckling was observed to take place from 10 to 60 min after birth.

During both rutting periods, males were observed to sire the females successfully, and courtship behaviour was as described in MacNamara and Eldridge (1987). In addition, just before mounting an oestrous female, the males in our study population gently nudged her hind legs. Their attempt to copulate persisted over several hours.

The endocrine cycle of the adult male pudu is rather unique among the deer species (Bubenik *et al*. 2002). Unlike most other temperate deer, the male of this species exhibits two seasonal peaks of equal magnitude for the reproductive hormones, FSH and testosterone, spaced ~6 months apart (Bubenik *et al*. 1996). Although two seasonal peaks can also be detected in various other deer species, coinciding with the summer and winter solstices and equinoxes (Bubenik 1982; Rolf and Fischer 1990), the peak outside the rutting season is much smaller than that found for pudu. The non-rutting period for these deer is characterised by a small reactivation of reproductive function and, hence, a testosterone pulse (Bartoš and Bubenik 2010), while in other species, only one seasonal peak of testosterone coinciding with the reproductive period has been detected (Bubenik *et al*. 1982; Suttie *et al*. 1984). The seasonal variation of reproductive hormones in male pudu most closely resembles that of roe deer (Semperé 1990; Bubenik *et. al* 1996; Reyes *et al*. 1997). This may not be coincidental because of similar phylogenic roots

of pudu and roe deer. Randi *et al*. (2001) analysed Cervinae by using mitochondrial DNA. Their study indicated *Capreolus* being closest to *Mazama*, a south American cervid (*Pudu* was not included in that study). Subsequently, Ruiz-García *et al*. (2007) found close roots between *Pudu* and *Mazama* (*Capreolus* was not included). Yet, even though both roe deer and pudu have two circannual peaks of reproductive hormones, in contrast, the two hormonal peaks of the blood plasma concentrations of luteinizing hormone and testosterone in the roe deer occur much closer together in time, with the spring peak being considerably smaller than the summer one (Semperé 1990; Semperé *et al*. 1992).

Whereas most tropical and subtropical species exhibit asynchronous reproductive cycles independent of the photoperiod, most temperate and boreal cervids exhibit annual rutting seasons, synchronised by photoperiod (Bubenik *et al.* 1990; Bubenik 2006). To our knowledge, with the exception of Pere David's deer, *Elaphurus davidianus* (Li *et al*. 2004), until now the roe deer has been considered the only other temperate cervid in which sexual activity is initiated by increasing daylength and which breeds in early summer, with the onset of seasonal pituitary activity occurring in January and the beginning of testicular function following in spring (Semperé 1990). All other cervids of temperate and boreal regions are short-day season breeders (Bubenik 2006). However, the observations made at LCC indicate that the southern pudu has a second breeding season in spring, shortly following the vernal equinox, with males demonstrating full mating behaviour. For roe deer, the first smaller peak in testosterone, occurring in spring, was associated with mineralisation of antlers, while the second peak, occurring in summer, was related to the rut (Semperé 1990). However, for the LCC pudu population, the observed rut activity in the austral spring and fall coincides with the two annual testosterone peaks, suggesting therefore, that the first peak is associated not only with mineralisation, but also rutting behaviour. This concurs with Bubenik *et al*. (1982) in that maximal levels of testosterone appear to be essential for rutting behaviour.

Comparably, the roe deer and southern pudu are both small-bodied temperate deer (Lincoln 1992), historically found at latitudes ranging from 19°N to 70°N and at least from 33°S to 50–53°S (Osgood 1943; Saavedra and Simonetti 1991; Jimenez 2010), respectively. Delayed implantation in roe deer may have allowed it to inhabit extremely seasonal environments, whereas in general, smaller species with shorter gestation periods inhabit mostly tropical and subtropical regions; in contrast, larger cervids, exhibiting longer gestation periods, more commonly live in the temperate and boreal regions (Bubenik 2006). Evidence suggests that ancestors of temperate cervids may have displayed two rutting periods per year (Bubenik 2006). Therefore, the bimodal rhythm could be relic behaviour of such or a vestige of some ancestral reproductive pattern such as aseasonal breeding that still persists in some extant tropical and temperate cervids (Bubenik *et al*. 2002). Regardless of their similarities, the roe deer is mostly monestrous (Semperé *et al*. 1992, 1998), and occasionally polyestrous (Strandgaard 1972), whereas the pudu appears to be seasonally polyestrous (Blanvillain *et al*. 1997). It remains to be determined to what

degree endogenous rhythms and photoperiod are driving the sexual cycle of pudu.

