

Horn asymmetry and fitness in gemsbok, *Oryx g. gazella*

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The relationship between fluctuating asymmetry in horns of gemsbok (*Oryx g. gazella*) and a number of fitness components was determined in a field study in Etosha National Park, Namibia. The length and width of horns and skull length demonstrated fluctuating asymmetry. Both males and females with asymmetric horns were in poorer condition than symmetric individuals. Individuals of both sexes with symmetric horns more often won aggressive interactions at waterholes. Although symmetric individuals spent more time in dense vegetation, their vigilance rate was not higher than that of asymmetric individuals. Territorial, single males had more symmetric horns than males in herds, suggesting that mating success was inversely related to horn asymmetry. Females with symmetric horns more often had calves than asymmetric females. Horn asymmetry thus appears to reliably reveal phenotypic quality as demonstrated by a suite of fitness components. *Key words*: developmental stability, dominance, mating success, natural selection, predation, sexual selection. [*Behav Ecol* 7:247–253 (1996)]

Natural and sexual selection act on phenotypes and phenotypes are the product of the interactions between genotypes and the environment. The way in which genotypes are translated into phenotypes is far from clear since the commonly presumed linear relationship between genotype and phenotype often appears to be erroneous (e.g., Moreno, 1994). A simple and efficient method to investigate the efficiency with which the genotype is translated into a well-functioning phenotype is by considering the level of developmental stability of the phenotype. Developmental stability reflects the ability of a genotype to control stable development of a specific phenotype under a wide range of environmental conditions (Lerner, 1954; Waddington, 1957). Developmentally unstable phenotypes can be recognized by deviations from bilateral symmetry in otherwise bilaterally symmetrical traits (so-called fluctuating asymmetry) and by missing traits on one side of the body (so-called phenodeviant). These measures of developmental stability integrate a wide range of environmental and genetic factors that are known from observations and experiments to affect the development of phenotypes. For example, environmental factors that increase developmental instability include food quality and quantity, pollutants, extreme temperatures, and parasites, while genetic factors that give rise to elevated instability include inbreeding, homozygosity, hybridization, and mutation (reviews in Møller and Swaddle, 1996; Palmer and Strobeck, 1986; Parsons, 1990). If individuals from a specific population are reared in a novel environment, there is also a dramatic increase in developmental instability, as shown by two studies (Zakharov, 1981, 1989). This suggests that developmental instability also reflects genotype-by-environment interactions and local adaptations.

The current burst of interest in developmental stability in field studies of organisms is mainly caused by the apparent use of deviations from perfect bilateral symmetry as a reliable measure of phenotypic quality. Although a large number of

studies have been reported, there are relatively few of free-living organisms, and there are particularly few studies of mammals. Recent studies of developmental stability in mammals have shown that stags of fallow deer (*Dama dama*) with symmetric antlers are dominant over males with asymmetric antlers (Malyon and Healy, 1994). This relationship may be due to a better health status of symmetric individuals. For example, reindeer (*Rangifer tarandus*) treated with antihelminth drugs developed more symmetric antlers the subsequent years than individuals receiving the control treatment (Folstad et al., in press). Individuals with symmetric antlers thus may be more resistant to parasites or may become less infected with parasites than others. A high dominance rank may confer fitness advantages such as access to females and thus elevate mating success. This was the case in oribi (*Ourebia ourebi*), in which males with symmetric horns had larger harem sizes than asymmetric males (Arcese, 1994). It is fully possible that a developmentally stable phenotype may provide individuals with better access to food and thus a high body condition. The extent to which body condition is related to morphological asymmetry remains unknown, and the role of body condition as a mediator of the relationship between developmental stability and fitness components needs investigation. In this study, we relate a number of behavioral variables and fitness components to measures of developmental stability and body condition. Fitness components in the present study include birth rate, territory occupation, which in the present case is presumed to be a substitute for mating success, and survival.

The gemsbok is one of three subspecies of the oryx. Both sexes have slightly curved, lancelike horns with ridges at the proximal end. Male horns are thicker at the base than female horns, but are of similar length (Packer, 1983). The basal area of gemsbok horns is small for its body size, and the frequency of horn breakage is among the highest in antelopes (Packer, 1983). Both males and females use horns for intraspecific interactions, while individuals of both sexes defend themselves and females defend their offspring against predators. Fights start with sparring contests that often escalate into fights consisting of clashes of horns and heads and attempts to stab the opponent (Huth, 1980; Walther, 1980). The contested resource among males is usually an estrous female or water (Hamilton et al., 1977; Walther, 1980). Males are slightly larg-

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er than females with average body masses of 176 kg and 162 kg, respectively (Estes, 1991). The social organization consists of evenly spaced territorial males with a territory size of a few square kilometers and mixed herds (Smithers, 1983; Walther, 1978; Williamson and Williamson, 1985). Mixed herds are composed of females, juveniles, and nonterritorial males, and territorial males are able to dominate herd males and court females in mixed herds (Walther, 1978). Herd males usually have small scrotums and are therefore sexually inactive, while territorial males have fully developed scrotums and are sexually active (Estes, 1991).

