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POSSIBILITY OF TWO REPRODUCTIVE SEASONS PER YEAR IN SOUTHERN PUDU (*PUDU PUDA*) FROM A SEMI-CAPTIVE POPULATION

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ABSTRACT

Pudu (*Pudu puda*), occurring in the southern cone of Latin America, has been classified as vulnerable by the IUCN, yet little is known about this animal in the wild, with most knowledge on the breeding behavior 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 based upon the accepted tenet that the breeding period occurs only once a year between March and June. However, in this study, birth dates from fawns born at the Los Canelos semi-captive breeding center in Chile and male courting behavior revealed possibility of two rutting periods: autumn and spring. To our knowledge, this is the first time that late fall/early winter births (May through early June) have been recorded for the southern pudu; two of these four births were conceived by females in the wild. From available zoo and captive birth records (n = 67), no fawns were born in the winter. For all births combined (n = 91), 64% 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 day length and which breed in early summer. Yet, the present results indicate a similar response from the southern pudu if 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 retained the capacity to be a breeder for a much more extended period of time than documented by earlier studies. Pudu, like other temperate deer, are responsive to photoperiod for timing their breeding period, but may further optimize their production of offspring by also responding to other environmental cues such as seasonal variation in food supply when the climatic conditions are favorable.

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

INTRODUCTION

The southern pudu (*Pudu puda*) occurs only in southern Chile and southwestern 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 less than 15 kg (Eldridge *et al.* 1987; Geist 1998), little has been published on the biology of this species. Even less is known about the only other species to share its genera, the northern pudu (*P. mephistophiles*),separated by about 3200 km (Whitehead 1993). The cryptic behavior 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 masl (meters above sea level). The individuals are often solitary or in small family groups, coming out to feed at the forest edge in undisturbed areas (Jimenez 2010). Given their elusive nature, most information on the southern pudu has been acquired through studies on physiology and behavior 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 in Jimenez 2010; Reyes *et al.* 1988; Hershkovitz 1982). 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 (Whitehead 1993; MacNamara and Eldridge 1987) 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 to February in the southern hemisphere (MacNamara and Eldridge 1987; Reyes *et al.* 1988), with the fawning period shifted by six months in northern hemisphere zoos (Hershkovitz 1982; Blanvillain *et al.* 1997); individuals translocated to the northern hemisphere synchronize quickly to the local photoperiod. Females remained receptive for about 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 about 11 days (Blanvillain *et al.* 1997). Given the wide variation of the estrous 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 northern temperate deer. Bubenik *et al.* (2000) on the other hand, 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 (Aitkens 1974; Semperé 1990; Lambert *et al.* 2001). To our knowledge, this hypothesis has never been investigated. Here we provide observations of reproductive behavior for the first time from a semi-captive population of pudu that challenges this hypothesis and suggests yet another strategy unique to a temperate deer.

METHODS AND STUDY AREA

The current population consists of 28 pudu at the semi-captive center operated by Fauna Andina - Los Canelos (39°16' S latitude), 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 min-max temperatures 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 m). The 13 ha enclosure at 330 masl consists of dense native vegetation common in the Valdivian temperate rainforest ecosystem, including approximately 2.5 ha grassland pastures, with *Nothofagus* and *Festuca* species predominating inside and surrounding the enclosure. All animals are free-roaming inside the enclosure. Disturbance and contact is minimal so that animals retain their elusive behavior and natural fear of man to facilitate their subsequent reintroduction. No one but the caretaker (F. Vidal) and authorized 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 animal or livestock before reaching the pudu.

