Earth by comets and meteorites. Further studies of these objects may elucidate whether their composition and membrane-like structures were important building blocks for the origin of life.

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Increasing Trend of Extreme Rain Events Over India in a Warming Environment

B. N. Goswami,[1]* V. Venugopal,[2] D. Sengupta,[2] M. S. Madhusoodanan,[2] Prince K. Xavier[2]

Against a backdrop of rising global surface temperature, the stability of the Indian monsoon rainfall over the past century has been a puzzle. By using a daily rainfall data set, we show (i) significant rising trends in the frequency and the magnitude of extreme rain events and (ii) a significant decreasing trend in the frequency of moderate events over central India during the monsoon seasons from 1951 to 2000. The seasonal mean rainfall does not show a significant trend, because the contribution from increasing heavy events is offset by decreasing moderate events. A substantial increase in hazards related to heavy rain is expected over central India in the future.

Analysis of rain gauge data shows that Indian monsoon rainfall has remained stable over the past century even though the global mean surface temperature has risen steadily (*1*–*3*). Although the amount of summer monsoon rain [June to September (JJAS) seasonal mean all-India rainfall, AIR] has some interdecadal variability (*4*), it has no significant long-term trend (Fig. 1). Physical considerations and model studies indicate that tropospheric warming leads to an enhancement of moisture content of the atmosphere (*5*) and is associated with an increase in heavy rainfall events (*6*–*11*). Extreme rainfall results in landslides, flash floods, and crop damage that have major impacts on society, the economy, and the environment. Although prediction of such extreme weather events is still fraught with uncertainties, a proper assessment of likely future trends would help in setting up infrastructure for disaster preparedness.

The number of severe cyclonic storms over the north Indian Ocean (IO) has shown an increasing trend in the past 3 decades (*12*, *13*), consistent with similar findings over other basins (*12*). However, no coherent signal has emerged from investigations of the trend of daily station rainfall data over India (*13*–*16*), with some stations showing an increasing trend whereas others show a decreasing trend. The ambiguity in the existence of a trend in monsoon rainfall extremes may be partly related to the data and the methodologies used so far. Short-duration extreme rain events are a consequence of small-scale convective instabilities in a moist atmosphere. Although a fraction of extreme rain events is triggered in the background of synoptic disturbances (*17*) and is preferentially located around the tracks of monsoon lows and depressions, a large fraction arises from processes like severe thunderstorms and is more uniformly distributed in space and time. Even if the total number of extreme events over a homogeneous large-scale environment were to have an increasing trend, no significant trend may appear in data from a single station because of the inherently large variability and/or sampling issues (*18*–*23*). Therefore, we examined the trend of daily heavy and very heavy rain events over a relatively large region.

We used daily gridded rainfall data at 1°-by-1° resolution from the India Meteorological Department (IMD), based on 1803 stations (*24*, *25*) that have at least 90% data availability, for the period 1951–2000. The interannual variability of JJAS all-India rainfall (AIR2) from this data set (Fig. 1B) is similar to AIR, which is a long-term data set based on 306 stations (*26*). Daily anomalies of rainfall at each grid box were constructed as deviations of observed daily values from a smoothed climatological annual cycle (the sum of the mean and first three harmonics of the daily climatology). The climatological mean and variance of daily summer monsoon rainfall have large spatial variability across the country (Fig. 1A and fig. S1). However, over central India (CI, 74.5°E to 86.5°E and 16.5°N to 26.5°N, containing 143 grid boxes) the mean and the standard deviation are reasonably homogeneous (spatially

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[1] Indian Institute of Tropical Meteorology, Doctor Homi Bhabha Road, Pashan, Pune 411 008, India. [2] Centre for Atmospheric and Oceanic Sciences, Indian Institute of Science, Bangalore, Karnataka 560 012, India.