The objectives of this study were to determine behavioral and fitness consequences of horn asymmetry in the gemsbok (*Oryx gazella gazella*), a large antelope in which both sexes have horns. This was done in a study of horn asymmetry in a collection of skulls and a field study of free-ranging gemsbok in the Etosha National Park, Namibia. More specifically, we determined (1) the degree of asymmetry in three horn and one skull character; (2) the relationship between body condition and horn asymmetry; (3) the relationship between vigilance, habitat use, and horn asymmetry; (4) the relationship between dominance and horn asymmetry; (5) the relationship between territorial status and horn asymmetry in males; and (6) whether horn asymmetry of adult females was related to fecundity.

MATERIALS AND METHODS

Study area

The field study took place in Etosha National Park, Namibia, during the periods 14–19 January 1991 and 9–17 January 1995. The park, which is 22,275 km² large, mainly consists of open, dry savanna with scattered trees and shrubs. Annual precipitation is low, and although the rainy season extends from November to March, both study periods were very dry with little fresh vegetation. The total population of gemsbok in the national park has been estimated to 3300 to 3700 individuals in 1995 (Brain C, personal communication).

Measurement of horn asymmetry and tests for fluctuating asymmetry

For direct assessment of fluctuating asymmetry in gemsbok horns, A.P.M. measured the 97 skulls of gemsbok shot mainly in the Etosha National Park during 1970–1985 and currently in the Ministry of Environment and Tourism, Windhoek, Namibia. The length of the right and the left horn was measured to the nearest millimeter along the horn on the front side using a flexible ruler. The direct distance from the base to the tip was also measured, but this measurement was strongly positively related to the first measurement of horn length ($r = .996$) and we therefore only present the results based on the former measurements. The width at the base of the right and the left horn at an angle perpendicular to the body axis was measured to the nearest 0.1 mm with a digital caliper. A measure of skull size was obtained by recording the distance to the nearest 0.1 mm with a digital caliper from the eye socket to the front of the first tooth on the right and the left side of the skull. This distance is hereafter termed skull length, because it is likely to be strongly positively correlated with overall skull size. However, real skull length could often not be measured because of missing bony parts.

Sex was determined from the width of the horn at the base, assuming that adult individuals with a horn width larger than 57.5 mm were males. This method was reliable as determined from information on labels of some of the skulls. Whenever possible, a small piece of skin was removed from the skull,

stored in EDTA buffer, and later used for sexing based on a sex-specific DNA probe. This method of sexing based on a molecular technique provided similar results as sexing based on the horn width criterion for a sample of 60 individuals.

We tested if horn characters demonstrated directional asymmetry or antisymmetry (Ludwig, 1932) by determining whether signed right-minus-left character values deviated significantly from normal frequency distributions with a mean of zero (Palmer and Strobeck, 1986). If that was not the case, the characters were supposed to demonstrate fluctuating asymmetry. Absolute asymmetry of a character was simply unsigned right-minus-left character size, while character size was the mean of left and right character value. The relationship between absolute fluctuating asymmetry and character size was determined using Spearman rank correlation analysis. Relative asymmetry was absolute asymmetry divided by character size.

The first five skulls were measured a second time for assessment of measurement errors after all skulls had been measured once. The repeatability (Becker, 1984; Falconer, 1989) of horn length and width were very high (horn length: $r = 1.00$, SE = 0.001, $F = 8819.49$, df = 4,5, $p < .0001$; horn width: $r = .99$, SE = 0.01, $F = 443.82$, df = 4,5, $p < .0001$), as was the repeatability of absolute fluctuating asymmetry in horn length and width (absolute asymmetry in length: $r = 1.00$, SE = 0.001, $F = 7105.32$, df = 4,5, $p < .0001$; absolute asymmetry in width: $r = .98$, SE = 0.01, $F = 332.76$, df = 4,5, $p < .001$). Hence, measurement errors were small for both size and asymmetry measurements.

