LIFE-HISTORY CORRELATES OF HORN ASYMMETRY IN MOUNTAIN GOATS

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Fluctuating asymmetry (FA) refers to small random deviations from perfect bilateral symmetry. Because FA reflects the ability of individuals to undergo stable development, it may provide a potential measure of individual quality. We assessed whether horn asymmetry was related to life-history traits in individually marked mountain goats (*Oreamnos americanus*) over 10 years. Horn length exhibited FA and was related positively to absolute asymmetry in both sexes. Relative asymmetry in horn length did not vary with either sex or age. Horns of surviving juvenile (1- and 2-year-old) males were more symmetrical than horns of those that died, but horn asymmetry did not affect survival of juvenile females or adults of either sex. Horn asymmetry was not related to body condition in juveniles of either sex or in adult males, but adult females with symmetrical horns were in better condition than those with asymmetrical horns. Similarly, horn asymmetry was related negatively to body mass in adult females but not in other sex–age classes. Horns of dominant females were more symmetrical than those of subordinate females. Females that produced a young in their year of capture had more symmetrical horns than females that did not reproduce, and horn asymmetry was correlated negatively with long-term reproductive success in females. Nonetheless, asymmetry in horn length of females did not influence survival of young and was not related to age of primiparity. Analysis of our results indicates that asymmetry in horn length is a phenotypic marker of individual quality in females but does not point to a strong relationship between horn asymmetry and life-history traits in adult males.

Key words: dominance, fitness, fluctuating asymmetry, horn growth, life-history traits, mountain goat, *Oreamnos americanus*, reproductive success

Developmental stability of an individual under particular environmental conditions often is measured with fluctuating asymmetry (FA) in bilaterally paired morphologic characters (Møller and Swaddle 1997). FA represents small random variations from perfect bilateral symmetry where the signed differences between the 2 sides are normally distributed with a mean of zero (Palmer and Strobeck 1992; Van Valen 1962). Deviations from perfect symmetry are thought to arise from the inability of individuals to compensate for stress during development, regardless of whether sources of stress are environmental (such as weather, food shortage, parasitism) or genetic (possibly caused by hybridization, inbreeding, mutation—Leary and Allendorf 1989; Møller and Swaddle 1997; Palmer and Strobeck 1986; Parsons 1990). FA recently has attracted considerable attention from behavioral ecologists because of its potential use in evaluating phenotypic quality of individuals (Gangestad and Thornhill 1999; Wat-

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son and Thornhill 1994). High-quality individuals should be better able to control their development and therefore should have relatively low levels of asymmetry (Møller and Pomiankowski 1993). Several recent studies suggested that individuals with high survival or dominance status were characterized by low levels of FA (Hill 1998; Møller 1994; Møller et al. 1996; Thornhill 1992a; Ueno 1994) and were selected preferentially as mates (Møller 1994; Swaddle and Cuthill 1994; Thornhill 1992b). Asymmetry also was correlated negatively with fitness in numerous species (Clarke 1995; Leung and Forbes 1996; Møller 1997, 1999a, 1999b, cf. Clarke 1998; Houle 1998). However, other studies, especially of birds, failed to support the relationship between asymmetry and fitness (Clarke 1998; Dufour and Weatherhead 1998a, 1998b, 1998c; Ligon et al. 1998).

For secondary sexual characters of males under directional selection, absolute asymmetry should correlate negatively with trait size because high-quality individuals should be able to develop the largest or longest characters and at the same time avoid stress occurring during development (Møller and Höglund 1991; Møller and Thornhill 1998; Thornhill and Møller 1998). Conversely, for traits not used in either mate choice or intrasexual competition for mates, flat, U-shaped or positive relationships between absolute asymmetry and trait size have been predicted (Møller 1994; Møller and Pomiankowski 1993, but see Evans et al. 1995).

