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SHORT NOTE

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Mating activity and parturition of the smooth snake *Coronella austriaca* in Norway

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INTRODUCTION

The smooth snake *Coronella austriaca* Laurenti, 1768, is distributed widely over the European mainland occurring as far south as Sicily and Greece and as far north as Sweden and Norway where it reaches 60° N (Artsobservasjoner, undated; Artportalen, undated). This is a slender snake with a total adult length of 70–90 cm that in Norway feeds mainly on slowworms *Anguis fragilis* and shrew species *Sorex* spp. The female is ovoviviparous, bearing live young mostly in August or September. The reproductive ecology of the smooth snake is poorly understood since mating and parturition have rarely been documented. Here we present the first records of smooth snake mating activity in both spring and autumn in Norway, and report how parturition date varies with summer temperature.

Mating activity

In Norway, smooth snake populations have been studied and monitored around the inner part of the Oslo Fjord since 1982 (Sørensen, 2014 & 2017) in Kristiansand, southern Norway, since 2014, and in Moss, south-east Norway, since 2019. Photography of unique snake head patterns and scalation has been used to identify individuals. Despite intense field work, the first observation of a spring copulation was recorded on 11 June 2018 (BHS video, 2022a), so highlighting the rarity of mating observations for this elusive species. During 2019, a citizen science project was launched (Johansen, 2019) asking the general public to submit photos of smooth snake observations (Johansen, 2021), so that there is now a total of seven observation of smooth snake copulation in both spring and autumn (Table 1) at various locations in southern Norway (Fig. 1).

Observations of smooth snake copulations in Norway reflect the known behaviour of males to bite the female's head during mating (Duguy, 1961; Braithwaite et al., 1989; Capula & Luiselli, 1997; Völkl & Käsewieter, 2003). Spring records of smooth snake copulation in Norway provide new evidence to support the belief that mating takes place in May and early June, after emerging from hibernation in April (Spellerberg & Phelps, 1977; Capula & Luiselli, 1997; Reading, 2012; Sørensen, 2017). The autumn copulation records from Norway reflect similar records from other European countries

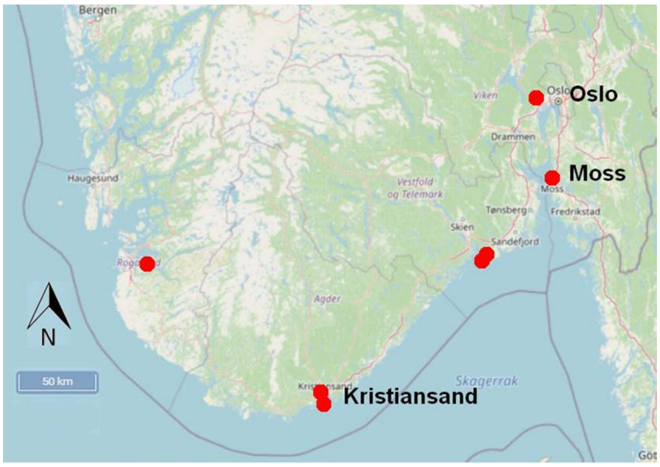


Figure 1. Locations (red circles) where smooth snakes have been observed to copulate in southern Norway 2003–2021. The map also shows the three towns of Oslo, Moss and Kristiansand, which are the main regions from where smooth snake field data were obtained. Copyright: Open Street Map contributors. Map prepared in www.artsobservasjoner.no.

(Table 2). Rollinat (in Duguy, 1961) found live sperm in the female oviduct during hibernation, concluding that autumn mating must have occurred.

Sperm storage

The fact that male smooth snakes engage in both springtime and autumn mating is not surprising considering the normal pattern of spermatogenesis for colubrid snakes in northern latitudes (Duguy, 1961; Saint Girons, 1982; Feriche et al., 2008; Fahgiri et al., 2011). While the main mating period for northern colubrids is spring, autumn mating is also reported for other species (Lankes, 1928; Winkler, 2008; Friesen et al., 2014). In an aestival spermatogenetic cycle, sperm production starts in summer, with a peak in late summer. Sperm is present in the vas deferens in autumn, and springtime mating is performed with stored sperm produced in the foregoing season. The mating period often coincides with a peak in sex hormone levels in male snakes (Graham et al., 2008) but can also be displaced in time (Saint Girons et al., 1993). The annual cycle of sex hormones in male smooth snakes is not known. Fighting males in the autumn may indicate