Photographs of the skulls were taken at a constant distance on a uniform background, with the vertical axis of the skull perpendicular to the ground level. Skulls were subsequently scored as asymmetric, if the horns differed noticeably in length or curvature, or symmetric, using the same method as described below for the field study. Two persons unaware of the aims of the study independently scored the skulls on the photographs for assessment of reliability of the scoring procedure. The Spearman rank correlation between scorers was for male gemsbok, $r_s = .96$, $N = 48$, $z = 6.58$, $p < .001$, and for female gemsbok, $r_s = .92$, $N = 49$, $z = 6.38$, $p < .001$. Hence, individuals were scored reliably with respect to horn asymmetry.

We assessed whether our procedure of scoring horn asymmetry reliably reflected real asymmetry by determining the absolute degree of horn asymmetry for individuals scored as either symmetric or asymmetric, respectively. For males, there was a clear relationship between asymmetry score and real asymmetry (horn length: scored as symmetric: 1.92 cm, SE = 0.48, $N = 22$; scored as asymmetric: 5.46 cm, SE = 0.95, $N = 26$, Mann-Whitney U test, $z = 3.42$, $p < .001$; horn width: scored as symmetric: 0.08 cm, SE = 0.01; scored as asymmetric: 0.17 cm, SE = 0.02, Mann-Whitney U test, $z = 2.50$, $p < .01$). Similarly, for females, scores of asymmetry reliably reflected real asymmetry (horn length: scored as symmetric: 1.26 cm, SE = 0.22, $N = 22$; scored as asymmetric: 3.31 cm, SE = 1.25, $N = 27$, Mann-Whitney U test, $z = 2.62$, $p < .001$; horn width: scored as symmetric: 0.10 cm, SE = 0.01; scored as asymmetric: 0.14 cm, SE = 0.01, Mann-Whitney U test, $z = 2.33$, $p < .01$). Hence, individuals scored as having asymmetric horns really had horns that were more asymmetric in length and width than individuals scored as symmetric.

Field procedures

We searched extensively for gemsbok along all public roads in the Etosha National Park from sunrise until 1100 h, when activity almost ceased completely because of heat, and from 1500 h until sunset. We recorded a total of 236 individuals in

1991 and 360 individuals in 1995. We drove slowly on all roads searching both sides of the road for gemsbok. Animals were not individually marked, and we attempted to avoid inclusion of the same individuals by covering most roads only once. Gemsbok are known to only travel short distances per day, usually less than 3 km and often less than 1 km (Smithers, 1983; Walther, 1978; Williamson and Williamson, 1985). We only included the first observation of an individual if sex and horn size and asymmetry of an individual seen on two different days were similar. Although we cannot be completely sure that no individual was included more than once, our field procedures ensured that we minimized such effects of pseudoreplication.

Sex was determined from the presence or absence of a scrotum. Animals were classified as either calves of the year, when having a light color and small horns, juveniles when having short horns and less than 14 ridges in the horns, or adults when having long horns and 14–30 ridges in the horns. Whenever an individual was sighted, we determined herd size as the number of individuals in a site traveling together. Herd size was not determined when we were uncertain whether animals could be hidden in the vegetation. Herd composition with respect to sex and age was determined as described above. Calves of the year were assigned to mothers based on suckling and attendance when animals traveled.

We determined horn size relative to the length of the head in units of one-quarter head lengths from the video recordings and the photographs of the skulls. This relative measure of horn length is justified because head length is relatively invariable relative to horn length (see “Tests for fluctuating asymmetry” in Results). Furthermore, the ratio between horn length and skull length from measurements was strongly positively correlated with the ratio estimated in terms of units of one-quarters head lengths for the skull sample ($r_s = .72$, $N = 97$, $p < .001$). Estimates of relative horn length in the field and from video recordings were also strongly positively correlated ($r_s = .82$, $N = 34$, $p < .001$).

We counted the number of visible ridges on the horns using binoculars or a telescope. This method is reliable as determined from independent estimates of the number of ridges on the same individuals determined by two observers ($r_s = .88$, $N = 50$, $p < .001$).

Horns were scored as either symmetric or asymmetric from side-on views (many from video films) depending on whether they visibly deviated in length or curvature from each other. Horns were scored as having similar or dissimilar lengths, as described in the section “Measurement of horn asymmetry and tests for fluctuating asymmetry,” or similar or dissimilar curvatures depending on whether horns overlapped or did not overlap when seen from the side. Independent assessment of asymmetry by two different observers gave highly consistent estimates; only two of 50 estimates differed between observers (length asymmetry: phi correlation coefficient = .92, $N = 50$, $\chi^2 = 38.28$, $p < .001$; curvature asymmetry: phi correlation coefficient = .75, $N = 50$, $\chi^2 = 25.09$, $p < .001$). If a horn was missing, this was recorded as horn breakage. All missing horns were broken at the base. However, we cannot exclude the possibility that some horns had broken at the tip, but were quickly worn again to rounded tip that no longer appeared as a break. The extent of this problem was probably minimal because horn asymmetry in length was strongly positively correlated with horn asymmetry in curvature (phi correlation coefficient = .85, $N = 50$, $p < .001$).

