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WINNING BY A NECK: SEXUAL SELECTION IN THE EVOLUTION OF GIRAFFE

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Abstract.—A classic example of extreme morphological adaptation to the environment is the neck of the giraffe (*Giraffa camelopardalis*), a trait that most biologists since Darwin have attributed to competition with other mammalian browsers. However, in searching for present-day evidence for the maintenance of the long neck, we find that during the dry season (when feeding competition should be most intense) giraffe generally feed from low shrubs, not tall trees; females spend over 50% of their time feeding with their necks horizontal; both sexes feed faster and most often with their necks bent; and other sympatric browsers show little foraging height partitioning. Each result suggests that long necks did not evolve specifically for feeding at higher levels. Isometric scaling of neck-to-leg ratios from the okapi *Okapia johnstoni* indicates that giraffe neck length has increased proportionately more than leg length—an unexpected and physiologically costly method of gaining height. We thus find little critical support for the Darwinian feeding competition idea. We suggest a novel alternative: increased neck length has a sexually selected origin. Males fight for dominance and access to females in a unique way: by clubbing opponents with well-armored heads on long necks. Injury and death during intrasexual combat is not uncommon, and larger-necked males are dominant and gain the greatest access to estrous females. Males' necks and skulls are not only larger and more armored than those of females' (which do not fight), but they also continue growing with age. Larger males also exhibit positive allometry, a prediction of sexually selected characters, investing relatively more in massive necks than smaller males. Despite being larger, males also incur higher predation costs than females. We conclude that sexual selection has been overlooked as a possible explanation for the giraffe's long neck, and on present evidence it provides a better explanation than one of natural selection via feeding competition.

Unlike almost every other branch of evolutionary biology, the evolution of the giraffe's (*Giraffa camelopardalis*) extraordinary height has attracted only one serious hypothesis. Darwin (1871) and many African folk legends before him (e.g., Greaves 1988) proposed a simple but powerful explanation for the large and elongated shape. Long necks allowed giraffe to outreach presumed competitors, particularly during dry-season bottlenecks when leaves become scarce; thus, interspecific competition could provide a selective pressure driving necks (and bodies) upward. So appealing is this hypothesis that students of giraffe behavior and evolutionary biologists alike accept it implicitly (Young 1950; Coe 1967; Dagg and Foster 1976; Smithers 1983; Pellew 1984*a;* Harvey and Pagel 1991). While

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some modifications to this feeding competition hypothesis have been attempted, neither predator avoidance (Pincher 1949) nor morphological adaptation to withstand intense solar radiation (Brownlee 1963) has gained subsequent support. Our aim in this article is both to evaluate the feeding competition idea and to suggest a novel alternative hypothesis. We do so by testing the interspecific feeding competition hypothesis with existing research, investigating evolutionary design by comparison with fossil and extant relatives of the giraffe, and subsequently suggesting and supporting an alternative explanation based on sexual selection.

Modern giraffes radiated on African savannas about 1 million (M) yr ago, from a large, morphologically similar species, *Giraffa jumae,* which had existed unchanged for at least 12 M yr (Churcher 1976; Harris 1976). Coexisting giraffids (e.g., Sivatheriinae) were characterized by massive but unelongated skeletons, with ossicones (horns) that were palmate, antlerlike structures, not found in modern giraffe (Singer and Bone 1960; Harris 1974; Churcher 1976). The ancestor of both types was a fast agile animal (*Palaeotragus primaevus*) similar in size and morphology to the extant forest-dwelling okapi *Okapia johnstoni*. Today, however, the genus is represented by only one species that shows greatly elongated limbs and neck and, at up to 5.3 m tall, stands 3 m higher than any present-day ungulate (Dagg and Foster 1976).

THE INTERSPECIFIC FEEDING COMPETITION HYPOTHESIS: ASSUMPTIONS AND PREDICTIONS

This hypothesis, like others explaining historical events, assumes that for the trait to remain, either similar selection pressures occur in present-day populations or, if not, that the costs in retaining the trait are trivial. Clearly, the alternative is that other selection pressures are acting to maintain the trait and may have given rise to it. We are aware that selective forces giving rise to morphological traits may not be the same as those maintaining them (Gould and Vrba 1982), but we start with these assumptions to generate and evaluate predictions associated with feeding competition.