To our knowledge, this is the first time that a peak in late autumn births has been shown for the southern pudu. The lack of expression of a second peak in the captive situations might be explained by husbandry practices in the zoos, yet even so, one southern pudu pair at the Seattle zoo produced two offspring 8.5 months apart with birth dates of 9 September 2007 and 24 May 2008 (Schürer 2009). Although the results from our semi-captive study population suggest that pudu can have two distinct seasonal reproductive periods per year, future observations might fill in the late summer–early autumn gap and necessitate an alternative explanation. The measurements of testicular parameters indicate a prolonged period of gonadal activity in southern pudu (Reyes *et al*. 1997), more than what should be the result of hormonal concentrations alone. From the study of Reyes *et al*. (1997), it is not clear whether or not spermatozoa were absent outside of the March rut. In September, they occasionally detected a few precursor cells (most probably spermatocytes) inside the lumen of epididymal tubules of pudu males. Therefore, unless investigated, we cannot reject the possibility that the males maintain the ability to produce spermatozoa for much longer periods than is currently believed. Males of many deer species are fertile for a prolonged part of the year and are capable of mating if females are in heat. For example, in one of the most studied temperate species, the red deer, *Cervus elaphus*, the rutting season occurs in September or October (according to the region) in the northern hemisphere. After the rut, the testosterone concentration decreases almost immediately, while spermatogenesis remains very active in November and December, and then declines until June (Lincoln 1971). Under certain circumstances, complete male sexual-behaviour patterns can be induced that result in production of motile spermatozoa outside the normal rutting season (Krzywiński and Jaczewski 1978; Bubenik *et al*. 1985). One male, incited by artificial stimulants, ejaculated up to June; however, his spermatozoal concentration in early April was nearly two-thirds lower than that in the sample collected a month earlier. By mid-April, the concentration had dropped further to nearly zero and by May and June the ejaculate from this individual was aspermic (table 2 in Krzywiński and Jaczewski 1978). Full scale, out-of-season spermatogenesis was observed in the seminiferous tubules of two stags in full winter (4 February) and was speculated to be initiated by pheromonal stimulation by hinds exhibiting signs of the oestrous (Bubenik *et al*. 1985). Females can follow a seasonal pattern similar to that of males. In the absence of conception, oestrous cyclicity in red deer can persist at least for 4–6 months, with a gradual increase in the length of the oestrous cycle being evident with later cycles (Guinness *et al*. 1971; Asher *et al*. 1993; García *et al*. 2002). That reproduction in this extended period may occur is documented by occasional delayed parturitions, as late as October and November instead of the typical May and June births, in many red deer populations across Europe (L. Bartoš, unpubl. data). Additionally, up to six oestrous cycles for black-tailed deer, *Odocoileus hemionus* (Wong and Parker 1988), and seven for white-tailed deer, *Odocoileus virginianus* (Knox *et al*. 1988), have been observed.

Today's extreme reduction in distributional range is likely to have resulted in a diminished variety of habitat types utilised, along with concomitant reduction in variability of behavioural expressions (Putman and Flueck 2011). For instance, migratory behaviour of the past has been eliminated in some areas. Older inhabitants from the Inferior Valley of the El Manso River, immediately outside the southern boundary of the Argentine Nahuel Huapi National Park, reported having seen solitary pudu individuals on various occasions in the past during winter months, while in a nearby, less disturbed area within the same park, fresh tracks and pudu remains found in summer of 2009 at 1200 masl indicate migratory behaviour because snow levels would not allow pudu to remain at that elevation during winter (J. M. Smith-Flueck, unpubl. data). Abbe Molina noted (1782, cited in Hershkovitz 1982) that pudus descended in flocks from the mountains to the warmer coastal plains of the southern provinces in winter. Gay (1847, cited in Hershkovitz 1982) mentioned them living in small flocks in the central valley of Chile between the Cordilleras. Such large formations of social groups and movement patterns no longer occur. Some historic habitats with no snowfall, particularly those towards the Pacific coast (within the temperate Mediterranean and temperate oceanic climatic zones), may have been sufficiently productive all year, such that two breeding seasons or aseasonality could have been a viable tactic for pudu. Accordingly, in order to time the optimal breeding season, pudu responds to photoperiod like other higher-latitude cervids, but may also have a pattern of conception directly influenced by the seasonal change of food quality, similar to deer adapted to tropical conditions (Lincoln 1985).