Condition was simply estimated as the number of visible ribs under the assumption that starved individuals will have more visible ribs than fat individuals. We have not found any reference to this simple index, but farmers have traditionally used visible ribs as a sign of poor condition. The condition

index was determined using either 10×50 Zeiss binoculars or a $25\text{--}50 \times 50$ Kowa telescope. This measure of condition was reliable since the Spearman rank correlation between independent scores by two observers was positive and statistically highly significant ($r_s = .98$, $N = 50$, $p < .001$).

Habitats were classified in four categories depending on visibility. These categories were (1) open habitats without bushes or trees and with good visibility, (2) open habitats with some bushes and therefore less visibility, (3) habitats with intermediate density of bushes and trees and an intermediate visibility, and (4) dense habitats with many bushes and trees and low visibility.

Recording behavior

Aggressive interactions and fighting were rare in foraging herds of gemsbok. Waterholes were a limited resource and the frequency of fighting was high in such sites. Only direct physical interactions were used in order to avoid problems of inclusion of covert aggressive interactions. Interactions were observed from a car at a distance of at least 30 m, a distance that did not disturb animals because of the continuous presence of tourists around waterholes. We determined the outcome of interactions by assigning a loss to an individual that yielded to another individual which therefore was recorded as the winner. Sex and the relative size of the horns of interacting animals, their asymmetry, and the number of visible ribs were determined after the fight. A total of 84 interactions involving 50 dyads of individuals were recorded.

We recorded two cases of predation encountered in 1991. Horn length and asymmetry were assessed as previously described.

Whenever a foraging gemsbok was sighted, we started a continuous video recording of behavior for a duration of 5 min, or until the animal moved out of sight. Videotapes were subsequently analyzed for head-up behavior, which was supposed to equal vigilance. Whenever the focal, standing animal lifted its head above the level of its back, we assumed that it had an opportunity to scan for predators and it was therefore considered to be vigilant. Time spent vigilant was simply the time with the head above the level of the back divided by total recording time. We also noted the sex of the individual, the number of individuals in the herd, the number of ridges on the horn, horn size relative to head length, horn asymmetry, the number of ribs, and the density of vegetation as defined above. The consistency of this estimate of vigilance for the same individual at different times was determined for 20 individuals by calculating the proportion of time being vigilant during the first 2.5 min and the last 2.5 min of an observation period. The rank correlation between these two estimates was positive and highly significant ($r_s = .77$, $z = 3.36$, $N = 20$, $p < .001$).

Statistical analyses

The frequency distributions of absolute asymmetries are truncated normal, and this fact violates the assumptions of parametric statistical tests. Nonparametric tests were therefore used in most cases. The relationship between horn asymmetry and various measures of behavior and fitness components, respectively, was determined using rank correlation analysis (Siegel and Castellan, 1988). The partial effect of horn asymmetry after controlling for the potentially confounding effects of body condition was determined by Kendall partial rank correlation analysis (Siegel and Castellan, 1988). The outcome of dominance interactions in relation to horn size and asymmetry was tested with a binomial test assuming a binomial probability of .5.

Table 1
Summary statistics for morphological characters of skulls of gemsbok

	Horn length	Horn width	Skull length
Males (<i>N</i> = 48)			
Character size	88.30 (1.70)	6.30 (0.05)	14.36 (0.10)
Signed right-minus-left character value	4.57 (7.31)	0.02 (0.04)	-0.07 (0.04)
Kurtosis	0.11	0.68	0.57
Skewness	0.31	0.58	-0.55
Absolute asymmetry	35.28 (5.39)	1.24 (0.32)	1.75 (0.28)
Relative asymmetry	0.042 (0.006)	0.019 (0.005)	0.012 (0.002)
Females (<i>N</i> = 49)			
Character size	85.81 (1.07)	5.04 (0.08)	14.07 (0.15)
Signed right-minus-left character value	-5.17 (7.40)	0.30 (0.18)	-0.01 (0.02)
Kurtosis	0.71	1.02	0.94
Skewness	-0.04	0.76	0.14
Absolute asymmetry	25.37 (6.64)	1.11 (0.11)	1.29 (0.15)
Relative asymmetry	0.031 (0.009)	0.024 (0.003)	0.009 (0.001)

All measurements in centimeters except for relative asymmetry which is dimensionless. Values are means (SE).

