

Assembly rules in large herbivores: a null model analysis of local and regional diversity patterns of ungulates in dry tropical forests of western India *

Sumanta BAGCHI^{1, 2**}

1. Biological Research Laboratories, Syracuse University, 130 College Place, Syracuse NY-13244, USA

2. Nature Conservation Foundation, 3076/5, IV-Cross, Gokulam Park, Mysore-570002, Karnataka, India

Abstract Competition can shape natural communities and give rise to general assembly rules that can be tested with null models. Yet, evidence for competitive structure is scarce from many animal assemblages. A null model analysis is done to test whether a local large herbivore assemblage of five ungulates (*Axis axis*, *Boselaphus tragocamelus*, *Cervus unicolor*, *Gazella bennetti* and *Sus scrofa*) in dry tropical forests of western India shows general assembly rules. Using Monte Carlo simulations, niche overlap and body size ratios are analysed in terms of limiting similarity. Results from niche overlap suggest the local assemblage is not competitively structured and has sub-optimal species richness with internal guild structuring. Two other ungulates are part of the regional species pool (*Antilope cervicapra*, and *Tetracerus quadricornis*), but are absent from this assemblage. Body size relationships show that size-ratios are non-random in the regional assemblage; whereas, they can be obtained by random chance in the local assemblage. Local extinctions leaving statistical ‘gaps’ in the extant assemblage seems the most plausible explanation for the observed patterns. Since predators (large carnivores) can potentially reduce competition between prey species; this irregular niche-apportionment is possibly maintained. The absence of *T. quadricornis* from this assemblage raise concerns since very little is known about its biology, including its conservation status. An urgent need for generating more ecological information on this rare and endemic antelope is perceived since it appears that conservation concerns of such lesser-known species have gone unnoticed [*Acta Zoologica Sinica* 52 (4): 634–640, 2006].

Key words Competition, Species coexistence, Monte Carlo simulation, Niche, Resource partitioning, *Tetracerus quadricornis*

大型食草动物的聚群规则：印度西部热带干旱森林中有蹄类动物局域和区域尺度的多样性格局 *

Sumanta BAGCHI^{1, 2**}

1. Biological Research Laboratories, Syracuse University, 130 College Place, Syracuse NY-13244, USA

2. Nature Conservation Foundation, 3076/5, IV-Cross, Gokulam Park, Mysore-570002, Karnataka, India

摘要 竞争能够塑造自然群落并由其给出可用备择模型检验的一般性聚集规则。关于多种动物集合的竞争结构证据至今还非常少见，我们给出了一个备择模型分析用于检验印度西部热带干旱森林中当地 5 种大型食草动物（花鹿 *Axis axis*，印度大蓝羚 *Boselaphus tragocamelus*，水鹿 *Cervus unicolor*，印度瞪羚 *Gazella bennetti*，野猪 *Sus scrofa*）是否符合一般性集合规则。使用蒙特卡罗模拟分析了动物的生态位重叠和身体大小比率的类似性，结果表明当地这些种的集合不是竞争结构决定的，其内部阶元结构处于亚最适种丰富度。另外 2 种有蹄类（印度黑羚 *Antilope cervicapra*，四角羚羊 *Tetracerus quadricornis*）属于地域性种库的组成部分，但缺失于这种集合；身体大小组合在地域性物种集合中不是随机的，然而在本地集合中能够通过随机性机会获得。对于观察到的类型，我们认为由于灭绝留下的统计学空缺似乎最能解释现存集合。由于天敌（大型食肉类）能够减少猎物物种的种间竞争，使得这种无规则生态位配置具有成立的可能性。由于对四角羚羊（*T. quadricornis*）的生物学和保

护现状知之甚少, 未将该种包括在该聚集中。我认为对这类较少被人类了解的物种其保护问题被忽视了, 今后获得这些稀少的地方特有物种的生态学资料是一项紧急课题 [动物学报 52 (4): 634–640, 2006]。

关键词 竞争 种间共存 蒙特卡罗模拟 生态位 资源分化 四角羚羊

Since Gause (1934), competition is regarded as a major force in ecological communities and has been widely encountered in nature (Schoener, 1983). Yet, its role in structuring natural communities continues to be debated as evidence from many assemblages seems controversial (Strong et al., 1984). Thus, coexistence of species sharing common resources remains of keen interest among ecologists.