Horns and antlers are secondary sexual characters that are used in intrasexual conflict. Some researchers have reported negative effects of horn and antler asymmetry on various life-history characteristics such as survival and reproductive success, but others reported little or no association of FA with life-history traits (Clarke 1998). Antler asymmetry decreased with age in some ungulates, suggesting that individuals with more symmetrical antlers survived longer (Pélabon and van Breukelen 1998; Solberg

and Sæther 1993). Few studies have addressed directly the question of asymmetry and survival with marked animals in natural conditions (Møller 1997). Similarly, effects of body condition on asymmetry of morphologic characters are largely unknown (Møller et al. 1996). In a study of gemsbok (*Oryx gazella*), Møller et al. (1996) suggested that individuals with asymmetrical horns were in poorer condition than individuals with symmetrical horns. However, studies on white-tailed deer (*Odocoileus virginianus*—Smith et al. 1982) and reindeer (*Rangifer tarandus*—Folstad et al. 1996) failed to find consistent relationships between body mass or kidney-fat index and antler asymmetry.

If low FA is correlated with high individual quality, we expected animals that are dominant and reproduce successfully to show low levels of asymmetry. Horn and antler asymmetry were related negatively to social dominance in gemsbok (Møller et al. 1996) and fallow deer (*Dama dama*—Malyon and Healy 1994). Female gemsbok with symmetrical horns were accompanied by young more often than were asymmetrical females (Møller et al. 1996), but a reanalysis showed that results were not quite statistically significant (Clarke 1998).

Male and female mountain goats (*Oreamnos americanus*) have similar pointed horns that are used in social interactions (Côté 1999). Males normally have longer horns than females because they grow a longer 1st annulus, but for a given body size, males have shorter horns than females (Côté et al. 1998b). Males have thicker horns than females at all ages, but most sexual dimorphism in horn growth is achieved by 2 years of age (Côté et al. 1998b). We tested if horn asymmetry was related to life-history traits of mountain goats and could therefore reflect individual quality. We 1st determined the pattern of FA in horn length of males and females and tested for size dependency. We then assessed if asymmetry in horn length was related to sex, age, survival, body condition, and body

mass. Finally, we tested if horn asymmetry was correlated with female reproductive success and social rank. Because high-quality females may reproduce at an earlier age than low-quality females, we also predicted that early age at primiparity would be associated with symmetrical horns.

MATERIALS AND METHODS

Study area.—We studied mountain goats on Caw Ridge (54°N, 119°W), west-central Alberta, Canada, a gently rolling mountain complex in the front range of the Rocky Mountains. Mountain goats used about 28 km² of alpine tundra and open subalpine coniferous forest at an elevation of about 2,000 m. Goats at Caw Ridge have not been hunted since 1969 and during our study, the population varied from 76 to 122 individuals, of which 60–90% were marked (Côté 1999).

Sampling procedures.—From 1988 to 1998, we marked and measured 142 different goats >1 year old (56 males, 86 females). Average capture date was 15 July and captures occurred from 30 May to 10 October. Goats were captured in remotely controlled wooden box traps and self-tripping Clover traps (Clover 1956) baited with salt. We drugged adult goats with xylazine hydrochloride (5 mg/kg), the effect of which was reversed by injection of idazoxan (Haviernick et al. 1998). We marked goats with canvas collars, plastic ear tags, and radio collars (Côté et al. 1998a).

In horns of mountain goat, the 1st distinct annual growth ring is formed at the beginning of the 2nd winter of life, or at about 1.5 years of age (Brandborg 1955; Smith 1988). Thereafter, each subsequent ring is formed in early winter. Age was determined by adding 1 year to the number of distinct rings observed at capture because trapping started in the spring and ended before formation of the new annual ring in early winter (Stevens and Houston 1989). We used a measuring tape to record to the nearest 1 mm the length of the first 2 annuli and total horn length along the anterior curve. We also measured basal circumference of the horn and the circumference of the first 2 annuli. We weighed goats to the nearest 0.5 kg with a spring scale hung from a tripod. Beginning in 1995, we assessed body condition of captured goats using a modification of the index proposed by Riney

(1960). The same observer (S. D. Côté) palpated the soft tissue covering bone at 3 different locations (Gerhart et al. 1996) and assessed condition of the animal on a scale from 1 to 5 (5 = best condition).