Although Bubenik *et al*. (2000) speculated that pudu might show delayed implantation similar to roe deer, the breeding and parturition dates of the LCC population and the wild fawn indicate instead that the species breeds twice annually, or possibly even aseasonally. The tropical northern pudu also seems to have two rutting periods, namely, one in March–April and another in October–November (Montulet 1984, cited in Whitehead 1993; Bubenik 2006). Furthermore, nearly full-term fetuses were taken from northern pudus killed in April and November (Grimwood 1969, cited in Hershkovitz 1982). These observations on northern pudu would concur with our hypothesis that the southern pudu also can breed twice per year. The adult pudus in the Chilean wild and at Los Canelos semi-captive centre may be responding to internal, environmental and/or social factors than are not available to individuals in captive centres and zoos. Considering that the females are seasonally polyestrous, one can speculate that those individuals that do not conceive in the fall are stimulated by some environmental or social cue, such as pheromonal stimulation, to ovulate again in the spring, which coincides with males entering their second annual peak in testosterone concentrations. The conception in the spring can therefore act as a back-up mechanism for a failed fall conception. Thus, this species might be more flexible than most other temperate deer in terms of their ovarian activity, by not being bound to one annual breeding season. Research should concentrate on the reproductive physiology of the female pudu to reveal the factors responsible for regulating a spring oestrous, and therefore elucidate further the unique physiological characteristics of this deer in relation to other temperate deer. Comparative studies with its tropical cousin can provide us with insight about their ancestors, and perhaps further demonstrate the flexible nature of cervids.

References

Aitken RJ (1974) Delayed implantation in roe deer (*Capreolus capreolus*). *Journal of Reproduction and Fertility* **39**, 225–233. doi:10.1530/jrf.0.0390225

Asher GW, Fisher MW, Fennessy PF, Mackintosh CG, Jabbour HN, Morrow CJ (1993) Oestrous synchronization, semen collection and artificial-insemination of farmed red deer (*Cervus-elaphus*) and fallow deer (*Dama-dama*). *Animal Reproduction Science* **33**, 241–265. doi:10.1016/0378-4320(93)90118-B

Bartoš L, Bubenik GA (2010) Relationships between rank-related behavior, antler cycle timing and antler growth in deer: behavioral aspects. *Animal Production Science* **51**, 303–310.

Blanvillain C, Berthier JL, Bomsel-Demontoy MC, Semperé AJ, Olbricht G, Schwarzenberg F (1997) Analysis of reproductive data and measurement of fecal progesterone metabolites to monitor the ovarian function in the pudu, *Pudu puda* (Artiodactyla, Cervidae). *Mammalia* **61**, 589–602.

Bubenik GA (1982) Endocrine regulation of the antler cycle. In 'Antler development in Cervidae'. (Ed. RD Brown) pp. 73–107. (Caesar Kleberg Wildlife Research Institute: Kingsville, TX)

Bubenik GA (2006) Seasonal versus non-seasonal reproduction in deer: from the arctic to the tropics. In 'Advances in deer biology: deer in a changing world'. (Eds L Bartoš, A Dušek, R Kotrba, J Bartošová-Víchová) p. 16. (Research Institute of Animal Production: Prague, Czech Rebublic)

Bubenik GA, Morris D, Schams D, Klaus C (1982) Photoperiodicity and circannual levels of LH, FSH, and testosterone in normal and castrated male, white-tailed deer. *Canadian Journal of Physiology and Pharmacology* **60**, 788–793. doi:10.1139/y82-110