The interspecific feeding competition idea implicitly assumes that fossil giraffids were shorter than modern giraffe and were sympatric, thereby acting as the closest presumed competitors. Both assumptions are supported (Singer and Bone 1960; Churcher 1976; Q. B. Hendy, personal communication). It also assumes that tall trees existed on African savannas that were exploited mainly by terrestrial folivores. Competition could then play a role in selecting for an elongated neck in the giraffe. In addition, as pointed out by Darwin (1871), food must be periodically scarce (or of poor quality) to provide a selective pressure pushing giraffe foraging heights above those of other folivores. Since leaves are scarce on savanna trees in dry seasons and have lower protein content (Sinclair and Norton-Griffiths 1979; Sauer et al. 1982), the selective pressure responsible is likely to have arisen in the dry season. Given these assumptions, the following predictions arise. First, present-day giraffes gain a feeding advantage over possible competitors mainly during the dry season when food is scarce and poor quality. Second, if dry-season competition does not occur, advantages of feeding on tall trees should exist at other times of year. Third, extant giraffes can simultaneously avoid interspecific competition by selecting different food types when feeding height overlap occurs and food is scarce. Finally, if feeding competition is (or was) the chief selective pressure increasing feeding height, anatomically giraffe should have achieved greater height by elongation of all body parts. Most species or genera exhibit predictable allometric variations in morphological traits, which reflect genetic correlations between body parts and metabolic and mechanical constraints (Huxley 1931; McMahon 1973, 1975; Peters 1983; Calder 1984; Grant 1986; Harvey and Pagel 1991). For example, among extinct vertebrates simple scaling can explain otherwise intractable problems associated with unusual morphological features (Gould 1973). One would therefore expect length increases in giraffe limbs to be allometrically scaled to their bodies and necks if the goal were increased feeding height. Quantitative data on neck length of fossil giraffids are unavailable, so we used ratios of leg to neck lengths from their only living relative, the okapi. We predicted that giraffe should exhibit similar morphometric ratios.

SEXUAL SELECTION AND NECK LENGTH: MODEL AND PREDICTIONS

The novel hypothesis developed here rests on the premise that the extraordinary length of the giraffe's neck arises from its use as a weapon during intrasexual combat. This behavior, called "necking" (Spinage 1959; Coe 1967), is well known and described in many studies (Innis 1958; Coe 1967; Dagg and Foster 1976; Estes 1991*a*). During combat two males stand side by side and exchange blows by swinging their necks first away from then at their opponents. The top or back of the well-armored skull (Spinage 1968) is used as a club to strike the neck, chest, ribs, or legs of the opponent with a force capable of knocking a competitor off balance or unconscious (Innis 1958; Coe 1967; Spinage 1968). Since the energy delivered by a club (the head) increases in proportion to the mass of the head and the length of the neck, we expect selection to have favored longer and more massive necks. These contests are called "sparring" among young males and are characterized by mutual neck rubbing and gentle blows (Coe 1967; Pratt and Anderson 1985). By contrast, violent combat may erupt between large males with few preliminaries (Innis 1958; Pratt and Anderson 1985; L. Scheepers, unpublished data) in the presence of estrous females. Male giraffes follow and defend single females, not herds or territories, chasing off other large males if they approach too closely (Dagg and Foster 1976; Pratt and Anderson 1985). Females can come into estrus at any time of year, and males search for such females by wandering from herd to herd (Dagg and Foster 1976).

Characteristically, sexually selected traits in other mammals (Darwin 1871; Andersson 1994) are bizarre or exaggerated in expression and of no immediate survival benefit, longer (or more exaggerated) in the chosen sex (Darwin 1871; Geist 1966), used in male-male dominance contests or courtship displays to females (unless sex roles are reversed), and bear a survival cost (Zahavi 1975; Grafen 1990). More recently, many such traits have been shown to be positively allometric (Petrie 1988, 1992). That is, larger individuals have relatively larger morphological characters: not only are such traits expected to indicate greater competitive ability in large individuals, but only larger animals can bear the costs of wearing them. We use these criteria to assess whether present morphological characteristics of giraffe conform to generally accepted patterns of sexually selected traits.

The following predictions arise. First, male giraffe should use only their necks (and heads) for intrasexual combat; typical ungulate fighting patterns (e.g., Clutton-Brock 1982; Berger 1986) are unexpected. Second, male giraffe should exhibit morphological adaptations such as longer and more muscular (powerful) necks than females if necks are used chiefly for intrasexual combat. Since the head is also used in combat, skulls of males should be better armored to deliver and absorb blows than those of females. Third, males with larger necks should be dominant and gain reproductive advantages over smaller-necked males. Fourth, fossil and modern skeletal evidence should reveal a disproportionate increase in neck length over and above expected isometric increases associated with lengthening of other body proportions. This would indicate that selection has been on the neck and not merely the lengthening of the body and limbs. This prediction can thus help distinguish between natural and sexual selection advantages. Finally, males should invest more than females in necks and skulls, and the largest males should exhibit relatively larger necks. This arises from the expected positive allometry of sexually selected traits (see also Gould 1973; Clutton-Brock et al. 1980; Petrie 1992).