We used spotting scopes (15–45×) to sample goat behavior from 200 to 700 m. Observations were conducted from mid-May to mid-September. We used direct observations of nursing behavior to determine lactation for marked females. Age at 1st reproduction was determined for females 1st caught when <2 years old. For analyses of reproduction, we only considered females ≥4 years old because only 2 of 45 females produced a young at 3 years of age (Côté 1999). Average reproductive success of females ≥4 years old was the number of young produced divided by the number of years females were monitored and therefore varied from 0 to 1. Only females with data from ≥3 years (6.1 years ± 2.1 *SD*) were included in analyses of average reproductive success. We had no information on the reproductive success of males.

We measured overwinter survival of marked goats by determining which individuals captured over the summer survived to 1 June the following year. Our sample for adults included all goats ≥3 years old. We are confident of our survival estimates because no goat was ever missed in 1 year and subsequently sighted, and almost all goats were seen >10 times each summer. Adult emigration seems rare and is probably limited at <1 goat/5 years (Côté and Festa-Bianchet, in press).

From 1991 to 1997, we noted all aggressive encounters (*n* = 3,262) observed between adult females (≥3 years old) and the identity of winner and loser (data for 1991 and 1992 are from Fournier and Festa-Bianchet 1995). Probability of winning an aggressive interaction was correlated strongly with age in adult females (Côté 2000). Therefore, we used the method of Clutton-Brock et al. (1986) to control for effects of age when determining social ranks. We divided number of adult females of the same age or older that each female dominated (D) by the number of individuals of the same age or younger that she was subordinate to (S), adding 1 to each side of the ratio to avoid divisions by 0: (D + 1)/(S + 1). We used that ratio to rank females within the same cohort. Because cohort size varied between years, we divided ranks by the number of animals in each cohort. Therefore, social

ranks varied from 0 (subordinate) to 1 (dominant).

Statistical analyses.—To reduce handling time, we did not repeat horn measurements during the same capture event (Côté et al. 1998a). We obtained 2–5 repeated measurements of the length and circumference of the 1st and 2nd horn annuli during 50 recaptures (10 males and 10 females) from 1992 to 1998. We used that subsample of 20 individuals to assess effects of measurement errors on asymmetry (Markusson and Folstad 1997; Palmer 1994). Observers did not know values of preceding measures or that repeated measurements would be used to assess measurement errors. Length of the 1st annulus is stable over years because virtually no horn wear occurs in mountain goats (Côté et al. 1998b). Therefore, horn wear did not affect horn measurements. Five goats were removed from the data set because of broken or damaged horns. We used total horn length rather than length of each annulus to conduct comparisons with life-history traits for several reasons. Total horn length increased sample size and allowed comparisons with variables that were measured in the year of capture (e.g., body mass, dominance status). Total horn length also facilitated comparisons with the few other published studies of horn asymmetry. To avoid nonindependence, each animal was included only once in the data set (Machlis et al. 1985). When recaptures were available, we randomly selected 1 sample/goat.

Fluctuating asymmetry was the signed right-minus-left measurements of horn length, whereas absolute asymmetry was the unsigned right-minus-left value (Palmer 1994). Relative asymmetry was absolute asymmetry divided by mean horn length (Palmer 1994). We assessed directional asymmetry or antisymmetry in horn length by testing if the signed right-minus-left values deviated significantly from a normal distribution with a mean of 0 using Kolmogorov–Smirnov tests and 1-sample t-tests (Palmer 1994; Palmer and Strobeck 1986; Sokal and Rohlf 1981). We used parametric tests to compare relative asymmetry in horn length to life-history traits, even if distributions of relative asymmetries were not normal, because Gangestad and Thornhill (1998) showed, by means of Monte Carlo simulations, that parametric statistics often were more robust than nonparametric tests for analyzing asymmetry data. We used 1-tailed probabilities, unless otherwise stated, because we expected to find negative effects of horn asymmetry on life-history traits as outlined in the recent literature on FA (Møller 1997, 1999b).

Because body condition increased during summer, residuals of the regression of body condition scores on capture date were used in comparisons with relative FA. We adjusted body mass of individuals to midsummer (15 July) using average summer mass accumulation rate of each sex–age class. To control for effects of age, we compared horn asymmetry to residuals of the curvilinear regression between adjusted body mass and age. We used the multivariate Mahalanobis distance to determine outliers. Data points that fell outside a bivariate ellipse representing a 95% density contour for a bivariate normal distribution were considered to be outliers (SAS Institute Inc. 1989). Analyses were conducted with JMP 2.0 (SAS Institute Inc. 1989).

