Contributed Papers

The Impact of Increased Environmental Stochasticity Due to Climate Change on the Dynamics of Asiatic Wild Ass

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Abstract: *Theory proposes that increased environmental stochasticity negatively impacts population viability. Thus, in addition to the directional changes predicted for weather parameters under global climate change (GCC), the increase in variance of these parameters may also have a negative effect on biodiversity. As a case study, we assessed the impact of interannual variance in precipitation on the viability of an Asiatic wild ass (Equus hemionus) population reintroduced in Makhtesh Ramon Nature Reserve, Israel. We monitored the population from 1985 to 1999 to determine what environmental factors affect reproductive success. Annual precipitation during the year before conception, drought conditions during gestation, and population size determined reproductive success. We used the parameters derived from this model to assess population performance under various scenarios in a Leslie matrix type model with demographic and environmental stochasticity. Specifically, we used a change in the precipitation regime in our study area to formulate a GCC scenario and compared the simulated dynamics of the population with a no-change scenario. The coefficient of variation in population size under the global change scenario was 30% higher than under the no-change scenario. Minor die-offs ($\geq 15\%$) following droughts increased extinction probability nearly 10-fold. Our results support the idea that an increase in environmental stochasticity due to GCC may, in itself, pose a significant threat to biodiversity.*

Keywords: *Equus hemionus*, population projection, reproductive success, simulation model

El Impacto del Incremento de la Estocasticidad Ambiental Debida al Cambio Climático sobre la Dinámica de *Equus hemionus*

Resumen: *La teoría propone que el incremento de la estocasticidad ambiental impacta negativamente a la viabilidad poblacional. Por lo tanto, adicionalmente a los cambios direccionales pronosticados bajo el cambio climático, el incremento en la varianza de estos parámetros también tendrá un efecto negativo sobre la biodiversidad. Como caso de estudio, evaluamos el impacto de la varianza interanual de la precipitación sobre la viabilidad de una población de* Equus hemionus *introducida en la Reserva Natural Makhtesh Ramon, Israel. Monitoreamos la población de 1985 a 1999 para determinar los factores ambientales que afectan el éxito reproductivo. La precipitación anual durante el año anterior a la concepción, condiciones de sequía durante la gestación y el tamaño poblacional determinaron el éxito reproductivo. Utilizamos los parámetros derivados de este modelo para evaluar el funcionamiento de la población en varios escenarios en un modelo tipo matricial de Leslie con estocasticidad ambiental y demográfica. Específicamente, utilizamos un cambio en el régimen de precipitación en nuestra área de estudio para formular un escenario de cambio climático global y comparamos las dinámicas de la población simulada con escenarios sin cambios. El coeficiente de*

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variación en el tamaño poblacional en el escenario de cambio global fue 30% mayor que en el escenario sin cambios. Mortalidades menores (≥15%) después de sequías incrementaron la probabilidad de extinción cerca de 10 veces. Nuestros resultados apoyan la idea de que un incremento en la estocasticidad ambiental debido al cambio climático global puede, por si mismo, ser una amenaza significativa para la bidiversidad.

Palabras Clave: *Equus hemionus*, éxito reproductivo, proyección de la población, modelo de simulación

Introduction

Directional changes in mean annual environmental conditions under global climate change (GCC) are expected to have a devastating impact on biodiversity (Sala et al. 2000; Cameron et al. 2004). However, GCC is predicted to manifest itself not only in directional changes in various weather parameters but also in an increase in their second moment (i.e., the interannual variance or what is termed environmental stochasticity) regardless of any directional change. For example, an increase in the interannual variance of precipitation due to GCC is expected even in areas where only minor or no changes in the mean are expected (Giorgi et al. 2001; Li & Xian 2003).

Of the various stochastic elements that affect wild populations (Shaffer 1981; White 2000), environmental stochasticity has the greatest and most variable impact on time of persistence and dynamics (Murdoch 1994; Simberloff 1998; Grevstad-Fritzi 1999). Depending on the average population growth rate and the variance of this rate due to environmental stochasticity, the function of persistence time versus population size may shift from an exponential to an asymptotic curve (Lande 1993, 1998). Specifically, for sufficiently large populations, mean time to extinction scales asymptotically as the carrying capacity raised to a power (K^c), where $c = 2r/V_e - 1$, r is the mean growth rate of the population, and V_e is the variance in r due to environmental stochasticity. If r remains unchanged, then as V_e increases, time to extinction declines. If $V_e > r$, then $c < 1$ and a higher K (i.e., larger populations) will contribute relatively little to reducing extinction probability. Thus, the second moment of GCC by itself may be a major contributing factor to the increased threat to biodiversity due to GCC.