Table 1. Observations of smooth snake copulations in the Oslo fjord region and the coast of south and south-eastern Norway, 2003 to 2021

Season	Date	Time	Photo/video reference	Recorder	Location	Behavioural notes
Spring	29/05/2003	11:50	Fig. 2	Trond Baugen	Larvik	Male bites females head (blood drawn)
Autumn	29/08/2014	14:00	-	Gro Pedersen	Sandnes, Rogaland	-
Spring	14/05/2018	19:40	-	Otto Munthe-Kaas	Rykkin, near Oslo	-
Spring	11/06/2018	15:20	BHS video (2022a)	Beate StrømJohansen	Kristiansand	-
Autumn	16/09/2020	14:12	-	Geir Hermansen	Moss	-
Spring	30/04/2021	15:30	-	Ståle Knutsen	Larvik	Male bites females head
Spring	01/05/2021	11:50	-	Beate StrømJohansen	Kristiansand	Male bites females head

Figure 2. Headbiting during mating attempt on 29 May 2003 at Mølen, Larvik. The female ended up quite bloody and escaped when disturbed by the photographer. This occurred during springtime which is the more common period for smooth snake mating.

greater sex hormone concentrations, which could then lead to autumn matings (Duguy, 1961). In Norway on 13 October 2020, a video was made of two male smooth snakes fighting at an overwintering site (BHS video, 2022b). Fighting males are also known from Germany and Italy (in Völkl & Käsewieter 2003; Capula & Luiselli, 1997), and Rollinat (in Duguy 1961) describes how males in France were observed fighting at the

Table 2. Records of autumn mating of the smooth snake in other European countries

Country	Date	Reference
England	9 August 1987	Braithwaite et al., 1989
England	6 September 2009	Bull, 2010
England	27 September 2013	Limburn et al., 2013
Germany	23 September 2010	Malkmus & Sauer, 2016
Italy	17 October 1989	Capula & Luiselli, 1997
Italy	3 October 1995	Capula & Luiselli, 1997
The Netherlands	Latter half of August	Strijbosch & van Gelder, 1993
France	End August – beginning October	Duguy, 1961

beginning of every mating season, both spring and autumn. Both the behavioural interactions between male smooth snakes and that of males towards females in different stages of the reproductive cycle have been little studied. The sexual behaviour of females is most likely influenced by the status of sex hormones and Saint Girons et al. (1993) found that in female aspic vipers *Vipera aspis* levels of progesterone were low after birth and also in the following spring. Most likely, autumn matings in Norwegian smooth snakes occur in females at the end of an otherwise non-reproducing season. Whether these females also engage in mating the following spring is not known. However, female red-sided garter snakes *Thamnophis sirtalis parietalis* are known to participate in both autumn and springtime mating (Friesen et al., 2014).

It appears to be the rule that female snakes in the northern temperate regions ovulate in late spring or early summer (Duguy, 1961; Saint Girons, 1982). Capula & Luiselli (1997) state that spring mating, early summer oviposition and late summer hatching is the more typical phenological pattern in Italian colubrids. Ovulation in late spring or early summer is also seen in species for which the normal mating season is autumn (Brito, 2003; Schuett et al., 2005). Springtime mating often occurs weeks before ovulation. In most temperate snake species, male and female gametes mature at different times of the year. Sperm storage and delayed fertilisation represent normal reproductive strategies whether mating takes place in spring or autumn the year before. Snake species have shown the ability to store sperm for exceptionally long periods of time (Booth & Schuett, 2011). Strugariu (2007) reports successful reproduction in a smooth snake after a minimum of 475 days of isolation. In this particular case the litter contained neonates of both sexes. This excludes the possibility of parthenogenesis, which is known to occur in snakes (Booth & Schuett, 2011), since the progeny would all have been female. Long-term sperm storage could be considered a reasonable strategy for small populations of snakes with low probabilities of meeting a partner (Strugariu, 2007). Such sperm storage could also be a factor when the female needs a longer period to build up energy reserves to sustain gestation (Reading, 2004), and/or when sperm storage can assure fertilisation in biennial reproduction.