RESULTS

To determine if asymmetry was larger than measurement error, we conducted a 2-way analysis of variance (side-by-individual) on lengths and circumferences of the 1st and 2nd annuli (Björklund and Merilä 1997; Merilä and Björklund 1995; Palmer and Strobeck 1986). The interaction (side-by-individual) was significant for the 1st (F = 3.02, $d.f.$ = 18, 58, P = 0.0008) and 2nd annuli (F = 2.10, $d.f.$ = 18, 36, P = 0.03), indicating that differences in FA (or directional asymmetry) existed among samples. Individuals 1st classified as having a longer horn on 1 side also had the same directional difference when recaptured (χ^2 goodness-of-fit = 21.04, $d.f.$ = 1, P < 0.0001, n = 57). However, we could not distinguish between measurement errors and FA for base circumference of horns (interaction side-by-individual; 1st annulus, F = 0.23, $d.f.$ = 19, 59, P = 1.0; 2nd annulus, F = 0.71, $d.f.$ = 19, 51, P = 0.8). Therefore, we restricted subsequent analyses to horn-length measurements.

The distribution of signed right-minus-left horn length did not differ from a normal

TABLE 1.—Characteristics of symmetry in total horn length of male and female mountain goats from Caw Ridge, Alberta, Canada, 1988–1998.

	Males n = 52		Females n = 82	
	$\bar{X}$	SE	$\bar{X}$	SE
Character size (mm)	187.2	6.5	192.5	5.1
Signed right-minus-left (mm)	0.87	0.48	−0.68	0.49
Skew[a]	0.44	0.33	0.32	0.27
Kurtosis[a]	1.02	0.65	3.73	0.53
Absolute asymmetry (mm)	2.52	0.35	3.15	0.36
Relative asymmetry	0.013	0.002	0.017	0.002

[a] For signed asymmetry (Palmer 1994).

distribution (males and females, 2-tailed Kolmogorov–Smirnov z-values = 1.3, P-values > 0.05) with a mean of 0 (males and females, 2-tailed t-values < 1.8, P-values > 0.05; Table 1), indicating that horn length exhibited FA for both sexes. The lower bound of the scatter plot of absolute asymmetry against horn length (Fig. 1) also included data points near 0 for all values of horn length, indicating that the data set was characterized by FA and not by antisymmetry (Rowe et al. 1997). Absolute asymmetry was weakly related to horn length in males (r^2 = 0.07, P = 0.03, n = 52) and females (r^2 = 0.03, P = 0.05, n = 82; Fig. 1). Therefore, relative asymmetries instead
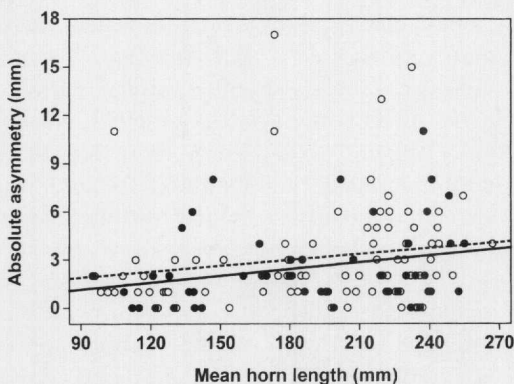

FIG. 1.—Absolute asymmetry as a function of mean horn length in mountain goats on Caw Ridge, Alberta, 1988–1998. Filled circles and solid line indicate males (P = 0.03); open circles and dotted line indicate females (P = 0.05).

of absolute asymmetries were used in subsequent comparisons.

Asymmetry in horn length did not differ between males and females (2-tailed t = −1.11, $d.f.$ = 132, P = 0.7; Table 1) and was not related to age (males, r^2 = 0.05, P = 0.1, n = 52; females, r^2 = 0.0004, P = 0.9, n = 82). Among yearlings and 2-year-olds, horn asymmetry was lower for males that survived the winter than for those that died (survived, 0.011 ± 0.003 SE; did not survive, 0.024 ± 0.005; t = 2.09, $d.f.$ = 26, P = 0.02), but no difference occurred in females (t = −1.41, $d.f.$ = 32, P = 0.9). Horn asymmetry was not related to survival in adult (≥3 years old) goats (males, t = −0.40, $d.f.$ = 17, P = 0.7; females, t = −0.37, $d.f.$ = 42, P = 0.6).