Assessment of the impact of GCC on population dynamics requires in-depth knowledge of the species' responses to environmental stochasticity (McCarty 2001). Specifically, good knowledge of an organism's response to environmental changes, such as the frequency and magnitude of extreme events, is especially pertinent. Current thinking is that in deserts loss of biodiversity due to climate change will be relatively minor (Sala et al. 2000; Thomas et al. 2004). These extrapolations are based mostly on expected changes in habitat due to overall changes in mean annual precipitation and temperatures and restriction of range derived from these changes and consequent anthropogenic-related fragmentation. Ungulate dynamics, for example, are influenced by stochastic variation in the environment (Sæther 1997), but because most ungulates are relatively large homeotherms, they are generally considered to be able to respond and adapt to minor changes in the environment both behaviorally and physiologically. Thus, the minor projected changes in mean annual precipitation due to GCC in many arid environments (IPCC 2001) may lead researchers and managers to erroneously conclude that GCC in these regions is not a serious threat to biodiversity. However, extreme events (droughts) do have a severe impact on desert ungulates (Young 1994; Saltz 2002; Epps et al. 2004), and interannual variance is expected to increase (i.e., more extreme events and more droughts) in most regions (Collins 2000). Thus, the impact of the second moment under GCC should not be ignored.

Because the interannual variance in productivity in arid environments is high (Archer et al. 1999), the dynamics of populations inhabiting them should be influenced strongly by environmental stochasticity. We assessed the impact of an increase in the interannual variance in rainfall on the viability of an Asiatic wild ass (*Equus hemionus*) population reintroduced into the Negev Desert, Israel. The Asiatic wild ass is a midsized equid (approximately 200 kg) inhabiting arid environments. Precipitation records for the northern Negev Desert, Israel, from the past 50 years suggest an increase in the interannual variation of rainfall (Ben-Gai et al. 1998; Alpert et al. 2002). We based our analysis on recorded changes in rainfall patterns at the site of the reintroduction (which also agree with GCC projections for the region—Giorgi et al. 2001) and their impact on the dynamics of the reintroduced population. We used these data to project future performance of this population under a GCC scenario, contrast the GCC scenario with a no-change scenario, and show that the second moment of changes caused by GCC is in itself a threat to this population.

Methods

Study Area and Local Rainfall Patterns

Asiatic wild asses were reintroduced in Israel into Makhtesh Ramon Nature Reserve. This is a 200-km² reserve established in and around an unusual anticlinal erosion cirque in the Negev Highlands (30°35′ N, 34°45′ E). The environment is hyperarid with cool, wet winters and dry,
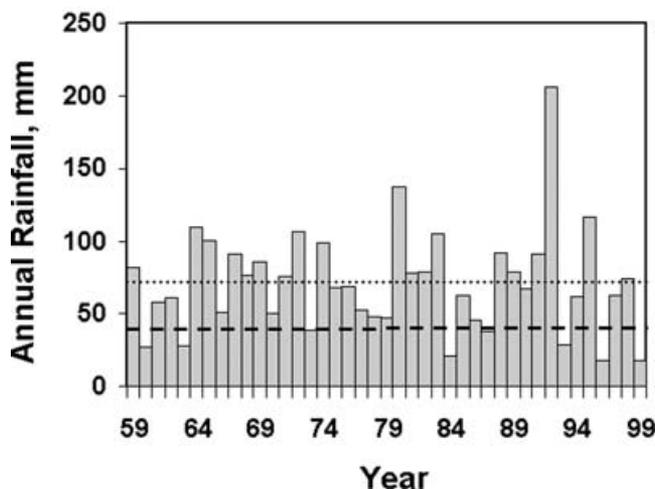
Figure 1. Annual rainfall recorded in the Makhtesh Ramon study area between 1959 and 1999. Mean rainfall was 71 mm (dotted line) and drought years are those with <41 mm (broken line).