*To whom correspondence should be addressed. E-mail: goswami@tropmet.res.in

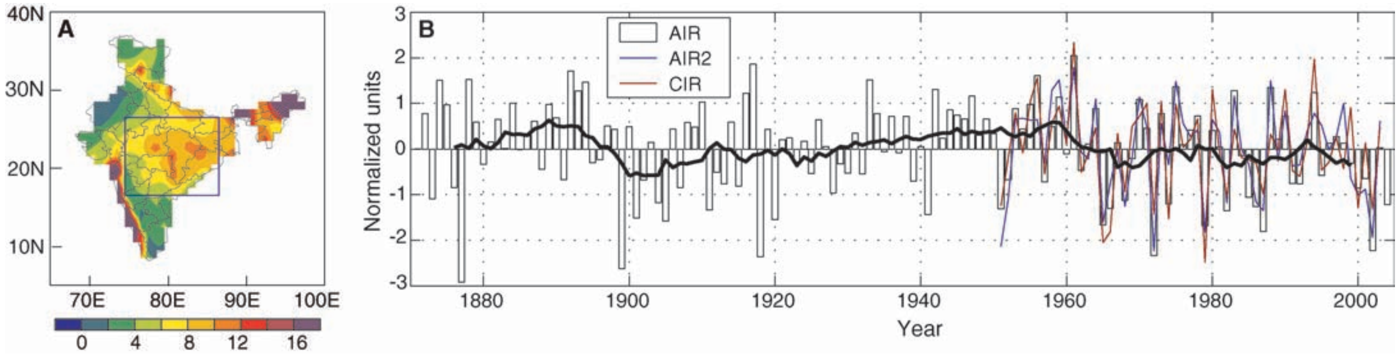


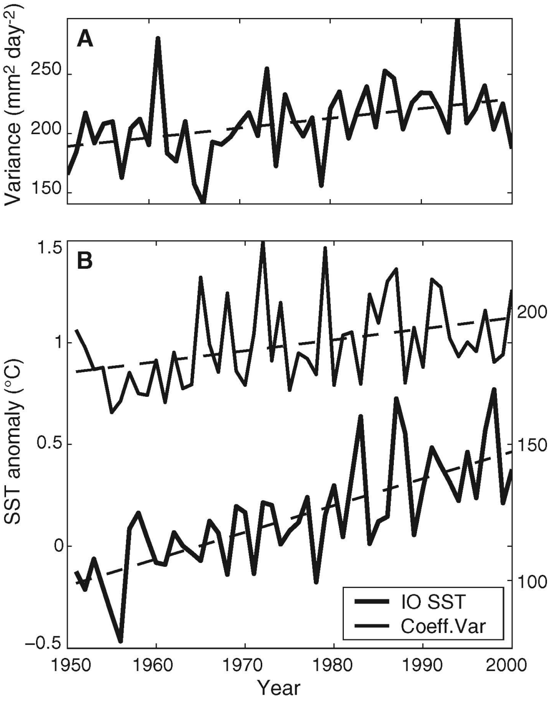
Fig. 1. (**A**) Climatological mean summer monsoon rainfall (mm/day). The box indicates the CI region used in our analysis. (**B**) Normalized (by the interannual standard deviation) JJAS AIR based on 306 stations (*26*) from 1871 to 2003 (bars). The mean is 84.9 cm, and the standard deviation is 8.4 cm. The solid black line represents an 11-year running mean indicating interdecadal variability but no trend. The AIR2 (blue) is the normalized seasonal mean AIR on the basis of the new gridded rainfall data (*24*). The seasonal mean and standard deviation are 94.0 cm and 9.1 cm, respectively. The CIR (red) is the normalized seasonal mean over CI on the basis of the gridded rainfall data set, the mean and the standard deviation of which are 69.5 cm and 11.2 cm, respectively.

uniform). Therefore, we select CI as the region to examine the trend of extreme rainfall over India.

The gridded daily data are smoother than the individual station data because of averaging over a 1°-by-1° box. The maximum 1-day rainfall during the summer monsoons of 1951 to 2003 in any box over CI is 58.2 cm. The seasonal mean over CI is 5.7 mm of rain in a day (mm/day), whereas the standard deviation of the daily anomalies is 11.5 mm/day. Although a fixed threshold for defining extreme events is not appropriate over regions where the mean climate has large spatial variability (*27*, *28*), a fixed threshold can be used to define extreme rain events over CI, where the seasonal mean climate as well as the daily variability is reasonably homogeneous (Fig. 1A and fig. S1). We used 100 mm/day in a 1°-by-1° box as a threshold to define a heavy rain event, whereas a threshold of 150 mm/day was used to define a very heavy event.

The temporal variance of daily rainfall anomalies averaged over CI shows a significant increasing trend (at 0.01 significance level) during 1951 to 2000 (Fig. 2A). The increasing trend of the coefficient of variability, defined as the ratio of the standard deviation to the mean, of daily monsoon rainfall (Fig. 2B) is a consequence of the absence of a trend in the seasonal mean (Fig. 1) and an increasing trend in the standard deviation. A trend in daily rainfall variance is related to a trend in large-scale moisture availability (*5*), which in turn is due to gradual warming of sea surface temperature (SST) (*7*). However, interannual changes in moisture content over CI can be influenced by regional-scale land surface processes as well as by atmospheric teleconnections associated with remote SST such as the El Niño and Southern Oscillation (ENSO). Although El Niño events are generally associated with positive SST anomaly over the tropical IO, they lead to drying of the atmosphere over CI through large-scale subsidence. As a result, daily CI rainfall variance and IO SST need not be correlated on a year-to-year basis. The long-term increase of daily rainfall variance is likely due to the warming trend of tropical IO JJAS SST (Fig. 2) and the associated increase in water vapor (*5*).