Assessing resource partitioning and coexistence in ungulates has received research attention in many parts of the world and these patterns were recently investigated in ungulates of dry-deciduous forests of western India (Bagchi et al., 2003a) which have a high potential to support a diverse assemblage of large herbivores (Olf et al., 2002). Seven species of ungulates are known to occur in this belt—two cervids: chital or spotted deer *Axis axis*, sambar *Cervus unicolor*, and four bovines: nilgai or blue bull *Boselaphus tragocamelus*, chinkara or Indian gazelle *Gazella bennetti*, blackbuck *Antelope cervicapra*, and four-horned antelope or chowsingha *Tetracerus quadricornis*, in addition to omnivorous wild pigs *Sus scrofa*. Ranthambhore National Park is a typical representative of this ecosystem. Its extant large herbivores include chital, sambar, nilgai, chinkara and wild pig. A small population of blackbuck occupies fringe agricultural and fallow lands, but four-horned antelope is missing, even though it occurs in very similar habitats in other parts of western and central India and coexists in similar assemblages. In this paper, I discuss whether competition and human-induced disturbances may have played a role in structuring this community.

Diamond (1975) suggested that competition leads to niche adjustments and discernible assembly rules. Connor and Simberloff (1979) argued whether an observed species pool suggests competitive structuring or merely a chance event needs to be tested using a null hypothesis. Null models are a means to test such hypotheses of non-interactive community assembly by contrasting a randomly generated pattern against empirical data (e.g. Fox, 1987). Monte Carlo simulations can be used to investigate mean niche overlap since competitively structured communities are expected to show less niche overlap than randomly generated ones (Gotelli and Graves, 1996). Also, since a species that is already present (functional group or guild) can influence the establishment of another new species from the same functional group (or guild), the variance of niche overlap can assess internal guild-structuring (Kelt et al., 1995; Gotelli and

Graves, 1996). Variance of niche overlap is least when competition imposes limits to similarity resulting in orderly niche apportionment. Consequently, a high observed variance of niche overlap in synecological data is interpreted as evidence for internal guild structuring or irregular niche apportionment. Some natural assemblages such as insects (Kobayashi, 1991), amphibians (Inger and Colwell, 1977), lizards (Pianka, 1986) and fishes (Winemiller and Pianka, 1990) have been studied in this context and this paper attempts to understand whether large herbivorous mammals, which dominate more than half of the earth's terrestrial realm (Owen-Smith, 1988) also follow such general rules.

Understanding how competition can have functional implications such as minimum size difference between coexisting species stems from Hutchinson's (1959) seminal paper "Homage to Santa Rosalia." Simberloff (1983) recognised that coexisting species have a minimum size difference (as seen in African grazers, Prins and Olf, 1998). Log-body weight has a linear relationship with the rank of body size, and the slope depends on species richness. Each member is a constant proportion larger than the nearest smaller species and this optimum weight ratio is calculated as e^{slope} (Prins and Olf, 1998; Mishra et al., 2002). This expected ratio depends on the underlying distribution of body sizes and on the possible end-points, and represents the probability that a particular body size will exist in a competitively structured community (Tonkyn and Cole, 1986). Monte Carlo simulations can be used to validate observed size-ratios against random patterns of non-interactive assembly (Strong et al., 1979; Mishra et al., 2002).

Here I investigate whether sympatric ungulates in dry tropical forests of western India, segregate by differential use of habitats using pellet group counts. I also analyse whether this assemblage is competitively structured by comparing similarity in habitat use (niche overlap) against a simulated competition-free environment using null models. Subsequently, I investigate species packing in this assemblage with body weight ratios. If this assemblage were competitively structured, then the observed patterns would differ significantly from randomly generated ones. Specifically: i) the mean niche overlap should be lower than by random chance, ii) variance of niche overlap should be lower than by random chance, and iii) it is unlikely that the observed body-size ratio be produced by random chance.