hot summers. Annual rainfall varies considerably (coefficient of variation = 51%). Average rainfall from 1959 (first recorded data) to 1999 (year the study of the Asiatic wild ass ended) was 71 ± 36 mm/year, with a minimum of 18 mm/year and a maximum 206 mm/year (Fig. 1), and was not normally distributed (Shapiro–Wilk statistic *W*:normal $= 0.92, p < 0.009$). When we divided these 41 years into two periods: 1959-1979 and 1980-1999, mean annual rainfall was not significantly different (64 ± 25 vs. 74 ± 45 mm; $t = -0.54, p > 0.59$, *t* test for unequal variances, respectively). However, the variance, in agreement with GCC scenarios for this region was higher in the latter years (test for equality of variances $F = 3.26, p = 0.012$).

Field Study and Reproductive Characteristics

Between 1982 and 1987, 28 animals (14 males and 14 females) were released in Makhtesh Ramon (Saltz & Rubenstein 1995). Until 1989 reproductive success was low due to a carry-over effect from the breeding core and\or an impact of the release process (Saltz & Rubenstein 1995). Thereafter, reproductive success increased. In 1997 the population was estimated at over 100 animals and ranged over 2500 km². As of 1997 the reintroduced population has had little effect on the vegetation in the region (Saltz et al. 1999).

The population was continuously monitored by direct observations since the first release until 1999. From 1982 to 1987 the Makhtesh Ramon ranger carried out postrelease monitoring with periodic surveys to record the presence and reproductive success of all animals in the cirque. From 1988 to 1992 and in 1995 we monitored the herd intensively and the reproductive success of all adult fe-

males was known. In 1993 the population was surveyed and monitored for 10 days (July and August). In 1994 and from 1996 to 1999 drive counts were carried out after the foaling season, and reproductive success was noted. Until 1995 all females in the population were individually recognized by scars, and reproductive success was recorded on an individual basis (Saltz et al. 2000) (i.e., the mother's age at the time of birth was known). Also, until 1995 we were able to determine adult survivorship.

Asiatic wild ass breed seasonally and most foals are born between May and July after the rainy season and when the standing vegetation biomass is at its peak. Gestation is 11 months at the end of which a single foal is born. Postpartum estrus occurs 1 month after foaling (i.e., well before the next wet season), and females may conceive in consecutive years. Females may live over 20 years in captivity. Primiparity is usually at age 3 (Saltz & Rubenstein 1995).

Data Analysis

Adult survival in most large ungulates is relatively constant and, except for extreme events (Young 1994), is generally unaffected by environmental stochasticity (Gaillard et al. 1998; Saltz 2002). Thus, mostly reproduction and recruitment were expected to determine the dynamics and facilitate density dependence in Asiatic wild ass. In the Negev Desert, as in all desert environments, primary production and standing biomass are strongly linked to precipitation. Consequently, we expected responses to environmental stochasticity in the reintroduced Asiatic wild ass population to manifest themselves in reproductive success and depend mostly on precipitation and to a lesser extent on population size.

We considered the following independent variables as predictors of reproductive success: annual precipitation (mm) in the year prior to parturition (i.e., during gestation); annual precipitation in the year prior to conception (an index of their body conditions when entering going into estrus); the lower of these two values (i.e., annual precipitation in the year prior to parturition and the year prior to conception); maternal age; and number of adult females in the population during the birthing season. Based on the data, we also included a binomial predictor based on annual precipitation whether the year prior to parturition was a drought year or not. We defined drought years as those falling below the lower twentieth percentile (≤ 40 mm, Fig. 1). The dependent variable was the proportion of adult females (≥ 3 years old) bearing foals. Due to postrelease impact on reproductive success (Saltz & Rubenstein 1995), all reintroduced adult females (i.e., not born in the wild) that were in the wild <4 years were excluded from analysis.

