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Evolutionary transitions among feeding styles and habitats in ungulates

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ABSTRACT

Using a phylogeny of extant species with a maximum likelihood model of trait evolution, the most likely pathway that led to the current diversification of feeding styles in the Ungulata is described and related to their habitat use. Habitat use and feeding style are intimately associated in extant species; grazing and mixed-feeder species are more likely to use open habitats than browsing species. From the ancestral state of a closed-habitat dweller/browser, the acquisition of an open-habitat/grazer state is likely to have occurred through a three-step transition. In the first step, the ancestral ungulate species evolved a mixed-feeder feeding style but retained the closed-habitat condition. Then, once the species had a mixed diet, it evolved to occupy open habitats. Finally, a grazer feeding style evolved with the open-habitat state being retained. The mixed-feeder state is a flexible evolutionary state that acts as a link between closed and open habitats. These findings are discussed from a comparative palaeoecological perspective.

Keywords: browser, diet, grazer, habitat use.

INTRODUCTION

The most widely accepted functional classification of ungulates, in relation to their dietary habits, is one which categorizes them into browsing, mixed-feeder and grazing species (Hofmann and Stewart, 1972; Owen-Smith, 1982, 1991; McNaughton, 1984; Demment and Longhurst, 1987; Gordon and Illius, 1988; Janis and Ehrhardt, 1988; Hofmann, 1989; Spalinger and Hobbs, 1992; Solounias *et al.*, 1994; Van Soest, 1996; Iason and Van Wieren, 1999). This classification is based on the proportion of different forages (grass or browse) that the animal includes in its diet (Hofmann, 1968). Species that feed predominantly on parts of woody plants are classified as browsers. Grazing species are considered to be those that eat mainly grasses. Mixed feeders are an intermediate group of species with a diet that includes a mixture of both browse and grasses. There is wide variation in the boundaries that demarcate these categories, since the use of grass/browse by herbivores depends, to a large extent, on food availability, competition between species of herbivores and avoidance of predation (F.J. Pérez-Barbería and I.J. Gordon, unpublished data). Relationships have

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also been established between gut morphology (Hofmann and Stewart, 1972; Hofmann, 1989), mouth morphology (Gordon and Illius, 1988; Hofmann, 1988; Janis and Ehrhardt, 1988), digestive physiology (Hofmann, 1989; but see Gordon and Illius, 1994, 1996; Robbins *et al.*, 1995), activity time (Mysterud, 1998) and feeding style. Nevertheless, the adaptive significance of many of these characteristics, and their relationship to feeding style, remain unclear, because most of the variation can be accounted for by phylogeny and body mass (Pérez-Barbería and Gordon, 1999a,b, 2000; Bashares *et al.*, 2000; Mysterud *et al.*, in press).

Gwynne and Bell (1968) and Jarman (1974) were the first to hypothesize that feeding style was fundamentally important to habitat use by ungulates. The fossil record suggests that the ungulate ancestor (a forest dweller and browser) rapidly evolved into an open-habitat dweller (a grassland inhabitant and grazer), probably in response to increased availability of open habitats, starting in the late Oligocene and continuing through the late Miocene (Janis, 1982). Mixed feeders are an intermediate transitional state between species that retain the use of closed habitats and those which become open-habitat dwellers. However, the evolutionary chronology of the relationship between habitat use and feeding style remains unclear. Was the selection to occupy new open habitats a consequence of a reduction in the area of forest habitats or an increase in predation pressure, which led to a change in feeding style? Or, was the nutritional advantage that the newly evolved grasses offered to ungulates the selective force for the shift in feeding style and then, as a consequence, the ancestral ungulate moved into open habitats?

The aims of this study were: (1) to establish the relationship between habitat use and feeding styles in ungulates, using a phylogeny of extant species and the application of statistical techniques; (2) to determine the sequence of evolutionary transitions from ancestral browsing to the derived grazing state; and (3) to establish the position of mixed feeders in this evolutionary landscape.

MATERIALS AND METHODS

Taxa

Information was collected on the habitat use and feeding styles of three of the five ungulate orders, Proboscidea ($n = 2$ species), Perissodactyla ($n = 12$ species) and Artiodactyla ($n = 94$ species). The number of extant taxa included was limited by both the biological and phylogenetic information available.