Fig. 2. (**A**) Temporal variation (1951 to 2000) in the variance of daily anomalies during summer monsoon seasons (June 1 to September 30), together with its linear trend (dashed line). (**B**) Coefficient of variability of daily precipitation during summer monsoon season and its trend (thin line) together with JJAS SST anomalies averaged over tropical IO and their trend (bold line). Statistically significant trends (0.01 significance level) are calculated on the basis of a *t* test, with a sample size of 50, under a null hypothesis of no trend.



The frequency histogram of daily rainfall at each 1° by 1° box (R) over CI during the summer monsoons of 1951 to 1970 and 1981 to 2000 was separately constructed (plotted as line curves in fig. S2) to assess the increase in variance in recent decades compared with those of the 1950s and 1960s. The tails of the histogram indicate a larger number of extreme events ($\geq$100 mm/day of rain) during 1981–2000. On the other hand, the number of light to moderate events ($\geq$5 mm/day but $<$100 mm/day) have decreased during 1981 to 2000 compared with 1951 to 1970. In fact, the frequency of heavy ($R \geq 100$ mm/day) and very heavy ($R \geq 150$ mm/day) events over CI shows clear and significant (at 0.01 significance level) increasing trends (Fig. 3) (*29*), whereas that of moderate events shows a significant (at 0.1 significance level) decreasing trend. There is a 10% increase per decade in the level of heavy rainfall activity since the early 1950s (Fig. 3A), whereas the number of very heavy events has more than doubled (Fig. 3B), indicating a large increase in disaster potential. These findings are in tune with model projections (*6*–*11*) and some observations (*30*) that indicate an increase in heavy rain events and a decrease in weak events under global warming scenarios.

In order to see whether the unambiguous increase in the frequency of heavy and very heavy events is also accompanied by an increase in the intensity of heavy events, we examined the rain intensity between 99 and 99.99 percentiles (*31*) of summer monsoon rainfall (Fig. 4A). The rainfall intensity that contributed to the 99.75 percentile in the early 1950s seems to contribute to only the 99.5 percentile in the early 1990s, with events of higher intensity contributing to the higher percentiles. For instance, the average intensity of the heaviest four events in each monsoon season (Fig. 4B) shows an ~10% per decade increase over the 50-year period (18 to 26 cm), significant at 0.01 significance level.

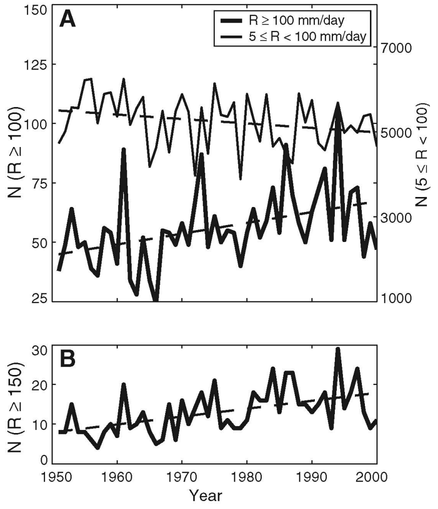


Fig. 3. Temporal variation (1951 to 2000) in the number (*N*) of (**A**) heavy ($R \geq 100$ mm/day, bold line) and moderate ($5 \leq R < 100$ mm/day, thin line) daily rain events and (**B**) very heavy events ($R \geq 150$ mm/day) during the summer monsoon season over CI. The statistical significance of the trends (dashed lines) was calculated as in Fig. 2.

Although the above results present strong evidence of an increase in the number of extreme monsoon weather events over India over the past half century, the Indian monsoon climate (seasonal mean monsoon rainfall) remains stable for the same period (Fig. 1). The findings in Fig. 3 help us piece this puzzle together. Note that although the frequency histograms for the two periods (1951 to 1970 and 1981 to 2000) have significant differences (fig. S2), the mean rainfall during these periods is nearly identical at 5.75 mm and 5.69 mm, respectively. The heavy events (≥100 mm/day of rain) contribute about 6.4% to the seasonal mean, whereas moderate events (from 5 mm/day to <100 mm/day) contribute about 85.8%. Although the relative contributions to the mean from these two classes do not balance in a given year, the contribution from the decreasing trend of moderate events is partially offset by that from increasing heavy rain events (*7*). Consequently, the seasonal total does not show any statistically significant change over longer time scales.