Authors offer different evidence regarding mating period for the smooth snake, although April and May are most frequently reported. However, they rarely report the number of observed copulations. Because mating is rarely observed, the true mating period may be incorrectly established based on a low number of observations. In Norway, the smooth snake shows an extended mating period compared to the sympatric grass snake *Natrix natrix* and northern viper *Vipera berus*. Grass snakes mate immediately after emerging from hibernation, whereas northern vipers copulate after the springtime molt of the male, normally in April in southern Norway. Like most ovoviviparous snakes in temperate regions, the smooth snake is generally regarded as a typical capital breeder (Bonnet et al., 1998). However, an extended mating period combined with a late ovulation may allow for a strategy defined as facultative income breeding (Lourdais et al., 2002). For southern England, Reading (2004) also concluded that breeding in the smooth snake is partly capital and partly income.

Parturition dates and temperature

Dates of parturition of smooth snakes in the Oslo fjord region and the coast of southern Norway have been established from a single observed birth in the wild, from 52 cases where females gave birth in captivity, 43 cases where neonates were observed at gestation sites, and 14 cases where females were observed post-partum close to gestation sites. Gestating females are highly sedentary and show a high site fidelity from one reproductive event to another. Fifty two gravid females from the Oslo region were brought into captivity at the end of their gestation period. Of these, 36 females (68 %) were collected after 10 August. The females were kept indoors in terraria at temperatures similar to those outdoors. Twenty three females (44 %) gave birth during the first 8 days. We believe that captive conditions did not significantly alter the date of parturition. The mothers and their offspring were then returned to the same place as they were found in the wild. The earliest recorded birth was 30 July, with the latest being 30 September (Fig. 3). This latest parturition date refers to an unusual case of a female that gave birth in two consecutive years. In the second year, vitellogenesis and ovulation were delayed and this would seem to account for the late parturition date. Most parturitions in Norway occurred in August (Fig. 3) and coincide with dates reported from France, Italy, Poland, Germany and The Netherlands (Duguy, 1961; Capula & Luiselli, 1997; Najbar, 2001; Käsewieter, 2002; Keijsers & Lenders, 2005) but occurs earlier than reported from England. Spellerberg & Phelps (1977) and Goddard & Spellerberg (1980) state that, in England, females give birth in September and October. A more continental climate around the inner Oslofjord and the south coast, with higher summer temperatures in smooth snake habitat compared to a more Atlantic climate in southern England may explain the difference. Mean temperature of the warmest month in Oslo is 17.6 °C compared to 16.1 °C at a study site in Dorset, England (Pernetta, 2009). Difference in duration of cloud cover may also result in an even larger difference in ground temperature. To examine the influence of summer temperature on the date of parturition in Norway we have subjected our data from the three regions to a statistical analysis that is reported in the next section.

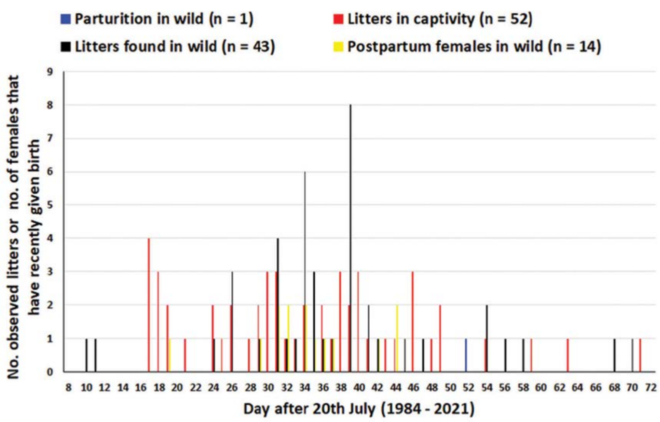


Figure 3. Distribution of smooth snake parturition dates in Norway from 1984-2021, based on observations of a parturition observed in the wild, litters from captive females collected from the wild, litters found in the wild and postpartum females found in the wild

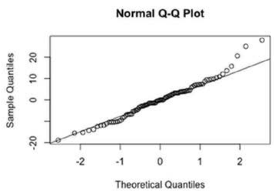
Statistical analysis - parturition dates, sites and temperatures

The parturition dates collected herein, were from three regions in Norway (Fig. 2); Moss (1 site), Oslo (10 sites), and Kristiansand (9 sites). To study the influence of temperature on parturition times, we used air temperature data measured 2 m above ground, from the nearest Norwegian Meteorological Institute weather station in each region - Gullholmen (SN17280) 59.4352° N, 10.578° E; Oslo (SN18700) 59.9423° N, 10.72° E; and Kjevik (SN39040) 58.2° N, 8.0767° E.