Ecological data

Two variables were included in the analysis (Fig. 1). First, *habitat use* was characterized following Janis (1988), Loison *et al.* (1990) and Pérez-Barbería and Gordon (unpublished data). Closed-habitat dwellers were defined as those species which spend most of the year in dense habitats (e.g. forests, woodlands, bushlands, thickets). Open-habitat dwelling species were considered those that predominantly use grasslands; mixed-habitat dwellers were defined as those species which use savanna, forest ecotone or both closed and open habitats depending upon the season or the population within a species. Secondly, *feeding style* was defined by predominant type of plant material in the year-round diet of the species (Janis, 1988). We simplified the classification for the purpose of adapting the data set to our

analytical requirements. Species whose diet was ≥90% monocotyledonous grass material were classified as grazers; species with ≥90% dicotyledonous herbage (i.e. tree and shrub foliage or fruit eaters) in their diet were classified as browsers. Mixed feeders were those species with 10–90% grass in their diet.

Although habitat use and feeding style vary within extant species between populations living in different environments (Novak, 1991), we chose the most representative habitat use and diet for each species. We assumed that this variation is similar to that of extinct fauna.

Phylogenetic information

The comparative method used does not support polytomies and, therefore, we constructed a fully dichotomous phylogenetic tree (Fig. 1) based on Pérez-Barbería and Gordon (1999a). Information on the branch lengths is not currently available for most nodes; sometimes discrepancies occur in divergence times estimated by palaeontological and molecular techniques (Gatesy *et al.*, 1997). Thus, we opted to use Pagel's (1992) arbitrary method to assign branch lengths (i.e. all inter-node branch segments of the tree are set equal to 1, but tips are constrained to be lined up across the top of the tree).

Comparative method

There is palaeoecological evidence that the primitive ungulates were browsers, living in closed woodland habitats (Janis, 1982). We took this state as the starting point of the analysis and then applied the method proposed by Pagel (1994) for the analysis of discrete characters based on a maximum-likelihood model of trait evolution to our phylogeny. The method estimates rates of character evolution for phylogenies by assessing: (1) the correlation between two discrete characters evolving among a group of hierarchically evolved species; (2) the temporal order of changes in two variables; and (3) whether the state of one variable makes changes in the other variable more or less likely (the contingent-changes test). The correlation between two variables is tested by comparing the fit to the data of a model in which the two variables evolve in a correlated fashion, to one in which they evolve independently. The temporal order of events is established by testing which of two variables changes most rapidly from the ancestral to the derived state; contingent changes are tested by comparing the rates of evolution of one variable dependent upon the state of another variable. All significance tests follow χ^2 distributions: the test for correlated change had four degrees of freedom and Monte Carlo simulations had to be used to estimate their significance; tests for rates and contingent changes had one degree of freedom and significance was assessed by using χ^2 distribution tables. The method is described in Pagel (1994, 1997).

RESULTS

Among the 108 species studied, 32% were closed-habitat dwellers, 25% were mixed-habitat dwellers and 43% were open-habitat dwellers. With respect to feeding style, 33% of species were browsers, 41% were mixed feeders and 31% were grazers (Table 1). The transition from closed and mixed habitats to open habitats was strongly associated with transitions from browsing to a mixed feeding style ($\chi^2 = 29.3$, d.f. = 4, $P < 0.01$; $\chi^2 = 20.8$, d.f. = 4, $P < 0.01$, respectively) or from browsing to grazing ($\chi^2 = 44.8$, d.f. = 4, $P < 0.01$; $\chi^2 = 22.2$, d.f. = 4,