1 Study site and methods

1.1 Study site

Data were collected between November 2000 and April 2001 in the semiarid dry deciduous forests of Ranthambhore National Park (392 km²), which is part of Ranthambhore Tiger Reserve (1 334 km²; 26° N, 76°E), Rajasthan, western India. The vegetation of this region is tropical dry deciduous forest and tropical thorn forest. *Anogeissus pendula*, *Acacia leucophloea* and *Butea monosperma* are the dominant trees, and *Grewia flavescens* and *Capparis sepiaria* are the common shrubs. Based on topography and vegetation cover, five habitat types have been recognized (Bagchi, 2001): A. *Anogeissus-Grewia* forest (600 trees and 800 shrubs/ha with canopy cover of 65%), B. *Anogeissus-Capparis* scrub (400 trees and 1 700 shrubs/ha with canopy cover of 50%), C. *Anogeissus forest* (900 trees and 700 shrubs/ha with canopy cover of 75%), D. *Anogeissus-Acacia-Butea* mixed woodlands (200 trees and 900 shrubs/ha and canopy cover of 20%), and E. Grassy slopes and plateaux (100 trees and 200 shrubs/ha without any canopy). Other details can be found in Bagchi et al. (2003a, 2003b, 2004a, 2004b).

1.2 Data collection

Rates of pellet deposition in different habitat categories provides insights into habitat selection in ungulates (Cairns and Telfer, 1980; Edge and Marcum, 1989). A total of 99 circular plots (10 m radius) were used for pellet counts, spread over different habitat types in a stratified random manner. The number of plots in a habitat type approximated its proportional acreage within the study site: A=36, B=9, C=10, D=28 and E=16. All pellets were cleared from a plot at the beginning of the study and left for further deposition to occur. A cluster of more than 10 pellets of a particular species was considered a pellet-group and indicated a single instance of habitat use (Rogers et al., 1958; Neff, 1968). But it was not possible to identify distinct pellet groups for wild pigs, and hence only their presence-absence was noted. Identification of species from pellets was done on site by observing shape and size characteristics. Plots were initially cleared and then given 135 to 150 days for pellet deposition and counts were standardized for 100 days (i. e., rate of deposition or intensity of resource utilization).

1.3 Data analysis

Distribution free Kruskal-Wallis ANOVA was used to compare rates of pellet deposition by the four species (except wild pigs) between different habitat types. Patterns of niche overlap and community structure were analysed through null models adapting Kobayashi (1991) using presence-absence of pellets

(all species) in plots. A measure of niche overlap between each species-pair was calculated as $O_{12} = O_{21}$

$$= 1 - \frac{\sum_{i=1}^n |P_{1j} - P_{2j}|}{2} \quad (\text{Czechanowski index, Feinsinger et al., 1981}),$$

where O_{12} is the overlap of species 1 with species 2 (conversely for O_{21}) in a community of n species, and P_{1j} the proportional use of resource state j by species 1 having $j = 99$ plots and $n = 5$ species. Observed niche overlap was compared against an expected niche overlap by 1 000 simulations using EcoSim software (Gotelli and Entsminger, 2001). The ‘conserved zeros’ randomization algorithm (Winemiller and Pianka, 1990; Gotelli and Graves, 1996) was used for the simulations since this retains observed niche-breadth. As they have strong habitat selection tendencies (Bagchi et al., 2003a), iterations were constrained to take into account that chital and sambar do not use open scrub, while chinkara does not use dense forest. During iterations, their absences from plots in such ‘unsuitable’ habitats were retained following Bagchi et al. (2004c). In literature, this algorithm is also known as RA4 (Lawlor, 1980; Winemiller and Pianka, 1990).

Body weights of species were taken from literature (Table 1). Least squares regression was performed to assess the relationship between log body weight and species ranks in a hypothetical ‘intact’ assemblage representing regional diversity, which includes blackbuck and four-horned antelope, and compared against the extant local assemblage. The regression equations were checked against random patterns following Mishra et al. (2002). A Monte Carlo simulation with 1 000 random iterations was carried out by resampling body weights and the corresponding species rank. During each iteration, a weight-rank datum was randomly selected from the possible range of sizes, thus fixing the lower and upper bounds to match the ‘real’ community. Five such data were picked for the local assemblage and 7 pairs were picked from the regional assemblage (Table 1) to provide 95% confidence limits for the 2 linear equations (Mishra et al., 2002). This provided a means of comparing the statistical significance of the regression equations (Mishra et al. 2002) that describe body weight ratios between species.