When more than a single test is performed on a data set, the probability of finding statistically significant results is inflated. In order to avoid this problem, probabilities were Bonferroni adjusted to a significance level of 0.05 following the procedures reported by Rice (1989). All tests are two-tailed. Values reported are means (SE).

RESULTS

Tests for fluctuating asymmetry

Horn length and width and skull length demonstrated fluctuating asymmetry as revealed by the summary statistics showing that frequency distributions of signed right-minus-left character values not deviating significantly from normal distributions (Table 1). None of the mean right-minus-left values differed significantly from zero (one-sample *t* tests, $p > .20$). Similarly, none of the skewness or kurtosis values differed significantly from expectations for normal distributions ($p > .10$).

Absolute asymmetry in morphological characters was unrelated to mean character size for horn length and skull length, but was positively related to horn width in males (horn length: Kendall rank order correlation, $\tau = -0.10$, $N = 49$, $z = 0.73$, ns; horn width: $\tau = 0.30$, $z = 2.09$, $p < .05$; skull length: $\tau = -0.02$, $z = 0.11$, ns). Absolute asymmetry was unrelated to character size for all three traits in females (horn length: Kendall rank order correlation, $\tau = 0.09$, $N = 49$, $z = 0.67$, ns; horn width: $\tau = -0.12$, $z = 0.92$, ns; skull length: $\tau = 0.01$, $z = 0.06$, ns). Relative rather than absolute asymmetries were therefore used for subsequent comparisons.

Horns in males were significantly longer and wider than in females (Table 1; horn length: Mann-Whitney *U* test, $z = 2.37$, $p < .01$; horn width: $z = 8.62$, $p < .001$), but skull length did not differ significantly between sexes ($z = 0.63$, ns). Six individuals in the field study had broken horns, and they were all males (4.5% of 134 males). Relative asymmetry in horn length and width was significantly larger in males than in females (horn length: Mann-Whitney *U* test, $z = 2.20$, $p < .05$; horn width: $z = 2.41$, $p < .05$), but there was no difference for skull length ($z = 0.90$, ns).

Relative asymmetries differed significantly among morphological characters in both sexes. Horn length asymmetry was

significantly larger than asymmetry for horn width and skull length in males (Table 1; Bonferroni adjusted Mann-Whitney *U* tests, $p < .05$). In females, relative horn length asymmetry was larger than skull length asymmetry, while horn width asymmetry did not differ significantly from the other two mean estimates (Table 1; Bonferroni adjusted Mann-Whitney *U* tests, $p < .05$).

The frequency of asymmetric individuals among adults in the field sample was lower than in the sample of skulls for both sexes (males: field: 37.3% of 134 individuals; skulls: 45.8% of 48 individuals; females: field: 31.2% of 186 individuals; skulls: 44.9% of 49 individuals). There was no statistically significant sex difference, but the difference between the field sample and the skull sample was significant ($G = 4.02$, $df = 1$, $p < .05$). This may indicate that the sample of skulls was biased.

Asymmetry and condition

Horn asymmetry reliably reflected the condition of individual gemsbok. Symmetrical individuals had fewer visible ribs than asymmetrical individuals in all four sex and age categories (Figure 1). There was also a direct negative relationship between horn asymmetry and condition since the rank correlations between horn asymmetry and number of ribs all were negative and statistically significant (juvenile males: $\tau = -0.54$, $N = 12$, $z = 3.53$, $p < .05$; adult males: $\tau = -0.34$, $N = 112$, $z = 3.53$, $p < .01$; juvenile females: $\tau = -0.44$, $N = 21$, $z = 1.99$, $p < .05$; adult females: $\tau = -0.28$, $N = 151$, $z = 3.42$, $p < .01$). Therefore, individuals with asymmetric horns were in poor body condition independent of sex and age.