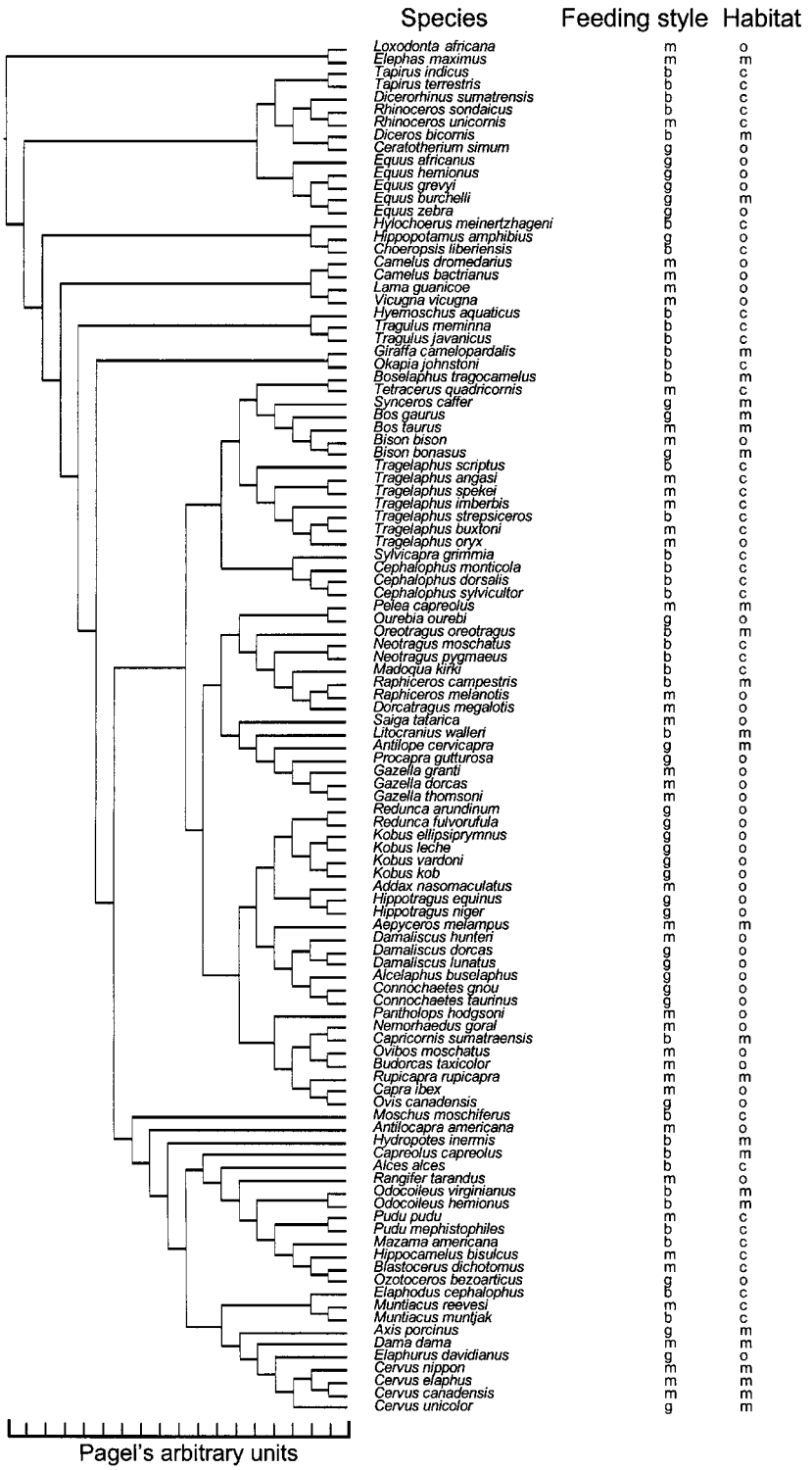
Species
Feeding style
Habitat
Loxodonta africana m o
Elephas maximus m m
Tapirus indicus b c
Tapirus terrestris b c
Dicerorhinus sumatrensis b c
Rhinoceros sondaicus b c
Rhinoceros unicornis m c
Diceros bicornis b m
Ceratotherium simum g o
Equus africanus g o
Equus hemionus g o
Equus grevyi g o
Equus burchelli g m
Equus zebra g o
Hylochoerus meinertzhageni b c
Hippopotamus amphibius g o
Choeropsis liberiensis b c
Camelus dromedarius m o
Camelus bactrianus m o
Lama guanicoe m o
Vicugna vicugna m o
Hyemoschus aquaticus b c
Tragulus meminna b c
Tragulus javanicus b c
Giraffa camelopardalis b m
Okapia johnstoni b c
Boselaphus tragocamelus b m
Tetracerus quadricornis m c
Synceros caffer g m
Bos gaurus g m
Bos taurus g m
Bison bison m o
Bison bonasus g m
Tragelaphus scriptus b c
Tragelaphus angasi m c
Tragelaphus spekei m c
Tragelaphus imberbis m c
Tragelaphus strepsiceros b c
Tragelaphus buxtoni m c
Tragelaphus oryx m o
Sylvicapra grimmia b c
Cephalophus monticola b c
Cephalophus dorsalis b c
Cephalophus sylvicultor b c
Pelea capreolus m m
Ourebia ourebi g o
Oreotragus oreotragus b m
Neotragus moschatus b c
Neotragus pygmaeus b c
Madoqua kirki b c
Raphiceros campestris b m
Raphiceros melanotis m o
Dorcatragus megalotis m o
Saiga tatarica m o
Litocranius walleri b m
Antilope cervicapra g m
Procapra gutturosa g o
Gazella granti m o
Gazella dorcas m o
Gazella thomsoni m o
Redunca arundinum g o
Redunca fulvorufula g o
Kobus ellipsiprymnus g o
Kobus leche g o
Kobus vardoni g o
Kobus kob g o
Addax nasomaculatus m o
Hippotragus equinus g o
Hippotragus niger g o
Aepyceros melampus m m
Damaliscus hunteri m o
Damaliscus dorcas g o
Damaliscus lunatus g o
Alcelaphus buselaphus g o
Connochaetes gnou g o
Connochaetes taurinus g o
Pantholops hodgsoni m o
Nemorhaedus goral m o
Capricornis sumatraensis b m
Ovibos moschatus m o
Budorcas taxicolor m o
Rupicapra rupicapra m m
Capra ibex m o
Ovis canadensis m o
Moschus moschiferus b c
Antilocapra americana m o
Hydropotes inermis b m
Capreolus capreolus b m
Alces alces b c
Rangifer tarandus m o
Odocoileus virginianus b m
Odocoileus hemionus b m
Pudu pudu m c
Pudu mephistophiles b c
Mazama americana b c
Hippocamelus bisulcus m c
Blastocerus dichotomus m c
Ozotoceros bezoarticus g o
Elaphodus cephalophus b c
Muntiacus reevesi m c
Muntiacus muntjak b c
Axis porcinus g m
Dama dama m m
Elaphurus davidianus g o
Cervus nippon m m
Cervus elaphus m m
Cervus canadensis m m
Cervus unicolor g m
Pagel's arbitrary units