Previous attempts to detect trends in extreme rain events by using station data were inconclusive, probably because of the large year-to-year variability in Indian monsoon rainfall. To assess the role of sampling and variability, we examined the number of heavy rain events over regions of increasing size (fig. S3). We find that for regions smaller than about 800 km by 800 km, it is difficult to find significant trends in heavy rain events. On the other hand, the whole of India cannot be taken as one unit to investigate such trends. The northeast and the west coast are regions of high mean (Fig. 1A) and high variability (fig. S1), and local orography has a strong influence on the rainfall over both regions. Therefore, trends in extreme rainfall due to a warming environment are difficult to discern in these regions.

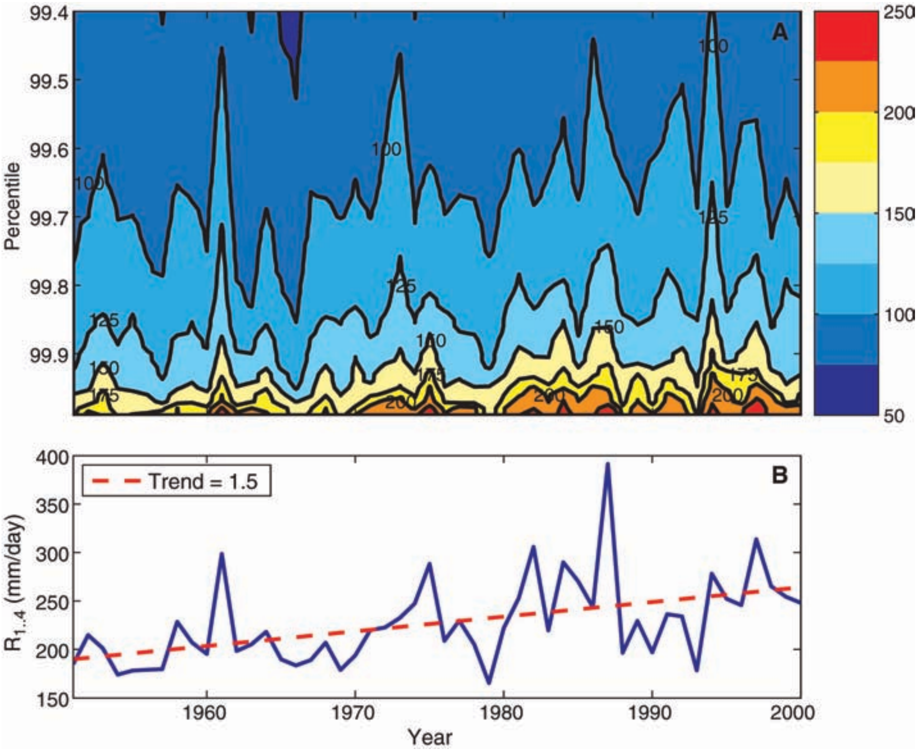


Fig. 4. Temporal variation (1951 to 2000) in (**A**) 99.4 to 99.99 percentiles of seasonal rainfall and (**B**) the mean rainfall of the four highest rain events every season ($R_{1..4}$). Color bar in (A) indicates rain intensity in mm/day. The statistical significance of the trend (dashed line) was calculated as in Fig. 2.

In spite of considerable year-to-year variability, there are significant increases in the frequency and the intensity of extreme monsoon rain events in central India over the past 50 years. Although desirable for applications, it is difficult to detect signals of climate change in extreme rain events at individual stations; instead, as we show, one needs a sufficiently large area to discern a trend reliably. The observed trends suggest enhanced risks associated with extreme rainfall over India in the coming decades.

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Male Fertility and Sex Ratio at Birth in Red Deer

Montserrat Gomendio,[1]* Aurelio F. Malo,[1] Ana J. Soler,[2] Maria R. Fernández-Santos,[2] Milagros C. Esteso,[2] Andrés J. García,[2] Eduardo R. S. Roldan,[1]*† Julian Garde[2]†

Efforts to test sex ratio theory have focused mostly on females. However, when males possess traits that could enhance the reproductive success of sons, males would also benefit from the manipulation of the offspring sex ratio. We tested the prediction that more-fertile red deer males produce more sons. Our findings reveal that male fertility is positively related to the proportion of male offspring. We also show that there is a positive correlation between the percentage of morphologically normal spermatozoa (a main determinant of male fertility) and the proportion of male offspring. Thus, males may contribute significantly to biases in sex ratio at birth among mammals, creating the potential for conflicts of interest between males and females.