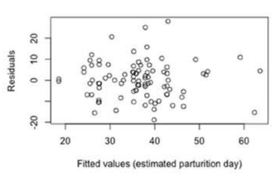
We used a multiple linear regression in R (R Core Team, 2022), using the lm command: lm($t \sim x_1 + x_2 + x_3 + x_4$) where i) t = parturition's date (in days after 20 July) ii) x_1 = the parturition site (20 sites) iii) x_2 to x_4 are based on the mean temperature in month of the year in which parturition was observed, where x_2 = the deviation from the average June temperature in 1989–2021 (Oslo), 2014–2021 (Kristiansand) and 2019–2021 (Moss), x_3 = the deviation from the average July temperature and x_4 = the deviation from the average August temperature.

Table 3. Anova table, testing the statistical significance of ‘site’ and monthly temperature deviation from average in June, July and August on smooth snake parturition date within the linear model for the three regions of Oslo, Moss & Kristiansand combined. Site and temperature deviation in July are both statistically significant factors.

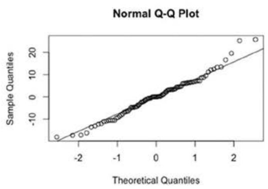
Country	Sum Sq	df	F value	Pr(>F) Exact probability
Site (x_1)	4585.9	19	2.5531	0.002284
June (x_2)	143.9	1	1.5219	0.221349
July (x_3)	972.4	1	10.2858	0.002001
August (x_4)	122.2	1	1.2928	0.259312
Residuals	6806.7	72		



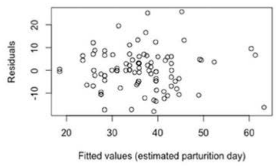
QQ plot for model with all 4 factors



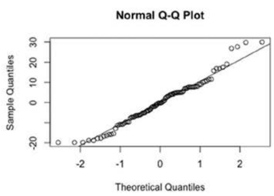
Residual fit plot for model with all 4 factors



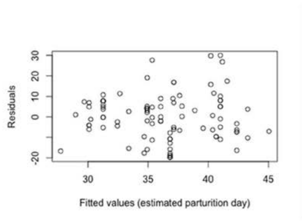
QQ plot for July temperature + location model



Residual fit plot, July temperature + location



QQ plot for July temperature alone model



Residual fit plot, July temperature alone

Figure 4. Residual-fit plots and quantile plots (QQ-plots) for the parturition date models

The output for a full-country linear regression with all four variables (site plus the three temperature deviations) gave $R^2 = 0.4926$. R^2 being a measure of how much of the variability in parturition date (t) can be predicted from variation in x_1, x_2, x_3 and x_4. Thus, approximately half the variability in the parturition date was explained by the four variables. We used residual-fit plots and quantile plots as quality controls to evaluate the fit of our model (Fig. 4, top pair). Although the results appear appreciable with all four variables, with only a slight and unproblematic right skew in the distribution, we elected to deploy the Anova command (in the R package car) (Fox & Weisberg, 2019) to explore which variables actually had a significant impact. The resulting Anova of the linear model informed us that only the variables ‘July’ and ‘site’ were statistically significant (i.e., $p < 0.05$) (see Table 3). In this case, significance was determined by how much of the variability (sum of squares) was explained by each variable, compared to its degrees of freedom (df). This is the number Pr(>F) in Table 3.

Table 4. Regression table for parturition date and July temperature deviation alone (lm(t ~ x_3)) for all three regions combined

	Estimate	Std. Error	t value Pr(>|t|)	Significance
(Intercept)	36.1670	1.1593	31.197 < 2e-16	p<0.0001
July (x_3)	-3.0455	0.8735	-3.487 0.000749	p<0.0001

Residual standard error = 11.29, df = 93
Multiple $R^2 = 0.1156$, Adjusted $R^2 = 0.1061$
F-statistic = 12.16, df = 1, 93, p = 0.0007489

Since the June and August temperatures were not statistically significant (Table 3), we revised the regression model to exclude those predictor variables, giving lm (t ~ $x_1 + x_3$). The result was that the appreciable fit of the model was maintained (middle row of Fig. 4).