Table 1. Numbers of ungulate species by type of habitat and feeding style (percentages in brackets)

Habitat	Browsers	Mixed feeders	Grazers	Total
Closed	25 (71)	10 (29)	—	35 (32)
Mixed	11 (41)	9 (33)	7 (26)	27 (25)
Open	—	22 (48)	24 (52)	46 (43)
Total	36 (33)	41 (38)	31 (29)	108

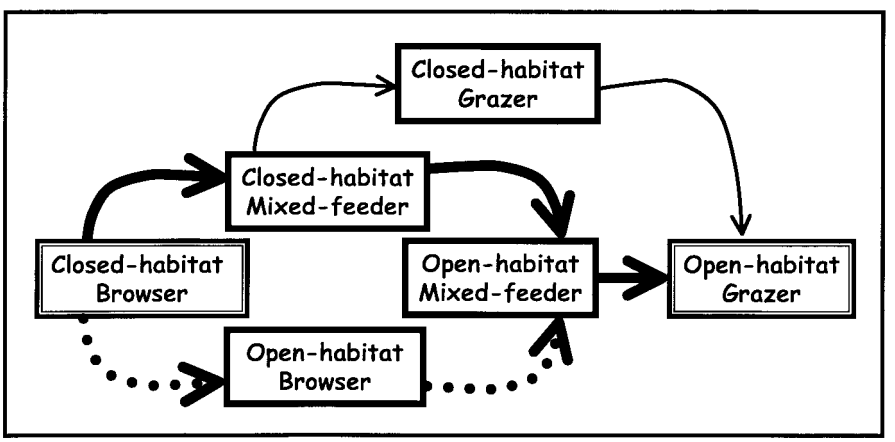

Fig. 2. Flow diagram showing the probable pathway from a closed-habitat/browser state towards an open-habitat/grazer state via two likely intermediate states. Solid bold arrows represent transition states that are significantly different from zero ($P < 0.05$); solid thin arrows represent another possible pathway that was not confirmed by the contingent-changes test (see Results); dotted arrows represent transitions that were not supported statistically.

$P < 0.01$, respectively). Not all transitions from closed to mixed habitat were associated with a change in feeding style ($\chi^2 < 6.92$, d.f. = 4, $P > 0.1$ in all cases) and not all transitions from mixed feeding to grazing were associated with a change in habitat use ($\chi^2 < 7.0$, d.f. = 4, $P > 0.1$ in all cases).