1.4 Limitations

The major assumption for niche analysis is that the scope for competitive interactions arises when species exploit limiting resources. In this case, availability of resources is assumed to be predictable (see Illius and O’Connor, 1998). Also, mechanisms behind body weight relationships can operate at the levels of discrete populations, but I have used species-

Table 1 Description of average body weights of 5 species found in Ranthambhore National Park, India

Species	Four-horned antelope	Chinkara	Wild pig	Blackbuck	Chital	Nilgai	Sambar
Weight (kg)	20	23	27	35	68	180	250

The five species includes chital *Axis axis*, sambar *Cervus unicolor*, nilgai *Boselaphus tragocamelus*, chinkara *Gazella bennetti*, and wild pig *Sus scrofa*. Two other species (blackbuck *Antelope cervicapra* and four-horned antelope *Tetracerus quadricornis*) that occur in adjoining areas are also shown.

level data for analyzing weight ratios (see Dayan and Simberloff, 1998).

2 Results

2.1 Habitat use

Proportional deposition rates by the four species in different habitat types (Fig. 1) suggest differential habitat selection by each species (Kruskal-Wallis

ANOVA $P < 0.01$ for all species). In general, chital and sambar have proportionately higher rates of pellet deposition in habitat A and D, and are forest-woodland dwellers under *Anogeissus*. On the other hand, nilgai and chinkara have higher relative rates of pellet deposition in habitat B and D, and seem to be scrub-woodland dwellers, related to *Acacia*.

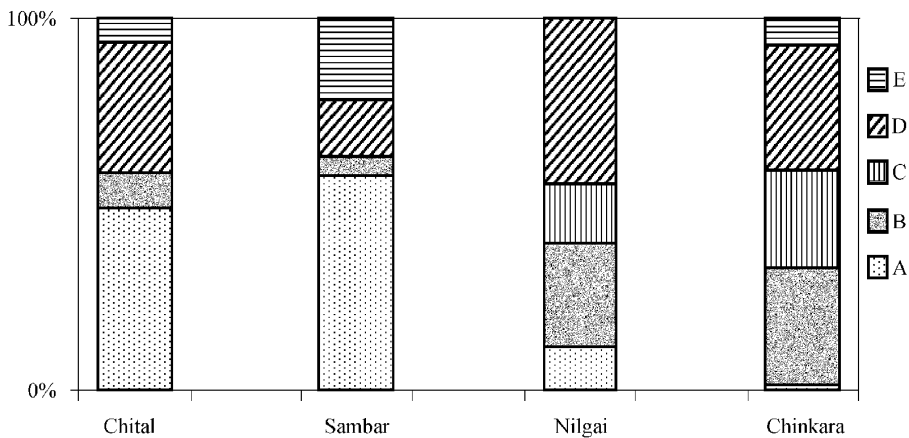


Fig. 1 Proportional use of different habitats (A – E) by four ungulates (chital *Axis axis*, sambar *Cervus unicolor*, nilgai *Boselaphus tragocamelus*, and chinkara *Gazella bennetti*) in Ranthambhore National Park, India

Wild pigs *Sus scrofa* were not part of this analysis. Habitat types are A: *Anogeissus-Grewia* forest; B: *Anogeissus-Capparis* scrub; C: *Anogeissus* forest with dwarf shrub layer; D: *Anogeissus-Acacia-Butea* mixed woodlands; and E: Grassy slopes and plateaux. Proportional use is derived from average number of pellet groups encountered in plots laid in different habitats.

2.2 Niche overlap

Observed mean niche overlap for all species (0.52) was not different from that expected by random chance (0.50, $P > 0.05$). The variance of niche overlap (0.05) was greater than expected by random chance (0.01, $P < 0.01$). In pair-wise comparison, certain species showed positive and/or negative associations with one other (Table 2). In general, the two deer tended to co-occur in the same plot, as did the 2 bovids. But any cervid-bovid pair tended not to co-occur in the same plot. And this is consistent with the trend that cervids relate to forest-woodland habitat while bovids exploit woodland-scrub. The habitat preference of the suid was similar to the cervids. This indicates some internal guild structuring within this assemblage.