METHODS

We surveyed literature on modern giraffe foraging behavior and social interactions (e.g., Coe 1967; Dagg and Foster 1976; Young and Isbell 1991), morphological comparisons of extinct and extant giraffids (Singer and Bone 1960; Harris 1974, 1976; Churcher 1976), and the function and morphology of sexually selected weapons (Geist 1966; Clutton-Brock 1982; Møller 1992). Because of the scarcity of published data on modern giraffe morphology, we requested data from zoos holding wild giraffe (ISIS 1989). Respondents (see Acknowledgments) were sent a diagram indicating the desired measurements and asked for details of mass, neck length, leg length, and horn length for male and female giraffe and okapi. While the data were insufficient for male-female statistical comparisons, we could use the okapi data to generate scaling components of leg to neck length. These were then compared to relative leg:neck ratios of giraffe to understand the direction in which giraffe have evolved morphologically.

During our own studies of wild giraffe in Etosha National Park, Namibia (19°15′ S, 14°31′ E), culled animals of all ages were dissected to determine the relative weights of body parts. Dissections were carried out only by L.S. on 45 females and 37 males over 1 yr of age. Heads were cut immediately below the skull and weighed, while necks were cut from the shoulder to include all cervical vertebrae. Only neck mass, not neck length, was recorded since other morphological aspects were under study. Nevertheless, neck mass and length are assumed to be correlated since males cannot grow longer necks without additional mass, and older giraffe have both thicker necks (below) and are taller than younger males. However, at some point they stop growing taller (L. Scheepers, unpublished data) while continuing to grow heavier necks. Shoulder height and horn proportions were noted, and each animal was aged using dentition formulas provided by Hall-Martin (1976) for South African giraffe. We plotted both head and neck mass against age to investigate relative sexual differences in investment in these organs and also relative investment in necks and heads in relation to body mass. As far as we know, these are the only systematic body mass data available for giraffe. Both curvilinear and linear regression procedures were performed using Statistical Package for the Social Sciences (SPSS 1992) programs, and those graphed represent the best fit to the data. Finally, we plotted neck mass against body mass (minus the neck) for males and females to determine whether males' necks were positively allometric as predicted. Relationships were investigated with linear and reduced major axis regression (Sokal and Rohlf 1981).

RESULTS

Foraging Studies Reviewed

In the Serengeti, giraffe spend almost all of the dry-season feeding from low Grewia bushes, while only in the wet season do they turn to tall *Acacia tortilis* trees, when new leaves are both proteinaceous and plentiful (Pellew 1984*a*) and no competition is expected. This behavior is contrary to the prediction that giraffe should use their feeding height advantage at times of food scarcity. Neither are giraffe exploiting better-quality (higher-protein) foods at such times since dry-season scarcity of leaves coincides with the lowest protein levels in *Acacia* leaves (Sauer et al. 1982). Similarly, in the Tsavo National Park, about 50% of all browsing is below 2 m (less than half the height of both sexes) and thus within reach of potential competitors such as gerenuk *Litocranius walleri* and lesser kudu *Tragelaphus imberbis* (Leuthold and Leuthold 1972). During the dry season, 37% of the browse taken by giraffe was below 2 m. Giraffe were not avoiding interspecific competition by selecting different food plants (the third prediction): considerable (unquantified) overlap was apparent between giraffe and sympatric browsers in Tsavo (Leuthold and Leuthold 1972). Only in South Africa were giraffe found to allocate 90% of their time to feeding above the average feeding height of browsers such as kudu *Tragelaphus strepsiceros* (1.0 m) and impala *Aepyceros melampus* (~0.3 m; du Toit 1990), but lower than their long necks allow (5–6 m). In each study both sexes frequently fed at or below shoulder height (~3.1 m and 2.8 m for adult males and females; L. Scheepers, unpublished data). For example, female giraffe spent over 50% of the time feeding with their necks at or below shoulder height in both South Africa (du Toit 1990) and Kenya (Young and Isbell 1991), contrary to the second prediction. So common is this behavior in females in eastern Africa that it is used as a field guide to sex individuals at a distance (Sinclair and Norton-Griffiths 1979; Pellew 1984*a*). However, low feeding heights are not restricted to females: males also regularly feed below or at shoulder height in Kenya, and only dominant bulls regularly fed at 5.0 m or more in both South and eastern Africa (du Toit 1990; Young and Isbell 1991). Thus, full neck extension was only used in a social context by dominant males in female groups (Young and Isbell 1991).