Asymmetry, habitat use, and vigilance

If asymmetric individuals are more susceptible to predation, we predicted that they may be able to reduce this risk by either spending more time in open habitats with good visibility or being more vigilant. Habitat distribution of gemsbok was indeed related to horn asymmetry (Figure 2). Symmetric individuals independent of sex were in more dense habitats than asymmetric individuals (Kendall rank correlation, $\tau =$

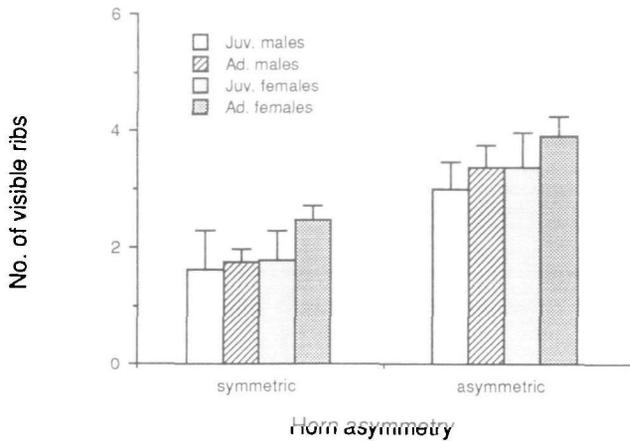


Figure 1
Number of visible ribs in relation to horn asymmetry in gemsbok. Values are means (SE). Sample sizes are 8, 73, 13, and 103, respectively, for the symmetric individuals and 4, 39, 8, and 48, respectively, for the asymmetric individuals.

-0.13, $N = 229$, $z = 2.89$, $p < .01$). Gemsbok with many visible ribs also tended to be in dense habitats ($\tau = 0.10$, $N = 191$, $z = 2.01$, $p < .05$). Females were in denser habitats than males ($\tau = 0.22$, $N = 217$, $z = 4.81$, $p < .001$). The negative relationship between horn asymmetry and habitat density could be confounded by individuals in poor condition, or of a specific sex, more often being found in dense habitats. However, the negative relationship between habitat density and horn asymmetry remained statistically significant after controlling for the effects of condition as reflected by the number of ribs and sex (partial Kendall rank correlation, partial $\tau = -0.15$, $N = 229$, $z = 3.38$, $p < .001$). Hence, gemsbok with asymmetric horns spent more time in open habitats with good visibility.

We recorded vigilance of a total of 41 individuals which spent on average 25.9% (2.8) of their time vigilant. There was no relationship between vigilance and horn asymmetry (Kendall rank order correlation, $\tau = 0.18$, ns). Vigilance was weakly negatively related to horn length ($\tau = -0.23$, $p < .10$). We found no relationship between time spent vigilant and sex, condition, group size, or vegetation density ($\tau = -0.10-0.03$, all ns). Time spent vigilant was still unrelated to horn asymmetry after simultaneously controlling for the potentially confounding effects of horn length, sex, condition, group size, and vegetation density (Kendall partial rank correlation, partial $\tau = 0.20$, ns). Hence, there was little evidence that gemsbok with asymmetric horns countered a higher risk of predation by being more vigilant.

Two of all the observed individuals during 1991 and 1995 were visibly wounded; a male with a limp had asymmetric horns, and a female with a broken leg had asymmetric horns. We only recorded two predation events in 1991, and both involved gemsbok with asymmetric horns; a male with asymmetric horns was eaten by lions; and a second, recently killed male with asymmetric horns was eaten by hyenas.

Asymmetry and dominance

The outcome of 84 fights was recorded at five waterholes. Fighting success was clearly related to horn length. Fights were usually won by the individual with the longest and most symmetric horns independently of whether they involved two males, two females, or a male and a female (Table 2). The relationship between outcome and horn length was highly significant in a binomial test with a binomial probability of .5, as

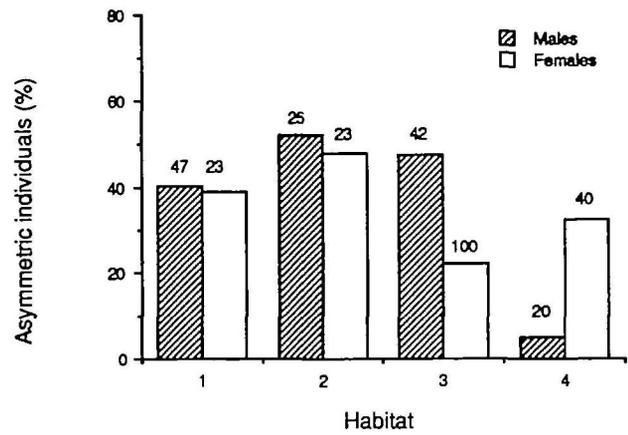


Figure 2
Habitat distribution of adult gemsbok in relation to horn asymmetry. Numbers are number of individuals. Habitats increase in tree density and decrease in visibility from 1 to 4.

was the relationship between outcome and horn asymmetry (Table 2). Males usually won interactions with females (Table 2).