Our results indicate that ‘site’ was an important factor for parturition dates. However, there were no historical records of the local temperatures at the sites themselves, so instead we assigned the historical temperature data from the nearest regional meteorological station. This introduces a potential inaccuracy, since the temperature profiles of the sites may differ from that of their corresponding meteorological station. This means that much of the difference attributed to the site variable could simply reflect how the temperatures differ between the different sites and the meteorological stations, rather than any intrinsic influence from the site itself. We also note that the site variable could have become a significant factor solely due to the low number of observations per site. We do not know. Nonetheless, ‘not knowing’ is not the same as ‘knowing that not’, so we suggest that further studies be aware of the potential importance of the site variable as a factor in such a linear model. To improve future analysis, dataloggers should record the ground temperatures at the relevant sites themselves.

At least for this pioneering analysis, we do not believe that the site variable matters as much as our results would suggest, since when we excluded the site variable from the model and ran the final regression for all sites combined for the July temperature deviations, the residual-fit and quantile plots (bottom row of Fig. 4) were still appreciable. This conclusion holds even though this reduced model accounted for less of the observed variability, as $R^2 = 0.1156$ (Table 4).

The mean parturition day, given July temperature deviation (x_3), is given by the formula $t = 36.1670 - 3.0455\ x_3$. This implies that for every 1 °C rise in mean July temperature, the mean parturition date will be 3.0455 days earlier.

We also tested each of the three regions separately. For Oslo, using all four factors $R^2 = 0.4097$. Using temperatures only (all three months) resulted in $R^2 = 0.1609$, with only the July temperature being statistically significant. The same held true for Moss. For Kristiansand, however, we obtained $R^2 =$

0.867, $p = 0.0004749$ when using all four factors. Even when looking at temperatures only, we obtained $R^2 = 0.6756$, $p = 0.00002336$ and all three months were significant, with June and August $p<0.01$ and July $p<0.001$. The equation for the mean parturition date in the Kristiansand region is $t = 44.106 - 6.021\, x_2 - 5.359\, x_3 - 11.381\, x_4$.

Our results indicate that deviation from average July temperature significantly influences the parturition date. Looking at the Kristiansand data, we revealed indications that the temperature deviations in June and August also made a significant contribution.

Although Norwegian smooth snake populations are among the northernmost populations of the species, the warm and dry summer climate along the southern coast helps speed up the gestation period of gravid females, so parturitions are mainly in August, as seen in continental Europe. It seems that England differs from the rest of Europe by having later parturition dates, probably because summers there are more cloudy and/or have lower mean temperatures. However, there are local variations, and we hope that researchers will look deeper into this in the future.

Gravid overwintering

Atkins (2011) reports hibernation of a gravid smooth snake in England, which showed clear signs of advanced gestation when found in April 2011. The specimen also had a substantially higher body mass/length ratio than 12 other female snakes. The pregnant snake was followed through spring and summer showing high site fidelity, a characteristic behaviour of gestating female smooth snakes (Sørensen, 2014, 2017; Stribosch & Van Gelder, 1993). Atkins comments on two more females showing signs of being gravid in that same spring. Spellerberg & Phelps (1977) also report from England that pregnant females were occasionally found in the spring. Gravid overwintering has later been confirmed by ultrasound scanning of three gravid female smooth snakes on 14 May 2017 in England (Atkins pers. comm.). In Norway, the smooth snake is at its northern edge of the species' range, but gravid overwintering has never been observed or reported. Nor has gravid overwintering been observed in an intensely monitored Alpine cool climate population (Capula & Luiselli, 1997). However, we would be interested in performing ultrasound scanning of potentially gravid female smooth snakes in spring in Norway. As parturition normally occurs later in the season in England compared to Norway, overwintering in a gravid state could be more common in England. We encourage researchers throughout the range of the smooth snake to perform ultrasound scanning of potentially gravid smooth snakes in the spring in order to add to the growing body of evidence that will advance our understanding of mating and parturition in this species.

To conclude, the parturition dates of smooth snakes in Norway depend on summer temperature, especially in July. Warm summers speed up the gestation period, resulting in parturition in August, which gives the neonates one to two months to forage before hibernation in October. Although Norway is on the northern range of the species, these higher latitudes, with colder winters compared to England and central Europe, seem to have no negative effect on the reproduction of the smooth snake in southern Norway. A relatively warm and dry summer climate in the distributional range in Norway normally assures successful reproduction for the smooth snake in Norway.