Do long necks allow advantages unassociated with out-reaching presumed competitors or advantages at other times of season? In a study of feeding height and rate, Young and Isbell (1991) found that giraffe feed at faster rates at 2.5 m for females and 3.0 m for males. Both feeding levels were at shoulder level, or 60% of their overall height. The lowest feeding rates were at the highest levels (Young and Isbell 1991). However, feeding rate may not be the best measure of food intake since bite rate and size may be inversely correlated if animals take longer to chew and ingest larger bites (Pellew 1984*b;* Spalinger and Hobbs 1992). A better assessment of preferred feeding height, therefore, is the proportion of feeding at different heights. This analysis (Young and Isbell 1991) confirmed the earlier results: females in female groups fed most frequently at 1.5 m, females in male groups fed most frequently at 2.5 m, and males in male groups fed at about 3.0 m. Only dominant males in female groups fed at a height (5.0 m) close to that expected of an animal of this height.

Scaling: Neck and Limb Morphology

The ratio of the okapi's foreleg to neck is approximately 1:0.44. For giraffe, the ratio is about 1:0.93. The 2-m-long neck of extant male giraffes is thus 2.1 times longer than expected based on isometric increases. Young giraffes, a few months old, exhibit a leg-to-neck ratio of 1:0.62, which reflects their shorter-necked ancestors. Skeletal study of the neck vertebrae also indicates a disproportionate 29% elongation over and above thoracic and lumbar vertebrae (Slijper 1946), and young giraffes exhibit high neck growth rates of 23 cm per week (Dagg and Foster 1976). Each suggests specific selection on neck length over other body proportions. Necks of female giraffe are about 35 cm shorter (Dagg and Foster 1976) than those of males, a difference not intuitively predictable from the interspecific feeding competition hypothesis.

Fossil Evidence: Selection on Neck or Limbs?

Among fossil giraffids two evolutionary lines are apparent. Among Pliocene Sivatheriinae, evolution favored massive oxlike animals with long robust anterior limbs to support great weight and more elaborate deerlike horns or ossicones (Harris 1974, 1976). Deep pits in the bones for the attachment of large neck muscles were also obvious (Foster and Dagg 1972; Churcher 1976), but necks were unelongated. This is characteristic of most Sivatheriinae giraffids (Singer and Bone 1960; Churcher 1976; Harris 1976). These and other examples indicate that the largest fossil giraffid (*Samotherium*), with a leg length 83% that of *Giraffa camelopardalis* (Colbert 1938), did not exhibit parallel increases in neck length. Instead, selection appeared to favor heavier bodies, large, heavy necks, and changes in horny growths on the skull. Such traits are typical of sexually selected armaments among extant mammals (Geist 1966; Clutton-Brock 1982). The other evolutionary trajectory was from savanna-dwelling okapi-like animals (*Palaeotragus primaevus* and *Palaeotragus stillei*) that were agile and fast with relatively long legs and necks. Fossil evidence suggests that a large species (*Giraffa jumae*), differing from modern giraffe only in its more flattened ossicones (Churcher 1976; Harris 1976), arose from this stock at least 12 M yr ago. This culminated about 1 M yr ago in a sudden radiation of other elongate *Giraffa*, most of which were less robust and tall than seen today (Colbert 1938; Churcher 1976). All showed disproportionate growth in leg and neck length and relatively short, stout horns, suggesting both a different mode of fighting and intense selection on necks. The present *G. camelopardalis* and extinct *G. jumae* were also about 1 m taller than the largest sympatric Sivatheriinae (Churcher 1976). Fossil evidence therefore suggests pressures other than feeding height stratification underlay (and maintain) the elongation.

SEXUAL SELECTION ON THE NECK OF THE GIRAFFE

In support of our first prediction, the only form of fighting recorded between males is by "necking" (Innis 1958; Coe 1967; Dagg and Foster 1976; Smithers 1983). Biting, kicking, head wrestling, or butting, common in other mammals (Geist 1966; Berger 1986; Estes 1991*a*), including okapi (Walther 1960), is unrecorded in giraffe. Necking is unique to giraffe (Estes 1991*a*). Female giraffe are never reported as fighting (reviewed in Dagg and Foster 1976; L. Scheepers unpublished data); thus, sexual dimorphism is expected.

In support of our second prediction, females carry smaller skulls that are less well armored and 3.5-fold lighter (2.2 vs. 7.8 kg) than males' (Spinage 1968). Total (wet) head mass differed almost twofold between the sexes for same-age animals in our study (fig. 1*a*). Neck lengths also differ between sexes: male giraffe average about 30–40 cm longer and up to 1.7-fold heavier necks than same-age females (Foster and Dagg 1972) (fig. 1*b*). The same relationship exists when sex differences in body mass are controlled for. By plotting neck (or head) mass against body mass using simple regression, we generated residuals for both sexes reflecting body mass–corrected values for heads and necks. A one-way ANOVA of residuals revealed, as expected, that males had significantly heavier heads per unit body mass than females ($F = 14.8$, df $= 1{,}76$, $P = .0002$; residuals $\overline{X}_{♂} = 0.98$, $n = 33$, $\overline{X}_{♀} = -0.80$, $n = 42$) and significantly heavier necks per unit body mass than females ($F = 12.4$, df $= 1{,}77$, $P = .007$; residuals $\overline{X}_{♂} = 3.21$, $n = 35$, $\overline{X}_{♀} = -2.55$, $n = 44$). In real terms, for males and females each weighing 800 kg, the respective head masses would be 20.3 kg and 18.0 kg, even though males of this mass would be at least 2 yr younger. Similarly, the neck masses of males and females weighing 800 kg would be 60 kg and 51 kg, respectively. Both age- and body mass–related results for head size and neck size are compatible with the idea that male attributes have undergone selection for increased size and strength. Data are unavailable for neck length per se.