Data were collected on births dates of pudu born at the Los Canelos Center between 2000 and 2010, either by directly observing the parturition or the neonate within two to three days after birth. This data set of a semi-captive population was compared to parturition dates of captive pudu in the northern and southern hemisphere and included: 20 births at western European zoos (Hershkovitz 1982); 22 births at the captive breeding center of La Victoria Island (41°05' S latitude) in the Argentine Nahuel Huapi National Park (MacNamara and Eldridge 1987); four births in the province of Neuquén (ca. 40°40' S latitude), Argentina (Schmidt 1944 in Hershkovitz 1982); two births in Osorno-Llanquihue (40°34' S latitude) region of Chile (Vanoli 1967 in Hershkovitz 1982); one birth in an unspecified Chilean location (Hick 1967 in Hershkovitz 1982); and six births at two breeding centers of the University of Concepción (36°50' S latitude) in Chile (Reyes *et al.* 1988). Recent births (n = 12) of the last five years at the North American zoos of Detroit (42°20' N latitude) and Woodland Park (Seattle, 47 36' N latitude), and the United Kingdom's Belfast Zoological Gardens (54°35' N latitude), Bristol Zoo Gardens (51°27' N latitude), Edinburgh Zoo (55°57' N latitude), Hamerton Zoo Park (52°24' N latitude), Marwell Wildlife (51°01' N latitude), and Paignton Zoo (50°26' N latitude) were obtained from the zoos' electronic news briefs. Given that the fawning period shifts by six months in northern hemisphere zoos, the comparisons are made by season. From the European zoos, three were conceived in Chile: for the analysis, these were included in the data set for captive centers in the S Hemisphere. A lone winter birth (January) at Germany's Cologne zoo was not included in the data set as 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 center to include in this analysis, plus an observation of a wild fawn in the Huilo Huilo Reserve (39 48' S latitude). For the analysis, we consider the meteorological season of winter to begin 1 June and 1 December for the southern and northern hemisphere, respectively.

On a daily basis at Los Canelos Center, animals were observed for health condition and any behavioral changes. Whenever opportunities arose to record mating copulations and parturition behavior, *ad libitum* sampling was conducted on those individuals.

RESULTS

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

For the entire data set, the majority of births fell in spring (64%), mostly falling on the last month of spring (52%), signifying May and November for the northern and southern hemisphere, respectively (Fig. 2). The births at the northern hemisphere zoos ranged from 27 April and 3 September (129 days). Captive center birth dates in Argentina and Chile (n = 38) were between October and February. Birth dates for the 20 fawns born in the spring/summer at the Los Canelos (LC) semi-captive center ranged from 19 October to 17 February (121 days), with 46% in November. Late fall/winter births (May and first week of June) were observed in 4 cases: of the three of these born at the LC centre, 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, personal observation). A May birth date was estimated based on 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; F. Vidal unpublished data). Births were absent for five months of the year with the exception of one at the initiation of autumn on 3 September at Germany's Erfurt zoo (Czernay 1977 in Hershkovitz 1982).

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 new born is dropped and begins to clean it intensively. Suckling was observed to take place from 10 to 60 minutes after birth.

During both rutting periods, males were observed to sire the females successfully, and courtship behavior was as described in MacNamara and Eldridge (1987). In addition, just prior to mounting an estrous female, the males in our study population gently nudged her hind legs. Their attempts were persistent over several hours.

The endocrine cycle of 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 about 6 months apart (Bubenik *et al.* 1996). Although two seasonal peaks can also be detected in various other deer species, coinciding with the solstices and equinoxes (Bubenik 1982; Rolf and Fischer 1990), the peak outside the rutting season is much smaller then that found for pudu. The non-rutting period for these deer is characterized by a small reactivation of reproductive function and hence, a testosterone pulse (Bartoš and Bubenik 2011), 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) analyzed Cervinae using mitochondrial DNA. Their study indicates *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 levels of LH and testosterone in the roe deer occur much closer together, 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, synchronized by

photoperiod (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 day length 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 Los Canelos Center indicate that the southern pudu has a second breeding season in spring, shortly following the vernal equinox with males demonstrating full mating behavior. For roe deer, the first smaller peak in testosterone was associated with mineralization of antlers, and the second summer peak was related to the rut (Semperé 1990). However, for the Los Canelos 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 mineralization, but also rutting behavior. This concurs with Bubenik *et al.* (1982) that maximal levels of testosterone appear to be essential for rutting behavior.