We regressed reproductive success on various combinations of the above predictors by logistic regression (PROC GENMOD, SAS, Cary, North Carolina). First we ran the most general model with the DSCALE option to

estimate overdispersion ($\hat{c}$). Thereafter, we selected a set of submodels (Burnham & Anderson 2002) concentrating on predictors that showed some promise based on the single-variable models and what made sense biologically. Specifically, we focused on rain prior to conception because females in poor conditions would not go into estrus and on droughts during the year of gestation because given the effort already invested, a female would be expected to abort only under extreme conditions. The drought predictor and annual precipitation in the year prior to parturition were not used in the same submodel because the former is derived from the latter. Being large social mammals, we expected their dynamics to be density dependent, thus the inclusion of the number of adult females. To correct for overdispersion, we set SCALE in all submodels to 1 so as not to use $\hat{c}$ values <1. We then selected the best models based on Akaike's information criterion (AIC; Burnham & Anderson 2002), which we corrected for small sample size (AIC_c).

Due to high survival during this period (only two adult females died) and the relatively long life span of the species in the wild (approximately 16 years), we were unable to assess what factors affected survival or constructed a survival curve. Foal survival was also high; only two female foals died (both road kills). We also could not determine postpartum mortality and incorporated it in reproductive success.

Projecting Performance under Various Scenarios

We simulated population performance under various rainfall-pattern scenarios with a Leslie matrix–type model with demographic and environmental stochasticity. Time step was 1 year. Simulations were for the female population only (Brook et al. 2000) and started with the number and age structure of the females that were in the population in 1999 (last year of the study).

The equation for annual reproductive success was derived from what we considered the best model from the logistic regressions. Specifically, we used the coefficients of the predictors multiplied by the values of the predictor variables in the model (precipitation, number of adult females, maternal age) at that specific time step. This value was then multiplied by the proportion of females expected at birth for mothers of that specific age (Saltz & Rubenstein 1995).

We incorporated environmental stochasticity by randomly determining the annual precipitation for each time step via bootstrapping from the Makhtesh Ramon rainfall data bank. We used two basic scenarios: the first was a no GCC scenario (control) in which bootstrapping was from the entire data set (1959–1999). The second scenario assumed GCC caused the higher variance in annual precipitation in the latter 20 years. Under this scenario, separate simulations were run for the two periods (1959–1979 and 1980–1999); in each simulation precipitation

data from the respective periods was bootstrapped. The early period can be viewed as pre-GCC and the later period as conditions post-GCC. We then compared the output from all three simulations by looking at the variance of population size over time.

Because we were unable to generate a survival curve for the reintroduced population and estimate the impact of environmental stochasticity on survival, we relied on the age-dependent survival curve developed by Spinage (1972) for zebras (*Equus burchelli*) and modified by Saltz and Rubenstein (1995) for Asiatic wild ass. The Spinage (1972) survival curve is based on skulls collected over 1 year. The skulls were assumed to be no older than 2 years postmortem and population density during this time did not indicate a recent die-off. Thus, the survival curve we used does not reflect drought-related die-offs. Although the dynamics of most large ungulates are determined mostly by recruitment (Gaillard et al. 1998; Saltz 2002), extreme conditions (e.g., droughts) can cause considerable adult mortality in equids (Georgiadis et al. 2003; Saltz 2002). Drought-related die-offs in other ungulates are also common and usually exceed 30% mortality (Young 1994). Drought years occurred toward the end of out field study in years when only general surveys were carried out (1993, 1996, and 1999). Thus, we had no data on the effect of drought on adult survival.

To test the possible impacts of reduced adult survival during droughts, we simulated population performance based on the above scenarios and repeated the simulations while gradually increasing the impact of the drought on survival. Specifically, we repeated our simulations reducing survival by an additional 5% in each consecutive simulation until a 40% reduction, relative to the original survival curve, was reached. Each simulation included 1000 repetitions, and each repetition began with the number and age structure of the females that were in the population in 1999 (the last year of the study). We ran each repetition for 100 time steps (years). Extinction probability was then calculated as the proportion of repetitions (out of 1000) that ended with no adult females. Finally, we included demographic stochasticity as a simple binomial, based on the number of adult females in a specific time step and age group and the proportion of adult females expected to produce a female offspring or survive (based on the values produced from the environmental parameters).