Effectiveness of Necking in Male-Male Combat

We know of eight anecdotal accounts of male giraffes injuring or killing their opponents during combat. In a fight between semicaptive giraffe, one animal was thrown sideways several feet by blows from the other (Innis 1958). Dagg and

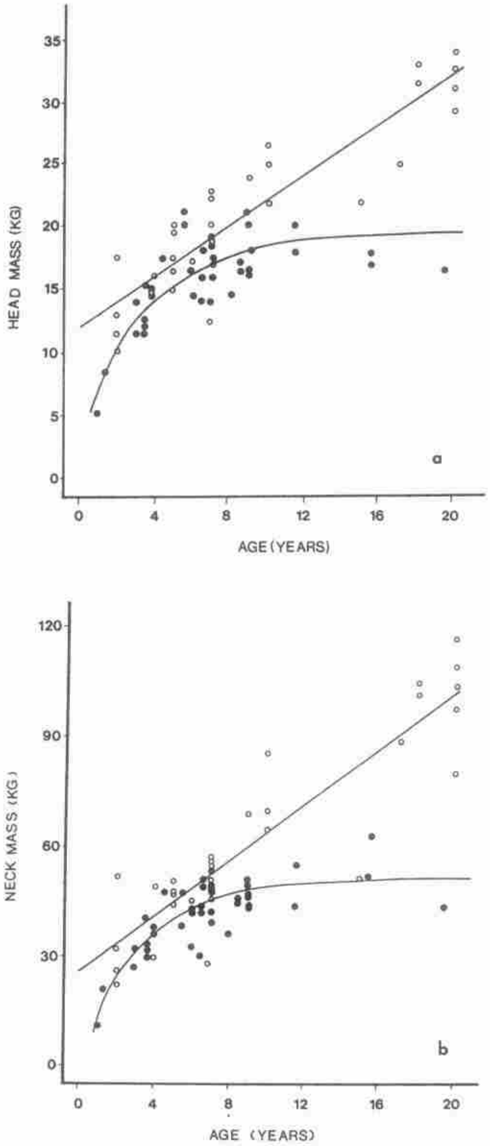

FIG. 1.—*a,* Age-related growth in the head mass of male (*open circles*) and female (*solid circles*) giraffes from Etosha National Park, Namibia. Significant patterns occurred for both males ($R^2 = 84\%$, $N = 31$) and females ($R^2 = 80\%$, $N = 43$), but lines of best fit indicate that females invest relatively little in head mass after 10 yr of age. Males continue to deposit bone throughout their lives at an average 1.0 kg per year (head mass = 12.0 + 1.0[year]). Males also invest more in this trait per unit body mass than females (see text). For females, head mass = $e^{(3.0 - 1.32/\mathrm{age})}$. *b,* Sexual differences in age-related neck mass increases for males (*open circles*) and females (*solid circles*). Males ($R^2 = 82\%$, $N = 33$) show continuous linear growth throughout their lives, while females ($R^2 = 80\%$, $N = 43$) stop investing in growth around age 10 yr. The increase in males is due to bone and muscle increment and is given by (neck mass = 25.6 + 3.82[year]). Males also invest more in necks per unit body mass than do females (see text). For females, neck mass = $e^{(4.0 - 1.5/\mathrm{age})}$.

Foster (1976) reported a male knocked unconscious by a blow from an opponent; another male was killed when the other punched a hole in its opponent's neck just below the ear, splintering the top vertebrae, which penetrated the spinal column (de Clerck 1965). Resnik (1989) photographed a male with a broken and twisted jaw following a blow from an opponent, and Coe (1967) recorded a death during "necking" of a captive male giraffe, mistakenly allowed into the enclosure of a similar-sized male. In three fights recorded in our study between large (old) bulls in northwestern Namibia, head clubbing resulted in the opponent being knocked to the ground on each occasion. The force was sufficient to break an opponent's leg in one encounter, and, in the most violent encounter, a male clubbed his rival to the ground, and the rival was prevented from standing by the opponent stamping its foreleg until death occurred. This is the only known record of a giraffe using its hooves in intraspecific aggression.

