

along with the geoid and dynamic topography. Thus the answer to the paradox posed by Gurnis²⁶, regarding the lack of observed continental flooding in response to Phanerozoic continental motions in a 'static' geoid-topography field, may be simply that neither the long-wavelength geoid nor associated dynamic topography have remained static.

Numerical mantle convection models are now approaching sufficient resolution to address such time-dependent problems in global geodynamics, and our results show how detailed knowledge of the history of plate motions can be used to constrain these models. For this purpose, estimates for the ages of subducted plates would be desirable so that their thermal loads could be estimated more accurately. □

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Why do female adders copulate so frequently?

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MALES of most animal species will enhance their reproductive success if they mate often and with many different partners, whereas promiscuous mating is unlikely to increase a female's reproductive success. Why then is multiple copulation by females so common^{1–6}? Many theoreticians have suggested that multiple copulations might enhance the viability of a female's offspring, either because of inadequate quantities of sperm from the first mating^{1,7}, additional nutrients derived from the seminal fluid^{7,8} or some genetic advantage^{9–14}. Our field studies on Swedish adders provide the first empirical evidence that multiple copulations, with different partners each time, increase offspring viability. This advantage apparently results from more intense sperm competition in the female's reproductive tract, resulting in a higher proportion of her ova being fertilized by genetically superior males.

Adders (*Vipera berus*) are small venomous snakes widely distributed through Europe. Like all snakes, they lack male parental care¹⁵, and female cooperation is required for successful copulation (forcible insemination is impossible¹²). After mating, females store sperm in their reproductive tracts for months before ovulation^{12,16,17}. For the past 10 years we have studied a small population of adders (mean number of reproducing adults per annum = 30, range 21–46) living in open grassy meadows in southern Sweden (Smygehuk, 55° 20' N, 13° 22' E). All snakes captured in the study area were individually marked by clipping ventral scales, and all reproductive females were force-fed miniature radiotransmitters each year. The snakes were monitored intensively throughout the three-week mating period each spring. Females were collected in midsummer, and maintained in the laboratory until they gave birth a week or two later. The neonates were measured, weighed, marked and

released, with their mothers, at her site of capture.

Most females mated with more than one male. The average number of copulations per female per season was 3.69 (s.d. = 1.58, $n = 45$ females), and ranged from one to eight. The number of times that a female copulated was independent of her body length ($r = 0.18$, $n = 45$, $P = 0.23$) or the number of males that we saw courting her during the mating season ($r = 0.11$, $n = 45$, $P = 0.45$). Female adders also tended to mate with a series of different males, rather than repeatedly with the same male. A female adder was courted by an average of seven males per season, and mated at least three times. Hence, the probability that she would have mated more than once with the same male is 38.5% under the null hypothesis of random choice of partners. In practice, the observed proportion of 'repeat matings' was much lower than this figure (16.1% of 124 matings), and the difference between these two proportions is highly significant ($\chi^2 = 26.21$, 1 d.f., $P < 0.001$). This test is conservative, because it does not take into account the fact that females actually mated an average of 3.7 times rather than 3.0, and that some males were much more successful than others in obtaining matings. These factors should have considerably increased the numbers of 'repeat' matings.

Why do female adders mate more than once per season, and usually with a different male each time? The female's reproductive success (litter size) is determined by the amount of energy she allocates to reproduction, so her reproductive output is not enhanced by additional matings: the number of copulations by a female was not significantly correlated with her litter size ($r = 0.15$, $n = 30$, $P = 0.44$) or with her fecundity relative to body size (residual scores from the regression of litter size to maternal snout-vent length: $r = 0.26$, $n = 30$, $P = 0.17$). The nutrient input from semen is insignificant: the number of matings by a female did not affect her mean offspring mass ($r = 0.21$, $n = 28$, $P = 0.29$), her total litter mass ($r = 0.17$, $n = 27$, $P = 0.38$) or her proportional loss in body mass during gestation ($r = 0.25$, $n = 28$, $P = 0.21$). A shortage of sperm to fertilize her ova is also not a problem: studies on captive adders show that a single mating is sufficient for this purpose¹⁸, and our field data show that almost all ova were fertilized in almost all litters (mean = 3.9% infertile, s.d. = 8.5, $n = 34$ litters), and that the proportions of unfertilized ova were not affected by the number of times that a female mated ($r = 0.02$, $n = 34$, $P = 0.90$).

Our data suggest, instead, that a female adder benefits from multiple copulations through the genetic quality of her offspring. Genetic factors may be particularly important in small isolated

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populations such as that of the Smygehuk adders, because of the high potential for inbreeding depression¹⁹. The mating system of adders, whereby a single large male may obtain most of the matings, reduces effective population size and thus amplifies this effect²⁰. The Smygehuk adders offer an ideal opportunity to look for an influence of multiple mating on offspring viability, because genetic bottlenecks and small effective population sizes have resulted in low genetic variability and high proportions of stillborn offspring in most litters (mean = 31.6% of offspring stillborn, s.d. = 27.4, range = 0–100%, $n = 34$ litters).