Comparably, the roe deer and southern pudu are both small-bodied temperate deer (Lincoln 1992), historically found at latitudes ranging from 19° to 70° N and at least 33° to 50-53° S, respectively. Delayed implantation in roe deer may have allowed it to inhabit extremely seasonal environment, 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 a relic behavior 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; Semperé *et al.*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 late fall/early winter births have been recorded for the southern pudu. Although these results suggest that pudu have 2 distinct seasonal reproductive periods per year, future observations may reveal births occurring throughout the current autumn gap, thus necessitating an alternative explanation. The measurements of testicular parameters indicate a prolonged period of gonadal activity in southern pudu (Reyes *et al*. 1997) than what should be the result of the hormonal levels only. 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 detected, only infrequently, 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 time than currently believed. Males of many deer species are fertile for a prolonged part of the year and are capable of mating if the females are in the 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 region) in the Northern Hemisphere. After the rut, the testosterone level decreases almost immediately, while spermatogenesis remains very active in November and December, and then declines until June (Lincoln 1971). Under certain circumstances it is possible to incite complete male's sexual behavior to obtain vital spermatozoa up to June (Krzywiński and Jaczewski 1978). Females can follow similar seasonal pattern. In the absence of conception, estrous cyclicity in red deer can persist at least for four to six months with a gradual increase in estrous cycle length 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 (Bartoš unpublished data). Additionally up to six estrous 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 likely has resulted in a diminished variety of habitat types utilized, along with concomitant reduction in variability of behavioral expressions (Putman and Flueck 2011). For instance, migratory behavior 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 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 at 1200 masl indicate migratory behavior as snow levels

would not allow pudu to remain at that elevation during winter (Smith-Flueck unpublished 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, pudu respond to photoperiod like other higher latitude cervids in order to time the optimal breeding season, 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 those at the Los Canelos population and the wild fawn indicate instead that the species breeds twice annually or possibly even aseasonally. The tropical northern Andean pudu also seems to have two rutting periods: one in March-April and another in Oct-Nov (Montulet 1984 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 pudu adults in the Chilean wild and at La Canelos semi-captive centre may be responding to internal, environmental and/or social factors than are not available to individuals in captive centers and zoos. Considering that the females are seasonally polyestrous, one can speculate that those which don't conceive in the fall are stimulated by some environmental or social cue to ovulate again in the spring, which coincides to when males enter their second annual peak in testosterone levels. Thus this species might be more flexible than most other temperate deer in terms of their ovarian activity and are not 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 estrous 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.

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REFERENCES

Aitkens RJ (1974) Delayed implantation in roe deer (*Capreolus capreolus*). *Journal of Reproduction and Fertility* **39**, 225-233.

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.

Bartoš L, Bubenik GA (2011) 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, Texas)

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) pp. 16. (Research Institute of Animal Production: Praha)

Bubenik GA, Morris D, Schams D, Klaus C (1982) Photoperiodicity and circannual levels of LH, FSH, and testoterone in normal and castrated male, white-tailed deer. *Canadian Journal of Physiology and Pharmacology* **60**, 788-793.

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* **97**, 253-257.

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* **15**, 417-420.

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*). *Journal of Experimental Zoology* **292**, 393-401.

Eldridge WD, MacNamara MM, Pacheco NV (1987) Activity patterns and habitat utilizations of pudus (*Pudu puda*) in south-central Chile. In 'Biology and Management of the Cervidae'. (Ed. CM Wemmer) pp. 352-370. (Smithonian Institution Press: Washington, D.C.)

García AJ, Landete-Castillejos T, Garde JJ, Gallego L (2002) Reproductive seasonality in female Iberian red deer (*Cervus elaphus hispanicus*). Theriogenology **58** 1553-1562.

Geist V (1998) 'Deer of the World. Their Evolution, Behavior, and Ecology'. (Stackpole Books: Pennsylvania, USA)

Guinness FE, Lincoln GA, Short RV (1971) The reproductive cycle of the female red deer, *Cervus elaphus*. *Journal of Reproduction & Fertility* **27** 427-438.

Hershkovitz P (1982) Neotropical deer (Cervidae). Part I. pudus, genus Pudu Gray. *Fieldiana* (Zoology, Field Museum of Natural History) **New Series No.11**, 1-86.