Dominance and Neck Size

Dominance displays in both okapi and giraffe (unlike other ungulates) involve lateral nose pointing, increasing the apparent length of the neck (Walther 1960; Dagg and Foster 1976). Nose pointing is often sufficient to signal dominance (Estes 1991*a*) and results in approaching males wheeling away and running from dominant bulls (L. Scheepers, unpublished data). This is unsurprising if neck length is a sexually selected character. Dominance by the largest individuals has been verified in both captive (Dagg and Foster 1976) and wild populations (Innis 1958; Backhaus 1961). But is body size or neck size per se the most important feature in male access to receptive females? This has been evaluated in a study by Pratt and Anderson (1982), who ranked wild males into three categories (A–C, largest to smallest) according to neck size and horn length at first sighting. The main distinguishing features were "stouter neck, the massive horns, and the addition of bone and knobs or even extra horns to the skull" (pp. 481–482). In some cases (Pratt and Anderson 1985), A bulls were smaller than B bulls but were ranked as A because of larger necks. Pratt and Anderson showed that morphological ranking equated closely with dominance hierarchies: the larger-necked A bulls were consistently dominant over B and C bulls, and they courted females significantly more often than B or C bulls did. Ranking also appeared to be important in female mate choice: females allowed themselves to be urine tested (a test of their sexual receptiveness) by A bulls more often than B bulls, and they refused to be urine tested by C bulls in two-thirds of all encounters (Pratt and Anderson 1985). Hence, males with the largest necks and horns gained increased dominance, courted more often, and were chosen as partners most often—all prerequisites of sexual selection (the third prediction).

In support of the fourth prediction, ratios of neck to leg length compared between okapi and giraffe above indicate that neck length has increased about twofold more than that expected for giraffe based on isometric considerations. This increase is reflected in the elongated neck vertebrae of giraffe relative to other parts of the spine (Slijper 1946). Both points suggest that selection has mainly been on the neck.

To evaluate relative sexual investment in head and neck size, we plotted each character against age for male and female giraffe. Significant correlations ($P \ll .001$) between age and head mass occurred for both sexes (fig. 1*a*) but showed markedly different trajectories. While female head mass reached a plateau mass of less than 22 kg, males continued investing in heavier skulls throughout their lives. Male head mass increased linearly by 1.0 kg per year, to over 30 kg, a phenomenon achieved by deposition of bone over the top portion of the skull (Spinage 1968). This leads to a large median horn in some specimens and gives rise to "five-horned" animals in other populations (Dagg and Foster 1976). The oldest males in Namibian populations have heads weighing up to 40 kg.

Similarly, neck mass was significantly correlated ($P \ll .001$) with age in both sexes (fig. 1*b*), but female neck growth leveled off at about 10 yr of age at 60 kg. Male giraffe, however, continued to invest linearly in larger necks as they aged. Older males attained necks in excess of 100 kg. Neck and head dimensions compared between dominant and subordinate (A and C) males are unavailable because of the difficulty in obtaining such measurements.

Positive Allometry

Male giraffe were tested for positive allometry by plotting neck mass against body mass. Significant positive correlations ($P \ll .001$) were found for both linear and reduced major axis (RMA) regression (Sokal and Rohlf 1981). There was a clear trend for heavier animals to have disproportionately heavier necks (slope $b = 1.27$; $b_{\mathrm{RMA}} = 1.35$; fig. 2): the slopes were significantly different from isometry ($t = 4.33$, $P < .005$). Females, by contrast, exhibited isometry between neck mass and body mass ($b_{\mathrm{RMA}} = 0.986$, $R^2 = 82\%$, $N = 43$).

DISCUSSION

We have argued here that the widely accepted explanation for the great height and long neck of giraffe, the feeding competition hypothesis, is unsupported by two lines of argument. The maintenance of the trait is poorly supported by studies of present-day feeding behavior, and the evolution of the long neck is puzzling in light of the morphological solutions employed to reach great heights. Critics will point out that past competitors such as other giraffids may have driven modern giraffe feeding patterns ever higher and left them with a trait that is retained because it is not overtly disadvantageous. While the evolution is not directly testable (because we know nothing about fossil giraffe browsing patterns), we can infer something of competitive interactions from the relative heights of extinct giraffe and present-day feeding stratification among sympatric browsers.