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REFERENCES

Artsobservasjoner (undated). Slettsnok *Coronella austriaca* Laurenti, 1768. https://www.artsobservasjoner.no/ViewSighting/ViewSightingAsMap?storedSearchCriterias=6208020

Artportalen (undated). *Coronella austriaca* Laurenti, 1768. https://www.artportalen.se/ViewSighting/ViewSightingAsMap

Atkins, W. (2011). *Coronella austriaca* Laurenti (smooth snake): Gravid overwintering. *The Herpetological Bulletin* 118: 35–36.

BHS video (2022a). Smooth snake *Coronella austriaca* mating in Norway, 11 June 2018. Filmed by Johansen, B.S. https://youtu.be/UFV1ue--ORQ

BHS video (2022b). Smooth snake *Coronella austriaca* aggressive behaviour in Norway, 13 October 2020. Filmed by Botnermyr, R. https://youtu.be/e3MSwSYbhik

Bonnet, X., Bradshaw S.D. & Shine, R. (1998). Capital versus income breeding: an ectothermic perspective. *Oikos* 83: 333–342.

Booth, W. & Schuett, G.W. (2011). Molecular genetic evidence for alternative reproductive strategies in North American pitvipers (Serpentes: Viperidae): long-term sperm storage and facultative parthenogenesis. *Biological Journal of the Linnean Society* 104(4): 934–942.

Braithwaite, A.C., Buckley, J., Corbett, K.F., Edgar, P.W., Haslewood, E.S., Haslewood, G.A.D., Langton, T.E.S. & Whitaker, W.J. (1989). The distribution in England of the smooth snake (*Coronella austriaca* Laurenti). *The Herpetological Journal* 1: 370–376.

Brito, J. (2003). Seasonal and daily activity patterns of *Vipera latastei* in northern Portugal. *Amphibia-Reptilia* 24(4): 497–508.

Bull, D. (2010). *Coronella austriaca* Laurenti (smooth snake): Reproduction. *The Herpetological Bulletin* 111: 36–38.

Capula, M. & Luiselli, L. (1997). A tentative review of sexual behavior and alternative reproductive strategies of the Italian colubrid snakes (Squamata: Serpentes:

Colubridae). *Herpetozoa* 10(3/4): 107–119.

Duguy, R. (1961). Le cycle annuel d'activité chez *Coronella austriaca* (d'après les observations manuscrites inédites de RAYMOND ROLLINAT). *La Terre et la Vie* 4: 401–435.

Faghiri, A., Shiravi, A., Hojati, V. & Kami, H.G. (2011). Observations on the spermatogenetic cycle of the grass snake, *Natrix* (Serpentes: Colubridae) in Northern Iran. *Asian Herpetological Research* 2(1): 55–59.

Feriche, M., Pleguezelos, J.M. & Santos, X. (2008). Reproductive Ecology of the Montpellier Snake, *Malpolon monspessulanus* (Colubridae), and comparison with other sympatric colubrids in the Iberian Peninsula. *Copeia* 2008(2): 279–285.

Fox, J. & Weisberg, S. (2019). An R companion to applied regression, Third edition. Sage, Thousand Oaks CA. https://socialsciences.mcmaster.ca/jfox/Books/Companion/

Friesen, C.R., Mason, R.T., Arnold, S.J. & Estes, S. (2014). Patterns of sperm use in two populations of red-sided garter snake (*Thamnophis sirtalis parietalis*) with long-term female sperm storage. *Canadian Journal of Zoology* 92: 33–40. (doi:10.1139/cjz-2013-0195)

Goddard, P. & Spellerberg, I.F. (1980). Reproduction as a factor in the conservation of *Coronella austriaca* Laur. in southern England. *Bulletin of Ecology* 11: 535–541.

Goddard, P. (1984). Morphology, growth, food habits and population characteristics of the smooth snake *Coronella austriaca* in southern Britain. *Journal of Zoology* 204: 241–257.

Graham, S.P., Earley, R.L., Hoss, S.K., Schuett, G.W. & Grober, M.S. (2008). The reproductive biology of male cottonmouths (*Agkistrodon piscivorus*): Do plasma steroid hormones predict the mating season? *General and Comparative Endocrinology* 159: 226–235.

Johansen, B.S. (2021). Kartlegging av slettsnokens utbredelse i Norge 2019. Naturblogg.uia.no 05.11.2021. https://naturblogg.uia.no/kartlegging-av-slettsnokens-utbredelse-i-norge-2019/).