Horn asymmetry was not related to body-condition scores adjusted for capture date in juvenile (r^2 = 0.004, P = 0.4, n = 20) or adult (r^2 = 0.03, P = 0.3, n = 10) males. Similarly, no relation between horn asymmetry and body condition was detected in juvenile females (r^2 = 0.005, P = 0.4, n = 21). However, body-condition scores were related negatively to horn asymmetry in adult females (r^2 = 0.18, P = 0.04, n = 17), indicating that females with symmetrical horns were in better physical condition than females with asymmetrical horns. Similarly, when we regressed relative asymmetry in horn length on residuals of the regression of age with midsummer body
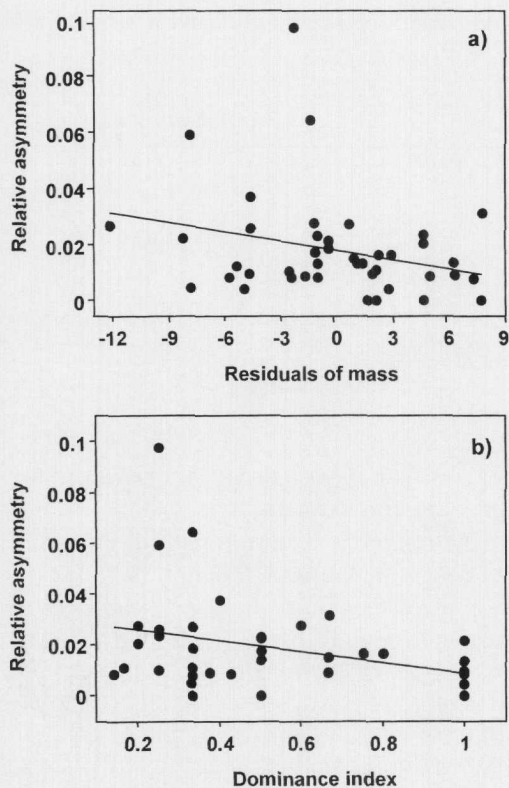
FIG. 2.—Relative asymmetry in horn length of adult (≥3-year-old) female mountain goats on Caw Ridge, Alberta, as a function of a) the residuals of the curvilinear regression between adjusted body mass and age ($P = 0.04$) and b) a dominance index that varies from 0 (subordinates) to 1 (dominants; $P = 0.02$).

mass, we observed that adult female mass was associated negatively with horn asymmetry ($r^2 = 0.08$, $P = 0.04$, $n = 43$; Fig. 2a). However, that relation did not occur in any other age-sex class (P-values > 0.05).

Horn asymmetry was related negatively to social rank in adult females ($r^2 = 0.11$, $P = 0.02$, $n = 39$; Fig. 2b), indicating that horns of dominant females were more symmetrical than those of subordinate females. An hyperbola or logarithmic curve did not provide a better fit to the data. Maternal dominance rank did not affect asymmetry in horn length of juvenile offspring (both sexes combined, $r^2 = 0.02$, $P = 0.2$, $n = 38$). The relationships between horn asym-

metry and body mass (Fig. 2a) and horn asymmetry and social rank (Fig. 2b) were affected by 3 females with asymmetrical horns. Only the female with the most asymmetrical horns was an outlier (multivariate Mahalanobis distance [Md]: body mass, $Md = 4.1$; dominance, $Md = 4.3$), and removal of that individual from those data did not modify the statistical significance.

Females that produced a young the year of capture had more symmetrical horns than did females that did not reproduce ($t = 1.82$, $d.f. = 35$, $P = 0.04$; Fig. 3a). We also observed a negative relationship between horn asymmetry and average reproductive success of females ($r^2 = 0.12$, $P = 0.02$, $n = 39$). Horn asymmetry was not related to survival of young to weaning ($t = -0.40$, $d.f. = 23$, $P = 0.7$; Fig. 3c) or to 1 year of age ($t = -0.31$, $d.f. = 20$, $P = 0.6$; Fig. 3d). Similarly, age at primiparity was not related to asymmetry in horn length ($t = 0.64$, $d.f. = 32$, $P = 0.3$; Fig. 3b). Juveniles born to primiparous females had similar levels of relative asymmetry as juveniles born to multiparous females (both sexes combined, $t = -0.87$, $d.f. = 41$, $P = 0.8$).