Fossil evidence shows that *Giraffa jumae,* the morphologically similar progenitor of *Giraffa camelopardalis,* was considerably taller (~1 m) than the massive oxlike *Sivatherium maurusium* that was widespread and sympatric (Churcher 1976). Another possible competitor was *Samotherium africanum* (Churcher 1976), but this animal had forelegs about 33 cm shorter than those of the extant giraffe and a neck described as "normal length" (Colbert 1938, p. 48). Thus, the immediate progenitors of the extant giraffe were also taller than required to out-

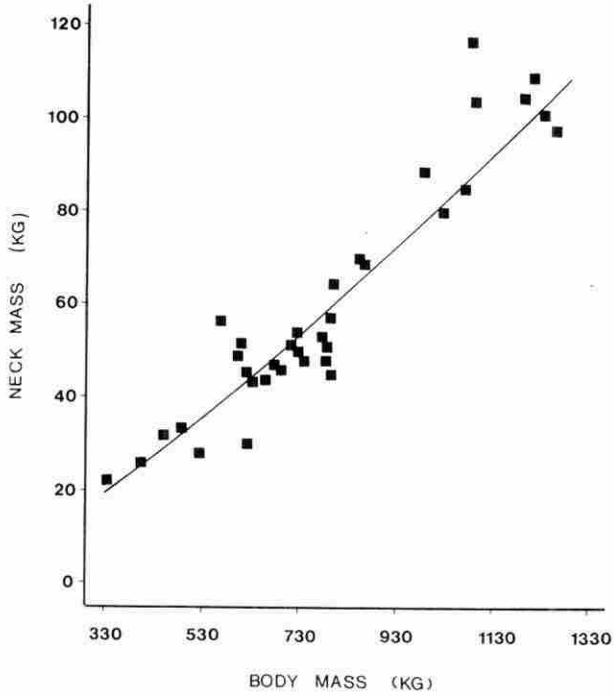

FIG. 2.—The relatively greater investment in neck mass with increasing body mass of male giraffe (R^2 = 88%, N = 34). Positive allometry in neck mass is given by neck mass = $-4.37(\text{body mass})^{1.27}$. Note that body mass in this graph does not include neck mass, and females (not shown) showed only isometric increases.

reach their presumed competitors. This does not rule out competition, but neither does it support it.

Nevertheless, feeding competition alone as an evolutionary explanation of long necks is unlikely for three reasons. First, we have shown that present-day giraffe, particularly females, appear to enjoy no direct advantage from their long necks, and neither sex feeds frequently with their necks extended. That giraffe can and do feed above possible competitors is undeniable and possibly a secondary consequence of other pressures. We are surprised, however, that it is not more common, especially when both leaves and protein levels are limited in the dry season. Neither do females time their period of greatest energy stress, birth and early lactation, to coincide with wet periods when higher feeding occurs (Pellew 1984*b*). Hence, the maintenance of the trait is poorly explained by feeding advantages. It has been suggested that neck extension aids both sexes when they feed low because they can reach the center of low-spreading bushes. This suggestion, like other possible advantages such as predator surveillance, are ad hoc explanations supported by little evidence and unlikely to provide major selective pressures favoring elongated skeletons.

Second, selection appears to have been primarily on the neck. This is contrary to expectation based on allometric and physiological grounds, since lengthening of the neck alone incurs "unnecessary" costs in the form of substantially increased blood pressure and heart size. The brain of the giraffe is almost 3 m above the heart (Warren 1974), and substantial enlargening of the heart and thickening of artery walls are required to push blood to the brain (Warren 1974; Lillywhite 1991). The result is that giraffe have higher blood pressure than any mammal (Warren 1974). Hence, a major physiological cost occurred during the evolution of elongated necks—an avoidable cost if all body proportions had lengthened. However, costs associated with sexually selected traits and the ability to bear them are an integral part of recent thinking on signals of viability and fitness (Zahavi 1975; Kodric-Brown and Brown 1984; Grafen 1990), particularly in the case of positively allometric sexual characters (Petrie 1988, 1992).

Further evidence of costs arising from sexual selection on males comes from studies of male mortality due to predation. In a 2-yr study of over 100 giraffe killed by lions *Panthera leo* in South Africa, Pienaar (1969) found that almost twice as many bulls were killed as cows (1.8:1). Female-skewed sex ratios are common elsewhere (Pellew 1984*a;* du Toit 1990) and suggest similar sex-related mortality. This is unusual in light of the mass difference between adult male and female giraffe in which the largest males (~1,300 kg) are 53% heavier than the largest females (850 kg; L. Scheepers, unpublished data). The proximate reasons are unstudied for giraffe, but see Owen-Smith (1993) for other ungulates.

The third main reason for doubting feeding competition as a driving force behind the giraffe's elongated neck comes from present-day studies of coexisting browsers. While feeding competition is often expected because it helps explain partitioning between grazers (Jarman 1974; McNaughton and Georgiadis 1986), there is conflicting evidence for browsers. For example, du Toit (1990) showed that contrary to qualitative assessments (e.g., Leuthold 1978), considerable overlap occurred in the feeding heights of three small South African browsers, including critical dry-season foraging. Guy (1976) similarly found substantial overlap of elephant *Loxidonta africana* feeding patterns with low-level browsers. Neither quantitative study found substantial partitioning that might suggest competition between browsers. That browsers enjoy higher year-round energy returns by feeding on high-protein leaves than do grazers feeding on grasses (Pellew 1984*b*) may explain the lack of any need to partition among browsers. In sum, all three approaches assessing feeding competition as a driving force behind giraffe evolution give limited support for the hypothesis.