The transition from closed habitat to open habitat is more likely to occur once the species acquires a mixed feeding style (see below). There was no direct transition from browsing to grazing ($P \geq 0.16$) without having first passed through a mixed-feeder state (Fig. 2).

The transition from the ancestral closed-habitat/browser state to the final open-habitat/grazer state is most likely to have occurred through a three-step transition. First, the mixed-feeder state evolved ($\chi^2 = 9.5$, d.f. = 1, $P = 0.002$, Fig. 2) but the species retained the closed-habitat dweller state. Once the mixed-feeder style was well established, species

Fig. 1. Phylogenetic relationships, feeding styles and habitat use among 94 ungulate species. The branch lengths were obtained using Pagel's (1992) arbitrary method (see Methods). Feeding style: b = browsers; m = mixed feeders; g = grazers. Habitat: c = closed; m = mixed; o = open (see Methods for a definition of these categories).

rapidly radiated into the open habitat ($\chi^2 = 6.86$, d.f. = 1, $P = 0.009$, Fig. 2). Finally, the grazer feeding style evolved ($\chi^2 = 4.84$, d.f. = 1, $P = 0.028$, Fig. 2). There is a second possible (i.e. significant) pathway from closed-habitat/mixed-feeder to open-habitat/grazer via a closed-habitat/grazer state; however, this pathway is not supported by the contingent-changes test, as the transition from a closed to an open habitat is unlikely to occur in grazers ($\chi^2 = 1.94$, d.f. = 1, $P = 0.16$). Mixed-habitat dwellers did not contribute significantly to changes in feeding style ($P > 0.1$ in all cases).

DISCUSSION

Association between feeding style and habitat use

Feeding style and habitat use are very closely related in extant ungulates. We found significant correlations between the use of open habitats and the mixed and grazer feeding styles. This intimate association between habitat use and feeding style in ungulates is as expected; the Ungulata are dominated by herbivorous species, with only 3% being omnivorous (Janis, 1988; Novak, 1991). Herbivory requires the animal to spend long periods foraging as a consequence of the low nutritive value of the vegetation (Robbins, 1993) and because of mechanical protection, such as thorns or spines, which increase handling time (Cooper and Owen-Smith, 1986; Spalinger *et al.*, 1986; Pérez-Barbería and Gordon, 1998). Prolonged feeding usually requires the animal to rest in the same broad habitat type where feeding takes place. In many cases, this is a better strategy than switching between habitats for different activities, such as feeding and resting (Robbins, 1993). Although ungulates move between sites throughout the day in relation to the activity being performed (Weckerly, 1993; Main and Coblentz, 1996; Pérez-Barbería *et al.*, 1997; Mysterud, 1998; Owen-Smith, 1998), these movements usually take place within the same habitat, at least within the broad categories of habitat used in this paper.

In evolutionary terms, movements between habitats should not be equally advantageous for species that differ in body size. Many extant ungulates that utilize open habitats are large species or larger races within species (Kingdon, 1997). This could be a response to stronger sexual selection and predation pressure in open habitats (Jarman, 1974; Clutton-Brock, 1982, 1983). It has been suggested that the occupancy of open habitats led to the evolution of polygynous systems and, in turn, this led to sexual dimorphism in body size via sexual selection (F.J. Pérez-Barbería, I.J. Gordon and M. Pagel, unpublished data).

Large body size is not necessarily advantageous in relation to foraging, movement or anti-predation strategies within very closed habitats. In closed habitats, solitude, inconspicuous morphology and small body size appear to be the preferred strategies to reduce risk of predation by ambush (Novak, 1991). Large body size has been shown to be an efficient anti-predation strategy in open habitats where ungulates are likely to encounter predators face-to-face (Kromers, 1996; Brotherton and Manser, 1997).

There is only limited information on how predation evolved in closed and open habitats (Janis and Wilhelm, 1993); it is difficult, therefore, to know how predation pressure contributed to the occupancy of open habitats. However, it is probable that its role was secondary, since the fossil record provides evidence that the modern type of pursuit predator (responsible for the present anti-predation strategies used by ungulates in open habitats) appeared only relatively recently, in the Pliocene about 7 million years ago (Janis and Wilhelm, 1993). This is considerably later than the development of grasslands and the occupancy of open

habitats by ungulates (Janis, 1982). Medium-sized species would be the most likely to use different habitat types and they may have been a flexible evolutionary link between closed and open habitats at times when open habitats were expanding.