2.3 Body weight ratio

The body-weight relations in the regional and the local assemblages are shown in Fig. 2. The coefficient of determination in the intact assemblage ($r^2 = 0.92$) can be considered higher than in a random as-

semblage ($r^2 = 0.87$, $P = 0.06$). In the extant assemblage ($r^2 = 0.94$) this was statistically not different from random chance ($r^2 = 0.90$, $P = 0.32$). The proportional weight ratio for the extant assemblage ($e^{0.67} = 1.95$) was higher than the intact assemblage ($e^{0.45} = 1.56$).

Table 2 Pair wise niche overlap between 5 species (chital *Axis axis*, sambar *Cervus unicolor*, nilgai *Boselaphus tragocamelus*, chinkara *Gazella bennetti*, and wild pig *Sus scrofa*) in Ranthambhore National Park, India

	Chital	Sambar	Nilgai	Chinkara	Wild pig
Chital		0.53 ⁺	0.44	0.11 ⁻	0.75 ⁺
Sambar			0.27 ⁻	0.12 ⁻	0.66 ⁺
Nilgai				0.41 ⁺	0.54 ⁺
Chinkara					0.24
Wild pig					

This is based on the symmetric Czechanowski index, ranging between 0 (no overlap) and 1 (complete overlap). Superscripts denote nature of association between species (positive or negative) and internal guild structure. These were derived by 1000 Monte Carlo simulations in a null model. Positive association reveals a tendency of species to co-occupy a particular resource state, and negative association is a tendency to avoid each other.

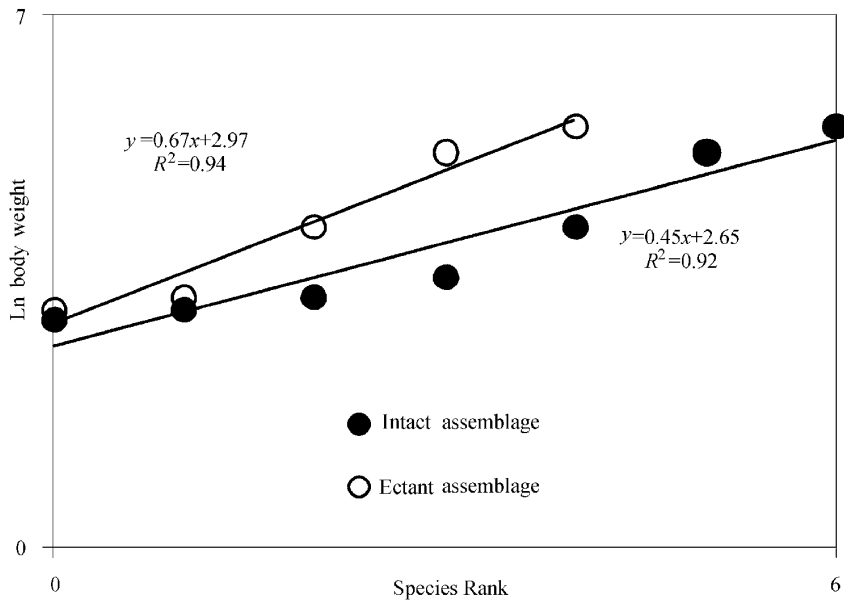


Fig. 2 Relationship between natural log-transformed body weight and species rank in two types of herbivore assemblage in western India

One of the two types of herbivore assemblage is the 'extant' local assemblage of Ranthambhore National Park, having only five species (chital *Axis axis*, sambar *Cervus unicolor*, nilgai, *Boselaphus tragocamelus*, wild pig *Sus scrofa*, and chinkara *Gazella bennetti*), whereas the other is an 'intact' assemblage representing the regional species pool of western India that includes blackbuck *Antelope cervicapra* and four-horned antelope *Tetracerus quadricornis*.

Thus, the strength of the relationship between body weight and species rank is significantly stronger in the regional assemblage than in the local assemblage such that there is an increase in the proportional weight ratio. Since the regional species pool seems to follow general assembly rules more closely than the local assemblage, it is possible that some species from the regional pool have been lost and the current local conditions reflect sub-optimal richness, caused by artificial gaps in the community.