Results

Overall mean annual reproductive success during the study was 0.5 foals/adult female and varied considerably, from 0.29 to 0.90. The variance, relative to the mean, was greater than expected given the number of adult females observed each year and assuming a random binomial, with the 95% confidence interval on the reproductive
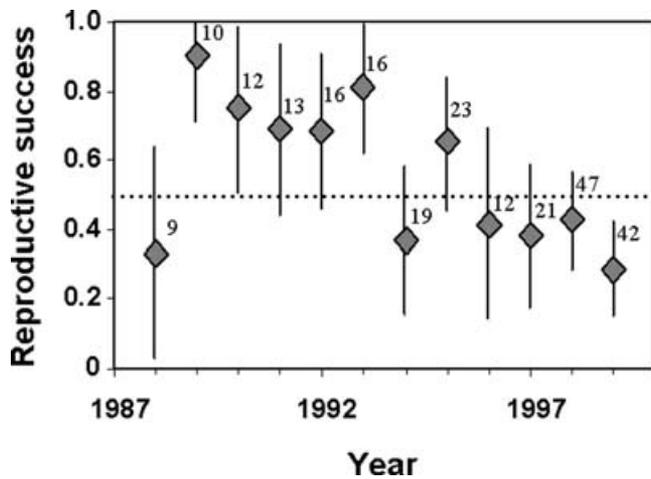
Figure 2. Annual reproductive success (diamonds) of Asiatic wild ass in the study area. The overall mean reproductive success was 0.5 (dotted line). The vertical solid lines represent the 95% confidence interval around each point, and the sample size for that year is the number over the diamond.

success for each year covering the overall mean in only 3 of the 12 years (Fig. 2) and the 50% confidence interval covering the overall mean in only 1 year ($P_{binomial} \leq 0.005$). Thus, factors other than demographic stochasticity affected reproductive success.

We initially carried out regressions and model selection on reproductive success, including maternal age as a predictor based on data from those years when the mother's age was known. After age was found to contribute little, we regressed reproductive success on various combinations of our predictor variables, including data from all years. From the most general model $\hat{c}$ was estimated to

0.7411. Therefore, we set the SCALE parameter to 1 for further analyses.

The two best models, in terms of AIC_c, were indistinguishable ($\Delta AIC_c < 2.0$, Table 1), with the first including two predictors: annual precipitation in the year prior to conception (positive correlation) and whether the year prior to parturition was a drought year (negative correlation) (Table 2). The second-best model included three predictors: the same two predictors as in the former model plus the number of adult females (a negative correlation), which is a density-dependent response. The combined Akaike weights of the two top models was 0.794, demonstrating that there was little uncertainty in selecting models with the two rainfall variables. Both models fit well (Hosmer and Lemeshow goodness-of-fit test $\chi^2 = 6.44$ and 4.55, df=6 and 7, $p = 0.375$ and 0.715, for the best and second best, respectively) and explained 75% and 83% (respectively) of the deviance relative to the saturated model.

The existence of a density-dependent term in the second model made it preferable for running the Leslie matrix population simulation because it eliminated the need for speculation concerning the carrying capacity of the area. Initially we ran the model with the basic survival curve of Saltz and Rubenstein (1995). Under these conditions there were no extinctions. Mean population size for adult females for the no-change scenario was 64.3 ($\pm$15.4 SD). Under the GCC, mean population size was similar for both pre- and post-GCC periods (65.6 and 63.3 for 1959–1979 and 1980–1999, respectively); however, the variance in population size over time was considerably larger for the post-GCC period (SD and CV = 17.7 and 27% [post] vs. 13.4 and 21% [pre]). Under GCC, when running 10,000 time steps, the adult female population fell below 40 2% of the time when bootstrapping from

Table 1. Logistic regression models of Asiatic wild ass annual reproductive success in the Negev Desert, with the number of parameters (*k*), including intercept, log-likelihood values, and AIC values and derivatives (Burnham & Anderson 2002).