Johansen, B.S. (2019). FacebookNaturmuseum og botanisk hage, Universitetet i Agder 12.08.2019 (https://www.facebook.com/naturmuseum/posts/2328986390472348).

Kãsewieter, D. (2002). *Ökologische Untersuchungen an der Schlingnatter* (*Coronella austriaca*). Dissertation Universität Bayreuth. 111 pp.

Keijsers, P.L.G. & Lenders, A.J.W. (2005). Het voortplantingsgedrag van de gladde slang. Een ecologische studie in het noordelijk peelgebied. *Natuurhistorisch Maandblad* 94: 263–268.

Lankes, K. (1928). Herbstpaarung bei der Ringelnatter. *Blätter für Aquarien- und Terrarienkunde*, Bd. 39, S. 489, Braunschweig.

Limburn, B., Woodley, S., Handyside, S. & Wilkinson, J.W. (2013). *Coronella austriaca* (smooth snake): Photographic record of autumn copulation. *The Herpetological Bulletin* 126: 32–34.

Lourdais, O., Bonnet, X.R., Shine, R., DeNardo, D., Naulleau, G. & Guillon, M. (2002). Capital-breeding and reproductive effort in a variable environment: a longitudinal study of a viviparous snake. *Journal of Animal Ecology* 71: 470–479.

Malkmus, R. & Sauer, H. (2016). Herbstpaarung bei der Schlingnatter. *Feldherpetologisches Magazin* Heft 6: 32–34.

Najbar, B. (2001). Reproduction of *Coronella austriaca* LAUR., 1768 in the Lubuskie region (western Poland) in the years 1995–2000. *Bulletin of the Polish Academy of Sciences, Biological Sciences* 49: 25–31.

Pernetta, A. (2009). Population ecology and conservation genetics of the smooth snake (*Coronella austriaca*) in a fragmented heath landscape, Doctor of Philosophy, University of Southampton.221 pp.

R Core Team (2022). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Reading, C.J. (2004). The influence of body condition and prey availability on female breeding success in the smooth snake (*Coronella austriaca* Laurenti). *Journal of Zoology* 264: 61–67.

Reading, C.J. (2012). Ranging behaviour and home range size of smooth snakes inhabiting lowland heath in southern England. *The Herpetological Journal* 22: 241–247.

Saint Girons, H. (1982). Reproductive cycles of male snakes and their relationships with climate and female reproductive cycles. *Herpetologica* 58: 3–16.

Saint Girons, H., Bradshaw, S.D. & Bradshaw, F.J. (1993). Sexual activity and plasma levels of sex steroids in the aspic viper *Vipera aspis* L. (Reptilia, Viperidae). *General and Comparative Endocrinology* 91(3): 287–297.

Schuett, G.W., Hardy Sr, D.L., Green, H.W., Early, R.L., Grober, M.S., van Kirk, E.A. & Murdoch, W.J. (2005). Sympatric rattlesnakes with contrasting mating systems show differences in seasonal patterns of plasma sex steroids. *Animal Behavior* 70: 257–266.

Spellerberg, I.F. & Phelps T.E. (1977). Biology, general ecology and behaviour of the snake, *Coronella austriaca* Laurenti. *Biological Journal of the Linnean Society* 9: 133–164.

Strijbosch, H. & van Gelder, J.J. (1993). Ökologie und biologie der Schlingnatter, *Coronella austriaca* LAURENTI 1768 in den Niederlanden. *Mertensiella* 3: 39–58.

Strugariu, A. (2007). A case of efficient long term sperm storage in Smooth snake *Coronella austriaca*. *Biota* 8: 79–82.

Sørensen, P. (2014). The smooth snake *Coronella austriaca* in Norway. *Fauna* 66(3–4): 110–123.

Sørensen, P. (2017). Vår sjeldneste slange. Norsk Herpetologisk Forening, *Slettsnoken* 1, 17–31. http://herpetologisk.org/2017/01/22/slettsnoken-var-sjeldneste-slange/

Völkl, W. & Käsewieter, D. (2003). Die Schlingnatter, ein heimlicher Jäger. *Beiheft der Zeitschrift für Feldherpetologie* 6. Laurenti Verlag, Bielefeld. 151 pp.

Winkler, C. (2008). Nachweis einer Herbstpaarung der Ringelnatter (*Natrix natrix*) in Schleswig-Holstein. RANA, *Mitteilungen für Feldherpetologie und Ichthyofaunistik* 9: 28–29.

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