DISCUSSION

Møller (1990) suggested that if ornaments or weapons evolve according to the predictions for models of sexual selection (Zahavi 1975) and therefore reflect male quality, then males with the largest ornaments or weapons should exhibit the lowest levels of asymmetry (Møller 1992; Møller and Pomiankowski 1993). Horn length in mountain goats demonstrated FA and was correlated positively with absolute asymmetry in males and females. Horns are secondary sexual characters and are used as weapons in intraspecific interactions; therefore, our results for males do not support the predictions of Møller and coworkers. Several studies on birds also failed to find a significant negative relationship between absolute asymmetry and trait size (Evans and Hatchwell 1993; Evans et al. 1995; Kimball et al. 1997). Among ungulates,
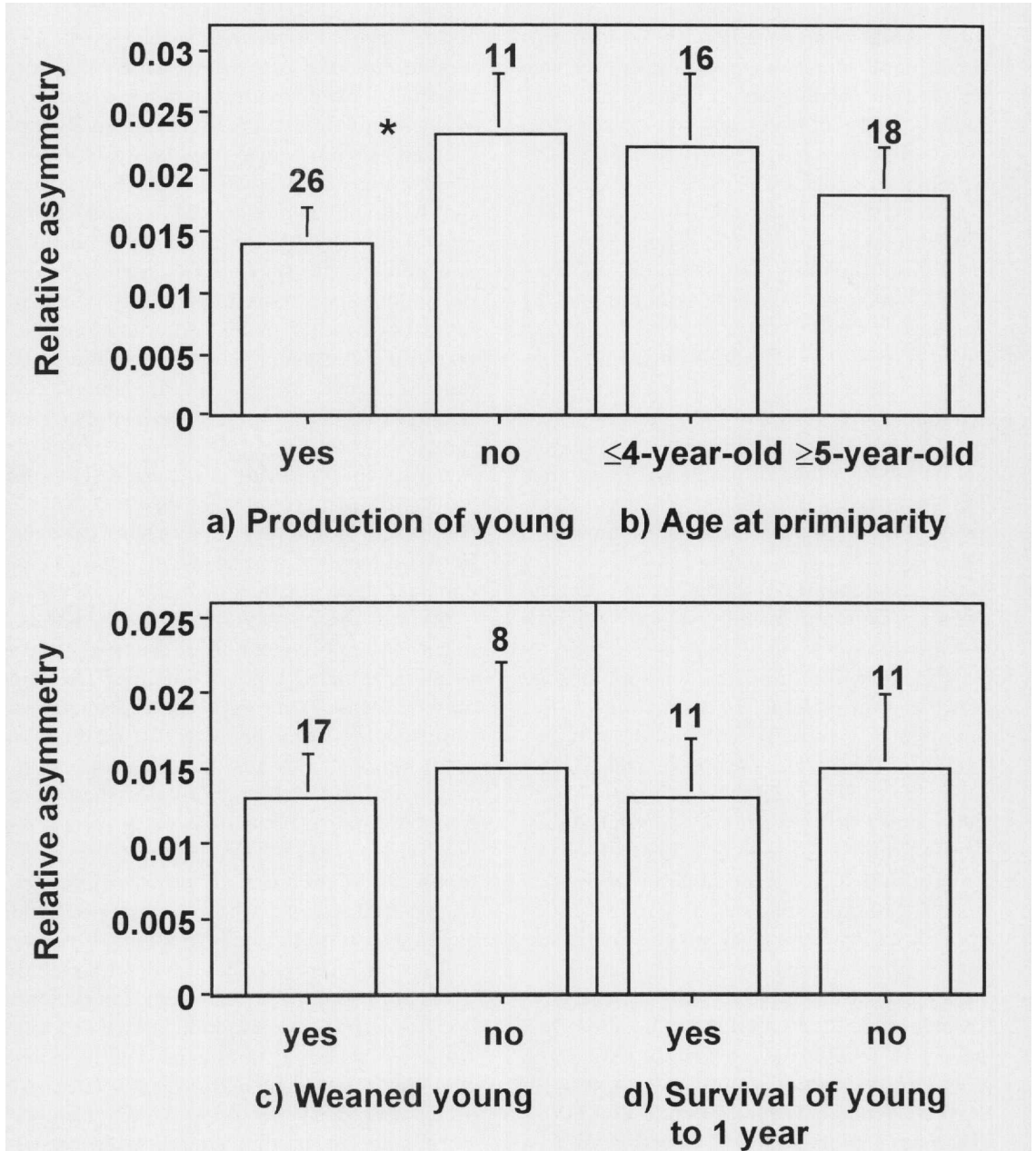
FIG. 3.—Mean (±*SE*) relative asymmetry of horn length in adult female mountain goats on Caw Ridge, Alberta, in relation to various measures of fitness (1989–1997). Samples sizes are shown above each bar; an asterisk (*) indicates $P < 0.05$.