The independent effect of horn length and horn asymmetry was determined by only considering fights in which the horns of the contestants were judged to be of similar length, or in which the winner had shorter horns. The winner had asymmetric horns in 29% of 14 fights, while all the losers had asymmetric horns ($G = 26.32$, $df = 1$, $p < .001$). Hence, the probability of winning was higher for individuals with symmetric horns.

Asymmetry and male territoriality

Horn asymmetry was related to male territoriality. Single males defend large territories, while nonterritorial males occur in pure male herds or herds of mixed composition. Horn asymmetry was more common among male gemsbok in herds than among territorial males (1991: herd males: 44.0% of 84 individuals; territorial males: 20.0% of 15 individuals; $G = 3.03$, $df = 1$, $p < .10$; 1995: herd males: 47.2% of 98 individuals; territorial males: 29.6% of 36 individuals; $G = 16.45$, $df = 1$, $p < .001$). Therefore, males with symmetric horns tended to be territorial, while males with asymmetric horns tended to be in herds.

Asymmetry and female fecundity

Horn asymmetry may be a predictor of female fecundity. Adult females with calves more often had symmetric horns

Table 2
Outcome of aggressive interactions between gemsbok at waterholes

	Winner	Loser	<i>p</i>
Individual with the longest horns			
Male-male fights	16	2	.002
Female-female fights	16	4	.012
Male-female fights	10	2	.11
Individual with the most symmetric horns			
Male-male fights	15	3	.036
Female-female fights	15	5	.042
Male-female fights	10	2	.11

Each observation refers to an interaction between two individuals. Each individual is only represented once.

(87% of 23 females) than females without calves (69% of 163 females; $G = 26.96$, $df = 1$, $p < .001$). Adult females with calves did not have longer horns or horns with more ridges than females without calves (Mann-Whitney U test, ns). However, mothers also had more visible ribs than nonmothers (Mann-Whitney U test, $z = 2.12$, $p < .05$; mothers: 3.29 (.63), $N = 23$; nonmothers: 2.52 (.31), $N = 163$). A partial correlation analysis revealed that presence of calves was significantly negatively related to horn asymmetry (partial $\tau = -0.28$, $N = 186$, $z = 5.67$, $p < .001$), but not to condition as indicated by the number of ribs (partial $\tau = -0.02$, $N = 186$, $z = 0.40$, ns). Hence, females with symmetric horns more often had calves than females with asymmetric horns.

DISCUSSION

Developmental stability and fitness components

The field study of developmental stability in horns of gemsbok revealed a number of different correlates of horn asymmetry. Most importantly, body condition as reflected by the number of visible ribs was higher among individuals with symmetric horns. The rainy seasons of 1990–1991 and 1994–1995 were both very dry, and low levels of precipitation are likely to reduce overall body condition. The correlation between condition and horn asymmetry could either be due to a direct link between metabolic efficiency and developmental stability (e.g., Mitton and Grant, 1984), or an indirect effect of developmentally unstable individuals having a higher parasite burden or being restricted to poor habitats with forage of inferior quality or quantity. Parasitism has been shown to be related to developmental instability in a range of studies (Folstad et al., in press; Møller, 1992b, 1995; Polak, 1993). Dominance was shown to be negatively related to fluctuating asymmetry in horn length of gemsbok of both sexes in the present study, and other studies have also indicated negative relationships (Malyon and Healy, 1994; Witter and Swaddle, 1994). Both these mechanisms thus appear to be feasible.

Gemsbok with symmetric horns were dominant over asymmetric individuals at waterholes, even when the effects of horn length and body condition as reflected by number of visible ribs were controlled statistically. Water is often a very important and limiting resource in arid environments, and fatal body attacks by gemsbok have been seen to take place during severe water restriction caused by drought (Hamilton et al., 1977; Walther, 1980). Asymmetries in horn length or shape may under serious sparring or stabbing contests prove to be a severe handicap that is fatal. Males are usually dominant over most females, and reproductively active males with a fully developed scrotum are dominant over reproductively inactive males (Hamilton et al., 1977; Stanley Price, 1978; Walther, 1978; Williamson and Williamson, 1985). Social dominance may confer a number of advantages in terms of mating and reproduction (e.g., Morse, 1980). This also appeared to be the case in gemsbok in which dominant individuals with symmetric horns more often won fights at waterholes. Such symmetric individuals were often territorial males or females with offspring.