Model*	k	Log likelihood	AIC	AIC_c	ΔAIC_c	Likelihood	Akaike weights
Rainprior, drought	3	−152.55	311.09	314.09	0.00	1	0.568
Rainprior, drought, adfem	4	−151.11	310.22	315.93	1.84	0.399	0.226
Minrain, rainprior	3	−154.34	314.67	317.67	3.58	0.167	0.095
Minrain, adfem	3	−154.39	314.77	317.77	3.68	0.159	0.090
Minrain, rainprior, rainthis	4	−154.19	316.39	322.10	8.01	0.018	0.010
Minrain	2	−159.43	322.85	324.19	10.09	0.006	0.004
Rainprior, rainthis	4	−155.27	318.55	324.26	10.17	0.006	0.004
Adfem	2	−160.35	324.71	326.04	11.95	0.003	0.001
Rainprior	2	−161.10	326.19	327.52	13.43	0.001	0.001
Minrain, rainthis	3	−159.28	324.56	327.56	13.47	0.001	0.001
Rainprior, rainthis, minrain, drought, adfem	6	−150.29	312.57	329.37	15.28	<0.001	<0.001
Rainthis	2	−162.83	329.65	330.99	16.89	<0.000	<0.001
Drought	2	−165.21	334.43	335.76	21.67	<0.001	<0.001

Models are ranked from best to worst. Predictor variables include annual precipitation in the year prior to conception (rainprior) and in the year of gestation (rainthis), the lower value of rainprev and rainthis (minrain), whether the year of gestation was a drought year (<40 mm of rain) (drought), and the number of adult females (adfem).
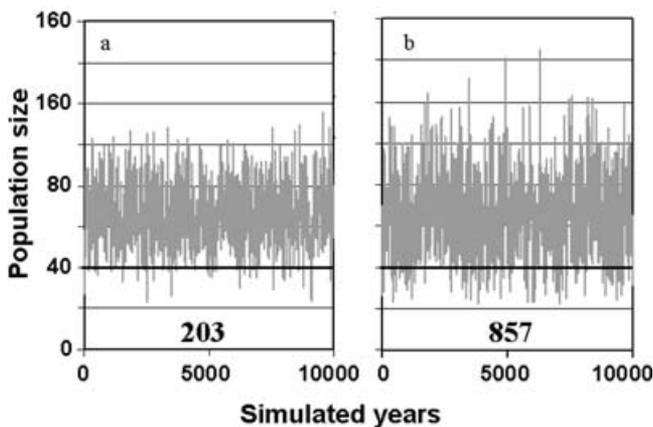
Table 2. Significance and parameter estimation for the two best models explaining reproductive success of Asiatic wild ass.*

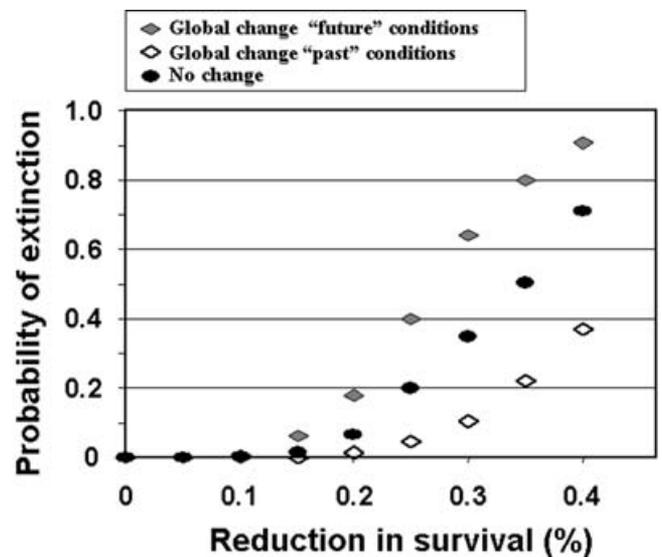| Model and parameter	df	Estimate	SE	χ^2	p
Best model					
intercept	1	−1.0318	0.3008	11.765	0.0006
drought	1	−1.5025	0.3798	15.646	0.0001
rainprev	1	0.0203	0.0044	20.923	0.0001
scale		0.9983			
Second-best model					
intercept	1	−0.4719	0.4461	1.12	0.2252
drought	1	−1.3149	0.4041	15.33	0.0001
rainprev	1	0.0182	0.0041	10.59	0.0011
adfem	1	−0.0171	0.0101	2.86	0.0906
scale		0.8728			

**The parameters used for the simulations were taken from the second-best model.*

the early 1959–1979 period (Fig. 3) as opposed to 8.6% of the time for the latter period ($p < 0.001$).