positive and negative relationships of absolute asymmetry and horn or antler size have been reported, often in the same study (Markusson and Folstad 1997; Møller et al. 1996; Pélabon and van Breukelen 1998; Solberg and Sæther 1993). These conflicting results could be interpreted as evidence that larger ornaments or weapons show higher asymmetry simply because they are costlier to produce (Møller and Höglund

1991; Solberg and Sæther 1993). Although directional selection on sexually selected traits often produces high degrees of asymmetry (>10% of trait size), most other characters that demonstrate FA usually display asymmetries that are <1% of character size (Møller 1992; Møller and Höglund 1991). Directional selection for longer horns is probably limited in mountain goats because 93% of total horn growth is completed by 3 years of age (Côté et al. 1998b). In addition, most sexual dimorphism in horn growth is achieved by 2 years of age, whereas dimorphism in body mass increases until ≥6 years of age (Côté 1999; Côté et al. 1998b). Therefore, body mass may have a stronger role than horn length in affecting male mating success in mountain goats.

We expected asymmetry in weapons to decrease with age because selective mortality should remove at a younger age individuals in poor condition that presumably are more asymmetrical. In Cervidae, antler asymmetry generally decreased with age (moose, *Alces alces*—Solberg and Sæther 1993; roe deer, *Capreolus capreolus*—Pélabon and van Breukelen 1998; white-tailed deer—Smith et al. 1982). Nonetheless, we did not find such a relationship in mountain goats. Although the negative correlations sometimes reported between age and asymmetry of ornaments or weapons are interpreted as evidence that symmetrical individuals survive longer than asymmetrical ones, few studies have tested directly a link between asymmetry and survival with marked animals under natural conditions (Badyaev et al. 1998; Møller 1994). If a link exists between horn or antler asymmetry and survival, it should be more evident for age classes where survival is low and more variable, therefore among juveniles for ungulates (Gaillard et al. 1998). If the relationship of horn asymmetry and probability of survival was only evident for juveniles, differences among older individuals may be more difficult to detect. We noted that asymmetrical individuals had

lower survival than symmetrical ones only among juvenile males. Absence of a correlation between horn asymmetry and survival in juvenile females is not easily explained. In our study population, survival of juvenile males is about 10% lower than that of juvenile females (73% versus 82%; S. D. Côté and M. Festa-Bianchet, in litt.), and perhaps the survival of females is less dependent upon individual quality than survival of juvenile males. Alternatively, because juvenile males may allocate more energy to growth than juvenile females, males could suffer a greater energetic stress than females, which might affect their developmental stability during this period (Parsons 1990). In oribi (*Ourebia ourebi*), Arcese (1994) did not find a relationship between horn asymmetry and survival but did not consider age-specific survival.

Overall, horn asymmetry was related negatively to body condition and body mass in adult females but not in other sex–age classes. We also showed that asymmetry in horn length was an indicator of quality for adult females, because the lowest asymmetry occurred among females that were dominant and produced a young. In gemsbok, Møller et al. (1996) reported that symmetrical individuals had fewer visible ribs (a possible index of body condition) than asymmetrical individuals in all age–sex categories. Similarly, a negative relationship between asymmetry in antler length and body weight was documented in yearling white-tailed deer (Smith et al. 1982). However, no relationships between kidney fat index and measures of antler asymmetry were detected in that study (Smith et al. 1982), or in a study of reindeer (Folstad et al. 1996; Markusson and Folstad 1997). Similarly, asymmetry in reindeer antlers was not correlated with body weight (Folstad et al. 1996; Markusson and Folstad 1997). Therefore, the relationships between horn or antler asymmetry and body condition or body mass seem to be equivocal in ungulates.