Multiple matings strongly reduced the proportions of offspring that were dead at birth (correlating proportion of stillborn young against number of matings, $r = -0.40$, $n = 34$, $P < 0.02$; against number of different males mated with, $r = -0.40$, $n = 34$, $P < 0.02$). No other variable that we measured on females or their litters was significantly correlated with the proportion of stillborn young (for example litter size, $r = 0.04$, $n = 34$, $P = 0.25$; mean offspring mass, $r = 0.24$, $n = 30$, $P = 0.20$), and there were no consistent differences in this respect between first and second litters of the same female (t -test, 8 d.f., $t_8 = 0.24$, $P = 0.81$), or among individual females (using a one-factor analysis of variance, with identification number of the female as the factor, $F_{5,6} = 1.18$, $P = 0.42$). The number of times that a female mated also did not differ consistently among individual females between years ($F_{5,6} = 1.24$, $P = 0.39$), or between first and second litters ($t_8 = 0.79$, $P = 0.45$). Hence the number of matings (or numbers of different mates, which is highly correlated with number of matings: $r = 0.90$, $n = 34$, $P < 0.001$) seems to be the primary determinant of the proportion of viable offspring produced by a female adder.

More detailed analysis shows that offspring viability depends on a female's choice of mates as well as the number of times she copulates. We looked for a paternal effect on offspring viability by restricting analysis to litters that had been sired by only one or two males, and comparing the proportion of stillborn offspring among fathers. The resulting one-factor analysis of variance (with identification number of the male as the factor) revealed strong differences among the seven males for which data were available ($F_{6,2} = 101.8$, $P < 0.01$), with matings by two of the males producing 100% inviable offspring, 67% in two others and 29–33% stillborn offspring in litters sired by the other three males. Multiple mating results in shared paternity of the resulting litter¹⁸, and our data suggest that the ova of females that mate more frequently are fertilized mostly by the sperm of 'better' males. If this were not the case, a higher number of copulations might reduce the variance in proportions of inviable offspring in a litter, but should not affect the mean proportion of inviable neonates. Instead, our data show that the proportion of viable offspring increases with additional matings.

Why should a higher number of matings per litter result in fertilization of a female's ova by a 'better' male? Multiple mating increases the potential for intrauterine competition among sperm from different males. If sperm that are more successful in fertilizing the ova are also more effective in producing viable offspring (as shown in some inbred populations of mammals²¹), then multiple mating should increase the average viability of offspring^{11–13}. Such an effect would normally be difficult to detect because of the problems inherent in assessing offspring quality, and the high proportion of stillbirths in the Smygehuk population overcomes this problem. Nonetheless, the same effect may well be widespread among other populations of adders (and many other types of animals). The enhancement of offspring quality through intrauterine sperm competition offers a plausible selective advantage for the willingness of females of many species to mate frequently, with many partners. □

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Retinoid X receptor is an auxiliary protein for thyroid hormone and retinoic acid receptors

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THYROID hormones and retinoic acid function through nuclear receptors that belong to the steroid/thyroid-hormone receptor superfamily (reviewed in refs 1–4). Thyroid hormone receptors (TRs) and retinoic acid receptors (RARs) require auxiliary nuclear proteins for efficient DNA binding^{5–10}. Here we report that retinoid X receptors RXR α (ref. 11) is one of these nuclear proteins. RXR α interacts both with TRs and with RARs, forming heterodimers in solution that strongly interact with a variety of T3/retinoic acid response elements. Transfection experiments show that RXR α can greatly enhance the transcriptional activity of TR and RAR at low retinoic acid concentrations that do not significantly activate RXR α itself. Thus, RXR α enhances the transcriptional activity of other receptors and its own ligand sensitivity by heterodimer formation. Our studies reveal a new subclass of receptors and a regulatory pathway controlling nuclear receptor activities by heterodimer formation.

We investigated the possibility that the auxiliary nuclear proteins might be members of the nuclear receptor proteins, in particular those that bind and activate the same or related response elements. Using a gel retardation assay, we observed that TR α DNA binding greatly increases in the presence of RXR α . A prominent complex which migrated much more slowly than the monomeric TR α complex⁵ was observed, whereas TR α binding was reduced (Fig. 1a). At the concentrations used, RXR α alone did not form visible complexes with the thyroid hormone response element (TRE). By contrast, there was no change of TR α binding when mixed with RAR α (Fig. 1a) or oestrogen receptor (ER) (Fig. 1b). In addition, when RXR α was mixed with oestrogen receptor and labelled oestrogen response element (ERE) (Fig. 1b), no increased binding or slow electrophoretic mobility complex was seen. When the carboxy-terminal variant TR α -2 (ref. 12), which is not a transcriptional activator^{13–15}, was used, a low-electrophoretic-mobility complex did not form either (Fig. 1a).

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