Bubenik GA, Bubenik AB, Frank A (1985) Aussersaisonale Brunft beim Edelhirsch (*Cervus elaphus maral*). *Zeitschrift fur Jagdwissenschaft* **31**, 129–133. doi:10.1007/BF02265741

Bubenik GA, Brown RD, Schams D (1990) The effect of latitude on the seasonal pattern of reproductive hormones in the male white-tailed deer. *Comparative Biochemistry and Physiology. A. Comparative Physiology* **97**, 253–257. doi:10.1016/0300-9629(90)90181-Q

Bubenik GA, Reyes E, Schams D, Lobos A, Bartoš L (1996) Seasonal levels of LH, FSH, testosterone and prolactin in adult male pudu (*Pudu puda*). *Comparative Biochemistry and Physiology. B, Comparative Biochemistry* **115**, 417–420. doi:10.1016/S0305-0491(96)00163-0

Bubenik GA, Reyes E, Schams D, Lobos A, Bartoš L (2000) Pudu, the smallest deer of the world: 10 years of endocrine studies of southern pudu (*Pudu puda*) in Chile. *European Journal of Wildlife Research* **46**, 129–212.

Bubenik GA, Reyes E, Schams D, Lobos A, Bartoš L, Koerner F (2002) Effect of antiandrogen cyproterone acetate on the development of the antler cycle in southern pudu (*Pudu puda*). *The Journal of Experimental Zoology* **292**, 393–401. doi:10.1002/jez.10046

García AJ, Landete-Castillejos T, Garde JJ, Gallego L (2002) Reproductive seasonality in female Iberian red deer (*Cervus elaphus hispanicus*). *Theriogenology* **58**, 1553–1562. doi:10.1016/S0093-691X(02)01048-8

Geist V (1998) 'Deer of the world. Their evolution, behavior, and ecology.' (Stackpole Books: Mechanicsburg, PA)

Guinness FE, Lincoln GA, Short RV (1971) The reproductive cycle of the female red deer, *Cervus elaphus. Journal of Reproduction and Fertility* **27**, 427–438. doi:10.1530/jrf.0.0270427

Hershkovitz P (1982) 'Neotropical deer (Cervidae). Part I. Pudus, genus *Pudu* Gray.' Fieldiana Zoology, New Series No.11. (Field Museum of Natural History: Chicago)

IUCN (2008) '*Pudu puda*. 2008 IUCN Red list of threatened species.' Available at www.iucnredlist.org [verified 10 January 2009].

Jimenez JE (2010) Southern *Pudu puda* (Molina 1782). In 'Neotropical cervidology'. (Eds JM Duarte, S González) pp. 140–150. (FUNEP: Jaboticabal, Brazil)

Knox WM, Miller KV, Marchinton RL (1988) Recurrent estrous cycles in white-tailed deer. *Journal of Mammalogy* **69**, 384–386. doi:10.2307/1381395

Krzywiński A, Jaczewski Z (1978) Observations of the artificial breeding of red deer. *Symposia of the Zoological Society of London* **43**, 271–278.

Lambert RT, Ashworth CJ, Beattie L, Gebbie FE, Hutchinson JSM, Kyle DJ, Racey PA (2001) Temporal changes in reproductive hormones and conceptus–endometrial interactions during embryonic diapause and reactivation of the blastocyst in European roe deer (*Capreolus capreolus*). *Reproduction* **121**, 863–871. doi:10.1530/rep.0.1210863

Li CW, Jiang ZG, Zeng Y, Yan C (2004) Relationship between serum testosterone, dominance and mating success in Pere David's deer stags. *Ethology* **110**, 681–691. doi:10.1111/j.1439-0310.2004.01003.x

Lincoln GA (1971) Puberty in a seasonally breeding male, the red deer stag (*Cervus elaphus* L.). *Journal of Reproduction and Fertility* **25**, 41–54. doi:10.1530/jrf.0.0250041

Lincoln GA (1985) Seasonal breeding in deer. In 'Biology of deer production'. (Eds P Fennessy, K Drew) pp. 165–180. Bulletin 22. (The Royal Society of New Zealand: Wellington, New Zealand)

Lincoln GA (1992) Biology of seasonal breeding in deer. In 'The biology of deer'. (Ed. RD Brown) pp. 565–574. (Springer Verlag: Berlin)

MacNamara M, Eldridge WD (1987) Behavior and reproduction in captive pudu (*Pudu puda*) and red brocket (*Mazama americana*), a descriptive and comparative analysis. In 'Biology and management of the Cervidae'. (Ed. CM Wemmer) pp. 371–387. (Smithsonian Institution Press: Washington, DC)

Osgood WH (1943) The mammals of Chile. *Field Museum of Natural History, Zoological Series* **30**, 1–268.