Horns of dominant females were more

symmetrical than those of subordinate females, suggesting that developmental stability (leading to low FA) may be related to an individual's ability to achieve high social status. Small variations among individuals in energy expenditure and acquisition could generate small differences in developmental stability that could affect competitive ability and dominance relationships (Møller and Swaddle 1997). However, age-specific social rank was not correlated with summer body mass in adult females (Côté 2000). Thornhill (1992a) showed that winners of fights for nuptial food in the Japanese scorpionfly (*Panorpa japonica*) were more symmetrical than losers. Although based on small sample sizes, 2 separate studies have shown that social rank was related negatively to horn or antler asymmetry in ungulates. In gemsbok, individuals of both sexes with symmetrical horns won aggressive encounters more often against asymmetrical individuals at water holes (Møller et al. 1996). Similarly, when antler height was controlled statistically, asymmetry in palm length of antlers was correlated negatively with dominance status in a captive group of 8 male fallow deer (Malyon and Healy 1994). Nonetheless, studies of the relationship between dominance and FA in birds have produced conflicting results (Dufour and Weatherhead 1998a; Swaddle and Witter 1994; Witter and Swaddle 1994).

Horn asymmetry was related negatively to reproductive success in female mountain goats, suggesting that symmetry in horn length indicated good-quality females. Although few studies have compared FA and fecundity of free-living large mammals, recent reviews suggest a negative relation between asymmetry and fecundity in animals of various taxa (Clarke 1998; Gangestad and Thornhill 1999; Leung and Forbes 1996; Møller 1997, 1999a, 1999b). In our study, horn asymmetry explained only 12% of the variance in average reproductive success of females and the significance of the regression was strongly affected by 1 asymmetrical female that had poor success.

Therefore, our results suggest that caution should be used in interpreting the relationship between FA and fitness (Houle 1998). Other studies of FA have reported similar weak effects of asymmetry on fitness traits (Clarke 1998). Many other factors could affect reproductive success of females, and previous studies suggest that regressions between asymmetry and fecundity will be unlikely to be characterized by strong coefficients of determination (Houle 1998; Leung and Forbes 1996; Møller 1997).

Horn asymmetry of mothers was not related to survival of young, indicating that although symmetrical females may have been more fecund than asymmetrical females, horn asymmetry was not related to the capacity of females to care for their offspring. To our knowledge, no study has looked at the relation between FA and age of primiparity. We expected that females producing their 1st young at 4 years of age would be of better quality than females that became primiparous at an older age and would show lower degrees of horn asymmetry. Contrary to our predictions, age of primiparity was not related to asymmetry in horn length. Perhaps young primiparous females were more symmetrical than old primiparous females, but then developed greater horn asymmetry during the year of primiparity. Early primiparity is costly for horn growth; horn increments are almost 3 times shorter for primiparous females than for nonreproductive females of similar age (Côté et al. 1998b).

The positive relationship observed between absolute asymmetry and horn length in male mountain goats contradicts the prediction that asymmetry should be correlated negatively with trait size in secondary sexual characters (Møller and Pomiankowski 1993). Asymmetry in horn length seems to be a phenotypic marker of individual quality in females, but results are equivocal for males. Highly symmetrical females had a higher social rank, were in better body condition, had higher body mass, and produced more young than did asymmetrical females,

suggesting that symmetry is indeed related to quality. For males (and perhaps juveniles), environmental conditions may not have been severe enough to create developmental instability in horn growth. The relationships between horn asymmetry and life-history traits possibly are weak in our study population because of low density. We have no evidence of density dependence in any life-history characteristic at Caw Ridge. Studies of animals under conditions of resource scarcity, and perhaps comparisons with captive populations, are likely to provide a better understanding of the relationship between asymmetry and life-history characteristics.

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