Tracing the origins of feeding style diversity

From this analysis, it would appear that there is a direct relationship between feeding style and habitat use in ungulates. The transition from the ancestral closed-habitat/browser state to the final open-habitat/grazer state evolved after a three-step process (Fig. 2). First, the ancestral ungulates evolved a mixed feeding style but retained their primitive closed-habitat dweller state; then mixed feeders radiated into open habitats before, finally, a grazing feeding style evolved. The appearance of a mixed-feeder state in closed habitats suggests an incipient diversification of feeding styles before open habitats were occupied, which makes the ecotone between closed and open habitats the key to ungulate diversity. More widespread use of the vegetation in closed habitats may have evolved in some primitive ungulate species, by adopting a diet consisting of a mixture of browse, herbs and grasses. Such a wide range of vegetation would allow these species to benefit from the increase in the forest/grassland ecotone that occurred in the late Miocene, when open habitats began to expand at the expense of tropical forest in Africa and Eurasia (Vrba, 1985). It is possible that the species with a wider range of foraging styles were the first to occupy the expanding open habitats in the late Miocene and, once they had colonized open habitats, they increased their consumption of grasses (Leopold, 1969; Wolfe, 1978; Janis, 1982). An example of how an incipient tendency for diet broadening could have occurred within forest dwellers is seen in the extant genus *Cephalophus*, which comprises 17 African species (although this genus may have re-occupied closed habitats from open habitats; Janis, 1982). All species in this genus are generally classified as browsers or frugivores and closed-habitat dwellers (Kingdon, 1997; Pérez-Barbería and Gordon, 1999a), but they show marked differences in habitat preference. Some of them use high-canopy forests with sparse undergrowth (e.g. *Cephalophus callipygus*); others prefer broken canopy with dense undergrowth (e.g. *C. spadix*, *C. silvicultor*), whereas still others utilize swamp forests, riverine habitats or forest edge (e.g. *C. nigrifrons*, *C. natalensis*, *C. monticola*). They also differ in terms of diet: some species show a marked tendency to use fruits, whereas others feed on leaves or flowers (Kingdon, 1997).

The acquisition of a mixed diet within closed habitats appears to be dependent on how open habitats developed from closed ones. The hypothesis presented here is more plausible if open habitat developed from closed habitat by means of small open patches that increased in area. This pattern of fragmentation of forests might have allowed closed-habitat ungulates to evolve a mixed diet by adding to their initial browse diet components of grasses obtained from patches of the open habitat within forests. However, from the current fossil record we cannot determine how the open habitat originated in the late Oligocene resulting in extensive grasslands by the late Miocene. Even information from high-resolution pollen analysis, which allows reconstruction of vegetation from more than 10,000 years B.P., is scarce (Bradshaw and Mitchell, 1999).

Our results suggest that the use of mixed habitats did not play a significant role in the evolution of feeding styles. This contrasts with the fact that mixed feeding was the main link between browsing and grazing and closed and open habitats. It appears counterintuitive that mixed habitats did not play a similar role to mixed feeding, because habitat use appears

to be more flexible than feeding style. A particular preference for a type of diet can be exhibited within different habitats; for example, in our data set, among mixed-habitat dwellers there were 41% browsers, 33% mixed feeders and 26% grazers. This is also consistent with the finding that the catalyst that primed ungulate species to evolve out of closed habitats was not the occupancy of mixed habitats while retaining a browsing feeding style, but the acquisition of a mixed feeding style within closed habitats.

The increase in open habitat has been more or less continuous from the Oligocene (Leopold, 1969; Wolfe, 1978; Vrba, 1985), resulting in increased transition to grazing. This is reflected in the composition of extant ungulates, 56% of which are open-habitat dwelling species. However, it is worth noting the important contribution of mixed feeding to the extant fauna (Kingdon, 1997), which suggests that this form of feeding represents a flexible strategy to deal with seasonal fluctuations in vegetation growth and biomass. This is consistent with the predominance of a mixed-feeding mouth morphology seen in artiodactyls (F.J. Pérez-Barbería and I.J. Gordon, unpublished data). Mixed feeding appears to be a transitional state that preceded the occupancy of open habitats; because of its ecological versality, it is still seen today.

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