Putman R, Flueck WT (2011) Intraspecific variation in biology and ecology of deer: magnitude and causation. *Animal Production Science* **51**, 277–291.

Randi E, Mucci N, Claro-Hergueta F, Bonnet A, Douzery EJP (2001) A mitochondrial DNA control region phylogeny of the Cervinae: speciation in *Cervus* and implications for conservation. *Animal Conservation* **4**, 1–11. doi:10.1017/S1367943001001019

Reyes E, Guzman R, Angulo A, Hermosilla Conejeros S (1988) Ciclo de vida y madurez sexual de *Pudu puda* (Molina) (Mammalia, Cervidae). *Boletin de la Sociedad Biologia de Concepcion* **59**, 143–150. [Chile]

Reyes E, Bubenik GA, Schams D, Lobos A, Enriquez R (1997) Seasonal changes of testicular parameters in southern pudu (*Pudu puda*) in relationship to circannual variation of its reproductive hormones. *Acta Theriologica* **42**, 25–35.

Rolf HJ, Fischer K (1990) Serum testosterone (T) and 5-alpha-dihydrotestosterone (DHT) in male fallow deer (*Dama-dama* L) – seasonality and age dependence. *Comparative Biochemistry and Physiology. A. Physiology* **95**, 445–452. doi:10.1016/0300-9629(90)90247-P

Ruiz-García M, Randi E, Martínez-Agüero M, Alvarez D (2007) Relaciones filogenéticas entre géneros de ciervos neotropicales (Artiodactyla: Cervidae) mediante secuenciación de ADN mitocondrial y marcadores microsatelitales. *Revista de Biologia Tropical* **55**, 723–741.

Saavedra B, Simonetti JA (1991) Archaeological evidence of *Pudu pudu* (Cervidae) in central Chile. *Zeitschrift fur Saugetierkunde* **56**, 252–253.

Schürer U (2009) Births 2007–2009. In 'International Studbook for the Chilean pudu (*Pudu pudu*) Vol. 12'. (Ed. A Stadler) pp. 78–80. (Zoological Garden Wuppertal: Wuppertal, Germany)

Semperé AJ (1990) The annual antler cycle of the European roe deer (*Capreolus capreolus*) in relation to the reproductive cycle. In 'Horns, pronghorns and antlers'. (Eds GA Bubenik, AB Bubenik) pp. 396–415. (Springer Verlag: New York)

Semperé AJ, Mauget R, Bubenik G (1992) Experimental induction of luteal cyclicity in roe deer (*Capreolus capreolus*). *Journal of Reproduction and Fertility* **96**, 379–384. doi:10.1530/jrf.0.0960379

Semperé AJ, Mauget R, Mauget C (1998) Why lactating monoestrous female roe deer can breed in summer? In 'Proceedings of the 4th international deer biology congress. Advances in deer biology'. (Ed. Z Zomborszky) pp. 140–144. (Pannon University of Agriculture: Kaposvar, Hungary)

Strandgaard H (1972) The roe deer (*Capreolus capreolus*) population at Kalø and the factors regulating its size. *Danish Review of Game Biology* **7**, 1–205.

Suttie JM, Lincoln GA, Kay RNB (1984) Endocrine control of antler growth in red deer stags. *Journal of Reproduction and Fertility* **71**, 7–15. doi:10.1530/jrf.0.0710007

Whitehead GK (1993) 'The Whitehead encyclopedia of deer.' (Swan Hill Press: Shrewsbury, UK)

Wong B, Parker K (1988) Estrus in black-tailed deer. *Journal of Mammalogy* **69**, 168–171. doi:10.2307/1381767