3 Discussion

Rates of pellet deposition across the different habitats were non-uniform, but overall niche overlap was not found to be less than by random chance, suggesting an apparent lack of competitive segregation (Glasser and Price, 1988). Alternately, there could be strong competition due to lack of divergence, and the real nature of the interaction does not become clear. The results from variance of niche overlap are more definitive. A high observed variance indicates some internal guild structure, and some species are very similar and these 'guilds' differ from other such groups (Inger and Colwell, 1977; Winemiller and Pianka, 1990). This is in line with the observed similarity between the two deer and the two bovids, as discussed in Bagchi et al. (2003a). Such guild structuring also implies that species richness is not maximised in this community (Inger and Colwell, 1977; Winemiller and Pianka, 1990), and that some species may have been lost in the past. As a result, the anal-

ysis of body weights was done. The relation between body weight ratios in the local assemblage was not different from what is expected by random chance, suggesting a lack of competitive structuring; unlike the more diverse regional assemblage where patterns differ significantly from random. And since this coincides with an increase in proportional weight ratios, it suggests that there are statistical 'gaps' in this assemblage and more species can potentially be accommodated. Since blackbuck still occur in small populations in this region, it is possible that four-horned antelope has suffered local extinction in certain parts of western India.

The role of competition in community structure is a central theme in much of ecological research on assembly rules (Weiher and Keddy, 1999). And empirical tests have sometimes generated controversial evidence (Strong et al., 1984). At least three aspects need discussion following the evidence of sub-optimal species richness in this assemblage. First, local extinction and colonization are natural processes in metapopulations, and might be responsible for the absence of four-horned antelope in a patch. But, with increasing fragmentation due to human pressures, recolonization processes and source-sink dynamics can often get disrupted, especially for the four-horned antelope as it occurs at low-densities in other parts of its range. Despite its taxonomic uniqueness (four-horned antelope is a monotypic species endemic to the India), little is known about its ecology, including its conservation status. And it appears that in these hu-

man modified landscapes, such lesser-known species may have grave conservation concerns that often go unnoticed.

Second, is the apparent low diversity in this assemblage (7 species regionally) despite the high potential predicted by Olff et al. (2002), and role of Pleistocene extinctions in shaping this assemblage needs to be assessed. Analysis of fossil assemblages has helped to place long-term diversity patterns of mammals on an empirical basis, but this is mostly restricted to North America (Potts and Behrensmeyer, 1992). But, parts of south Asia (the sub-Paratethyan region extending up to Arabia) record open-country large mammals consisting of bovids, equids, giraffids, rhinos among others; which had a diversity similar to the extant Old World savannah, especially in larger taxa (Bernor, 1984). Badam (1984) summarises this extinct Pleistocene fauna of India and investigations into long-term environmental patterns and diversity of large herbivores can provide a better understanding since these species are known to occur in sympatry from fossil records (Badam, 1979).

Third are various theoretical questions related to stability and diversity. Are these statistical 'gaps' due to transitional behaviour in variable environments (Inger and Colwell, 1977)? Or is such an assemblage non-equilibrial (Illius and O'Connor, 1998)? Predators are generally thought to promote coexistence of their prey (Noy-Meir, 1981) and these ungulates are known to be preferred prey of large carnivores. Possibly predation maintains such irregular niche-apportionment. Does this pattern suggest nestedness (Patterson and Atmar, 1986)? What implications does nestedness have on conservation planning for small populations (Patterson, 1987)? Unsaturated communities with sub-optimal species richness are common in nature (Cornell and Lawton, 1992) and theory predicts that local diversity is maximal at intermediate rates of dispersal (Mouquet and Loreau, 2003). But testing the interactions between local and regional processes in terms of dispersal and re-colonization (Thomas, 2000) is difficult for large mammals in such human-dominated landscapes where the only remaining habitats are small and isolated parks such as Ranthambhore National Park. However, dispersal and local competition are both thought to be linked with species co-occurrence patterns (Friedenberg, 2003) and these seem to have become uncoupled in the dry-forests of western India, raising conservation concerns about the rare-endemic species. Perhaps analysis of the distribution, abundance, and metapopulation-structure of the large mammals (especially the four-horned antelope) would provide answers to the hierarchical relation between α , β , and γ -diversity of this dry-deciduous ecosystem. In conclusion, the

analyses suggest that interactions of history with intrinsic processes may be central in determining community structure, rather than competition and predation alone.

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