The Trivers and Willard hypothesis (*1*) for sex allocation predicts that parents should increase the production of the sex with the higher fitness benefit. This hypothesis has been applied most often to mothers, who have a strong influence on offspring quality through maternal care. It can also apply to any trait that parents transmit to offspring that has a differential effect on the reproductive success of sons and daughters. Thus, among birds, offspring sex ratios may be adjusted in relation to the attractiveness of the father, because sons will inherit large sexual ornaments and will achieve high reproductive success (*2*). However, it is assumed that such manipulation is under female control, because in birds females are the heterogametic sex.

The possibility that males may also facultatively adjust sex ratio has seldom been considered. In haplodiploid insects, the offspring sex depends on whether the ovum is fertilized or not, and males may constrain sex ratios because males with poor-quality ejaculates fail to fertilize the ova (*3*). In mammals, males are the heterogametic sex, and offspring sex is determined by whether an X- or Y-chromosome–bearing spermatozoon fertilizes the ovum. Thus, mammalian males may have more control over the mechanisms of sex determination than they do in other taxa. In mammals, male fertility may have a great influence on the reproductive success of sons.

Ungulates are good models to test sex ratio theory because they are sexually dimorphic in body size, variance in reproductive success is greater among males, and the reproductive success of sons is more strongly influenced by maternal investment. Early studies on red deer (*Cervus elaphus*) found support for the prediction that high-quality mothers should produce sons (*4*), but subsequent studies have generated inconsistent results (*5*). Our previous studies have shown that in natural populations of red deer, males differ markedly in their fertility rates, and more-fertile males have faster swimming sperm and a greater proportion of normal spermatozoa (*6*). Thus, male reproductive success may not depend exclusively on body size, but also on the ability of males to fertilize females after copulation. Male fertility is advertised by antler size and complexity, so more-fertile males also have larger and more elaborate sexual characters, which may be inherited by their sons (*7*).

We tested the hypothesis that more-fertile red deer males produce more sons. The key challenge was to disentangle male and female effects by designing an experiment to retain the inter-male variation in fertility rates found in natural populations while minimizing differences between females (*8*). Thus, our experimental design was aimed at eliminating several female factors known to influence sex ratios: (i) We avoided the possibility that females may bias sex ratio in response to male quality by artificially inseminating females so that they had no direct experience with the males. (ii) We minimized differences in body condition by using a sample of females that were all in good physical condition, were kept under similar environmental conditions, and had access to an unlimited food supply. (iii) All females were inseminated at the same time in relation to ovulation, avoiding the confounding effects of insemination time. In contrast, by using sperm collected during the rut from males living in natural populations, we ensured a representative sample of the large degree of variation in male fertility previously described (*6*).

When the entire study sample is considered, a similar number of male and female offspring were produced (Table 1). However, among males, differences in fertility rates and in the proportion of male offspring were substantial. Male fertility rates ranged from 24 to 70%, and the proportion of male offspring ranged from 25 to 72% (Table 1).

Table 1. Descriptive statistics [mean, standard deviation (SD), and range] for male fertility rates, proportion of male offspring sired, percentage of normal sperm, sperm swimming-velocity parameters, and number of hinds inseminated per male (n = 14 red deer stags). VCL, curvilinear velocity; VSL, straight-line velocity; VAP, average path velocity.

Parameters	Mean	SD	Range min–max
Fertility rate (%)	50.39	13.06	24–70
Proportion of male offspring	0.50	0.14	0.25–0.72
Morphologically normal spermatozoa (%)	80.07	8.78	65–95
VCL (μm/s)	126.87	28.48	85–163
VSL (μm/s)	67.86	27.31	28–111
VAP (μm/s)	88.74	26.52	53–122
Hinds inseminated per male	24.57	16.00	11–69

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[1] Reproductive Ecology and Biology Group, Department of Evolutionary Ecology, Museo Nacional de Ciencias Naturales [Consejo Superior de Investigaciones Científicas (CSIC)], 28006-Madrid, Spain. [2] Instituto de Investigación en Recursos Cinegéticos [CSIC-Universidad de Castilla-La Mancha–Junta de Communidades de Castilla-La Mancha (JCCM)], 02071-Albacete, Spain.

*To whom correspondence should be addressed. E-mail: montseg@mncn.csic.es (M.G.); roldane@mncn.csic.es (E.R.S.R.)

†These authors contributed equally to this work.