When we reduced adult survival during drought years, there was little effect on extinction probability (there were no extinctions) until survival was reduced by 10%. Thereafter, extinction probability increased with considerable differences between the two scenarios and the two periods for the GCC scenario (Fig. 4). For example, a 15% adult die-off during droughts produced an extinc-

Figure 4. Impact of a reduction in adult survival due to drought on the probability of extinction over 100 years (based on 5000 simulations). Two scenarios are presented: (1) GCC scenario, which includes values estimated for "future" (bootstrapping rain data from 1980 to 1999) and "past" conditions (bootstrapping rain data from 1959 to 1979) and (2) the no-change scenario (bootstrapping rain data from 1959 to 1999).

tion probability of 6% under the post-GCC scenario versus 0.1% for the pre-GCC period and 1% for the no-change scenario. With a 20% reduction in survival, extinction probability for the post-GCC period rose to 18% as opposed to 1% for the pre-GC period and 7% for the no-change scenario.

Discussion

The possible impacts of GCC on biodiversity are mostly addressed by considering directional changes in mean annual measures of the environment (e.g., precipitation, temperature) and resulting changes in land-use intensity (Forchhammer et al. 1998; Sæther et al. 2000; Epps et al. 2004). Negative impacts of these directional trends have been documented mostly for small vertebrates and invertebrates (e.g., McCarty 2001). Sæther (1997) suggests that such effects might be difficult to show in ungulates due to the complex dynamics of these species. Here we present a new source of threat to ungulate populations, namely, the second moment of predicted GCC. Specifically, in our simulations of Asiatic wild ass dynamics under the GCC scenario, the increased variance in annual rainfall coupled with only moderate die-offs (relative to those documented; Young 1994) following drought years significantly reduced the viability of the population. This

Figure 3. Simulated population size of Asiatic wild ass over 10,000 years based on parameters derived from a logistic regression of reproductive success on precipitation in the year prior to conception, whether or not a drought occurred during gestation, and population density (indexed by the number of adult females). Environmental stochasticity was included by bootstrapping from the 41 years of recorded rain data: (a) high interannual variance by bootstrapping from 1959 to 1979 and (b) low interannual variance by bootstrapping from 1980 to 1999. Number at bottom of each figure is the number of times the population size dropped below 40.

occurred despite an actual increase in the simulated mean annual precipitation. The nonsignificant increase in mean annual precipitation from the period 1959–1979 to the period 1980–1999 became actual in the simulations because the precipitation data were bootstrapped only from these data. Thus, the precipitation data are not samples from two periods anymore, but rather entire populations.

The reduction in the viability of the Asiatic wild ass population under the GCC scenario (i.e., when the interannual variance of precipitation increased) was due to the fact that rainy years did not compensate for droughts. First, there is an upper limit to reproductive success regardless of precipitation. Second, droughts had a dual effect—inducing abortion during the dry winter and reducing conception rates in the following spring.

The change in precipitation patterns recorded in Makhtesh Ramon is not exclusive to this region. In many areas (e.g., East, South, and Southeast Asia) an increase in variance is projected, although little or no change is expected in the mean annual precipitation (Giorgi et al. 2001; Li & Xian 2003). Field data from many areas nearby agree with these projections (Intergovernmental Panel on Climate Change 2001), and increases in the frequency of droughts and dry spells have already been documented throughout the globe (Folland et al. 2001). Although there is no proof that past recorded changes in the weather parameters are due to GCC, if and when a change does occur, it will likely exhibit patterns at least as severe as the changes already recorded. Thus, the results of our case study are not unique and probably reflect a source of threat common to many species and systems.

Globally, climate projection models are in general agreement in terms of directional changes in the mean and variance of weather parameters. However, the exact outcome differs among models (Giorgi et al. 2001), and at the local scale the models may sometimes project opposite trends. Thus, deriving the parameters from such models to assess the performance of local populations is risky. On the other hand, because in many regions recorded weather parameters over the last few decades have exhibited changes that are in general agreement with the models (IPCC 2001, and next IPCC report), these parameters can be used to generate more realistic assessments of the impact of GCC on various components of biodiversity. Hence, the exercise we performed for the Asiatic wild ass in Makhtesh Ramon can and should be repeated elsewhere to broaden the knowledge and formulate rules via meta-analysis.

Acknowledgments

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