Support for Sexual Selection in Giraffe

It cannot be doubted that male giraffe use their necks and heads in combat and that larger-necked animals gain increased access to estrous females (Pratt and Anderson 1982, 1985). We have also shown that, as expected for a sexually selected trait, larger males exhibit proportionately larger necks and heads, and they continuously invest in these traits with age. Males also have larger necks and heads than females of the same body mass. Hence, there is good evidence that necks are maintained by sexual selection. What is arguable is whether success in male-male combat was the primary reason for the incipient evolution of elongated necks. We evaluated this by showing that the simplest morphological solution to increased height for feeding advantages did not occur. Hence, selection for mere height increase is unlikely to explain the initial evolution. This difficulty for feeding competition, however, offers direct support for the sexual selection idea, since it identifies intense selection on necks alone—an expected correlate of male-male competition. This analysis exposed two different physiological (increased heart size and blood pressure) and viability (higher male mortality) costs that are predicted by sexual selection theory.

Criticisms of Sexual Selection on Giraffe

While the sexual selection thesis developed here is supported by available morphological and behavioral evidence, the long necks of females are not used in combat or dominance; hence, they may seem problematic for this idea. Long-necked females also pose a difficulty for feeding competition ideas, since of the two sexes, females seem to gain less advantage by having long necks because they frequently feed with them bent. Thus, neither hypothesis directly explains long-necked females. Two explanations are possible. First, past selection pressures may have fashioned both male and female elongation, and these pressures are no longer identifiable. Second, female necks arose as neutral by-products of genetic correlation between the sexes. This explanation has been invoked by Darwin (1871), Fisher (1930), and Lande (1987) to explain malelike features present in females for which no other advantages (past or present) are identifiable. The explanation is often treated as one of "last resort" and unsatisfactory. However, artificial selection has shown close body size correlations among male and female *Drosophila* fruit flies, mammals, and birds, which have been verified in recent field studies (reviewed in Andersson 1994, p. 291; see also Pomiankowski and Sheridan 1994 for mate choice criteria). For giraffes we suggest that because sexual selection has driven male necks ever larger, female necks followed. Unlike elaborate tail ornaments of birds, the horns and antlers of female ungulates and giraffid necks are integral skeletal body parts, which cannot be genetically uncoupled from increases in body size. Unlike tail ornaments, they are not hormonally controlled and shed seasonally. Indeed, females of several mammals (Estes 1991*b*) but few female birds exhibit malelike characters, which suggests that genetic correlation is commoner for mammals than birds. Consider also a trait for which no function has been identified in female giraffe (Spinage 1968; Dagg and Foster 1976): the residual ossicones (mean adult male-to-female lengths, 9.0 cm vs. 15.0 cm). Females would lose such characters if genetic uncoupling of malelike attributes occurs, yet they have not. Genetic correlations appear, therefore, to be the best present-day explanation for the maintenance of long necks (and ossicones) in female giraffe, given that they do not fight.

If one accepts that necks may be present-day sexual traits, it is still arguable that giraffe necks are exaptations, not adaptations (sensu Gould and Vrba 1982). That is, elongated necks were primarily a response to other selection pressures and once lengthened could no longer be used in head-to-head combat. We do not reject this hypothesis because it is a parsimonious explanation for the switch from head butting (as in okapi) to head clubbing seen in giraffe, as necks became too long to wrestle with. That is, slightly elongated necks were not likely to have evolved just for clubbing but were increasingly effective once longer necks arose. Likewise, we cannot claim that longer legs did not allow other advantages, since most ancestral giraffids exhibited long legs. Long legs may have evolved for reasons such as antipredator responses (i.e., defense by kicking) or long-distance travel. Correlated responses with increasing body size must be considered in each case, and the okapi's long legs may be a clue to the long legs of extant and ancestral giraffe.

To summarize, our main criticism is that extreme lengthening of the neck is unlikely to have arisen from feeding competition alone because it is costly, its present-day maintenance is poorly supported by feeding data, and studies of extant sympatric folivores suggest that competition is unimportant. Sexual selection on male necks is a viable and overlooked alternative based on present-day fighting methods, disproportionate lengthening of the neck, enhanced access to receptive females by large-necked males, similarity in growth patterns with other sexually selected traits, and associated costs. Present evidence offers better support for sexual selection as a principal determinant of elongated necks than does natural selection through feeding competition. We hope that our critique of the feeding competition idea will stimulate its proponents to gather critical data to better support (or reject) it. At present it may be no more than a tall story.

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