Previous studies of the social organization of oryx have shown that territorial, solitary males constitute 11–28% of adult males in the population (Estes, 1991). Adult females often outnumber males by a factor two (Estes, 1991), but whether this is due to sampling bias or sex-specific mortality remains unknown. In our study of gemsbok in Etosha, solitary territorial males comprised 27% of all adult males. Adult males constituted 42% of all adult gemsbok recorded during our transects. Adult, territorial males were not a random sample of males, but more often had symmetric horns than herd

males. Territorial males have access to estrous females within their territories (Hamilton et al., 1977; Walther, 1980), and male mating success thus may be hypothesized to be inversely related to horn asymmetry. Negative relationships between degree of fluctuating asymmetry and mating success have been found in a large number of observational and experimental studies of both plants and animals (reviews in Møller, 1993; Møller and Eriksson, 1995).

Finally, female horn asymmetry was shown to be inversely related to fecundity as measured by the presence of dependent calves. Most female gemsbok give birth during the rainy season (Estes, 1991), and it is unlikely that gemsbok females could have postponed parturition due to drought conditions of the current season. The negative relationship between current fecundity and horn asymmetry thus is unlikely to have been influenced by our observations having been restricted to the late rainy season. Fecundity has never previously been related to developmental stability. High fecundity among female gemsbok with symmetric horns may be the result of developmental selection or a direct outcome of poor body condition. Developmental selection occurs when the number of offspring after fertilization is adjusted relative to their value to parents. Developmental errors such as fluctuating asymmetries or phenodevians may be the result of an inferior developmental program, and parents may select against developmentally unstable offspring and thus forego investment in offspring of low future reproductive potential. Chromosomally, genetically, or developmentally aberrant embryos may be aborted at an early stage of morphogenesis, and offspring with developmentally unstable phenotypes may be sacrificed during sib competition or deserted. Alternatively, poor body condition may directly influence female fecundity, although this does not appear to be the case in the gemsbok, since body condition measured as the number of visible ribs did not appear to account for the relationship between fecundity and horn asymmetry.

The present study of fluctuating asymmetry in gemsboks has demonstrated intense directional phenotypic selection against asymmetry. This result parallels similar studies of other organisms (review in Møller and Swaddle, 1996). High levels of additive quantitative genetic variation can be maintained for characters despite intense directional selection (Pomiankowski and Møller, 1995). Interestingly, a recent meta-analysis of published information on the quantitative genetics of developmental stability has provided evidence for a relatively large, highly significant additive genetic variance component (Møller and Thornhill, in press). Intense directional selection thus should result in microevolutionary responses to selection.

In conclusion, developmentally unstable horns in gemsbok of both sexes were a phenotypic marker of poor body condition and low social status. Females with symmetric horns tended more often to have offspring and symmetric males had access to a territory and therefore females, while asymmetric individuals either less often had offspring or were nonreproductive herd animals.

Developmental stability and conservation biology

Developmental instability at the individual level provides an extremely sensitive and wide-ranging blueprint for overall performance (e.g., Møller and Swaddle, 1996; Parsons, 1990). It is no surprise that a growing number of field studies of animals and plants have shown that, for example, growth rate, mating success, fecundity, and survival are strongly negatively correlated with various measures of developmental instability (review in Møller and Swaddle, 1996). If these patterns prove to be relatively general, this may have important implications for ecological and evolutionary biology, but also for conser-

vation biology, as suggested by Leary and Allendorf (1989). Conservation biology concerns the study of the well-being and the maintenance of viable populations of organisms (e.g., Meffe and Carroll, 1994). If developmental stability in morphological characters reliably reflects the interaction between organisms and their environment, and furthermore predicts performance in a number of domains related to fitness, then studies of developmental stability reliably may be used as tools for the conservation of viable populations. Our study of free-ranging gemsbok suggested that horn asymmetry was negatively related to a number of behavioral traits and fitness components. A relatively high frequency of horn asymmetry in the population may indicate that a relatively small fraction of the population with symmetric horns contributes disproportionately to reproduction and thus constitutes the effective population. Very few attempts have previously been made along these lines. For example, Manning and Chamberlain (1993) were able to show that fluctuating asymmetry in canine teeth, but not in sexually size monomorphic teeth, of gorillas (*Gorilla gorilla*) had increased during the last two centuries, possibly because of environmental stress due to habitat deterioration. A second example concerns the distribution of European blackbirds (*Turdus merula*) in a patchy environment of tree lots (Møller, 1995). Yearling birds were restricted to small habitat patches in which breeding success and developmental stability of offspring was low. Natural selection acted against asymmetric offspring, and the breeding population in small patches was maintained by immigration of developmentally stable individuals from large patches. We would like to emphasize, as already done by Leary and Allendorf (1989), that measures of developmental stability under field conditions may provide important and readily accessible information on the well-being of free-ranging organisms in their natural environment.

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