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.

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.

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.

Lincoln GA (1971) Puberty in a seasonally breeding male, the red deer stag (*Cervus elaphus* L.). *Journal of Reproduction & Fertility* **25**, 41-54.

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

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

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, D.C.)

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.

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* (Chile) **59**, 143-150.

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-Comparative Physiology* **95A**, 445-452.

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.

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 Reproductive Fertility* **96**, 379-384.

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

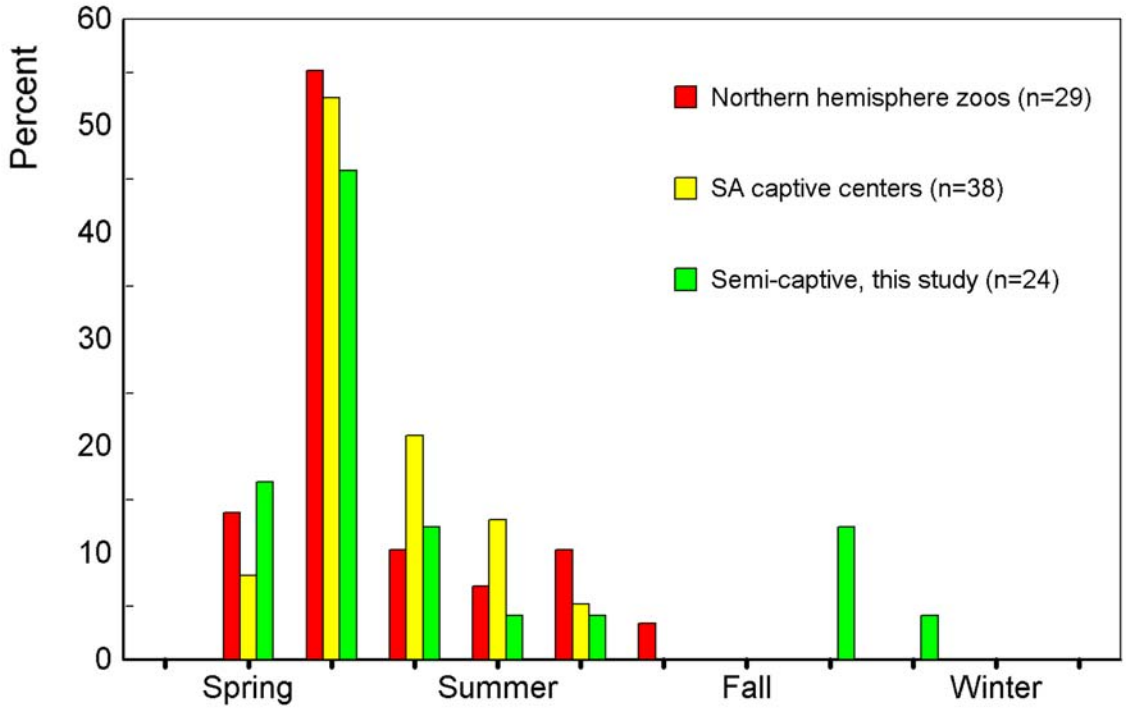
Suttie JM, Lincoln GA, Kay RNB 1984. Endocrine control of antler growth in red deer stags. *Journal of Reproduction and Fertility* **71**, 7-15.

Whitehead GK (1993) 'The Whitehead encyclopedia of deer'. (Swan Hill Press: England). p. 251.

Wong B, Parker K (1988) Estrus in black-tailed deer. *Journal of Mammalogy* **69**, 168-171.

Figure 1. Pudu male (*Pudu puda*) in August (winter, photo by Smith-Flueck).

Figure 2. Birth dates for southern pudu fawns born in northern hemisphere zoos, captive breeding centers in South America, and the Los Canelos semi-captive center 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. Northern spring: March-May; southern spring: Sept.-Nov.


Percent
60
50
40
30
20
10
0
Spring
Summer
Fall
Winter
Northern hemisphere zoos (n=29)
SA captive centers (n=38)
Semi-captive, this study (n=24)