

Diet selection by goats on a semi-arid shrubland in central Argentina

J. M. Pisani¹, R. A. Distel¹ and E. E. Bontti²

1. Departamento de Agronomía and CERZOS - CONICET Universidad Nacional del Sur, 8000 Bahía Blanca, Argentina. E-mail: cedistel@criba.edu.ar. 2. Departamento de Biología, Bioquímica y Farmacia and Comisión de Investigaciones Científicas (CIC), Universidad Nacional del Sur, 8000 Bahía Blanca, Argentina.

Abstract. *The objective of this study was to determine diet selection by goats on a semi-arid shrubland in the central part of Argentina. Ten goats grazed on a pasture for 10-days periods in winter, spring, and summer. The botanical composition of the pasture was estimated by a combined measure of cover and biomass, whereas the botanical composition of the diet was determined by the microhistological technique complemented with direct observation. Two shrub species (*Condalia microphylla* and *Prosopis caldenia*) and five soft grasses (*Piptochaetium napostaense*, *Poa* spp., *Stipa tennis*, *S. clarazii*, and *Pappophorum* spp.) were highly selected by goats. Shrubs represented 32%, 40% and 74% of goat diets in winter, spring and summer, respectively. For each season, the rest of goat diets was composed by the soft grasses. Although coarse grasses represented most (> 80%) of the available biomass in all seasons, they were always highly avoided by goats. The results showed that goats behave as mixed-feeders (eat grasses and shrubs) on semi-arid shrublands in central Argentina.*

Introduction

Goats present morphological and biochemical mechanisms that allow for a dietary plasticity not found in other livestock species. The small mouth and agile lips and tongue enable them the consumption of plant parts that are relatively inaccessible or protected by physical defenses (e.g., spines) (Hofmann 1988), whereas the ability to detoxify secondary compounds enables them the consumption of plants or plant parts with a high content of chemical defenses (e.g. phenols) (Distel and Provenza 1991, Silanikove et al. 1996). However, detoxification of plant secondary compounds can represent high metabolic costs (Freeland and Janzen 1974, McArthur et al. 1991, Cheeke 1994, Cheeke and Palo 1995), whereas to feed on spiny plants can result in a low consumption rate (Cooper and Owen-Smith 1986, Belovsky et al. 1991). Together, the mechanisms to counteract antiherbivore defenses and their limitations may explain why the diet of goats is commonly characterized by variety and frequent compositional changes (e.g. Riggs et al. 1988, Ricardi and Shimada 1992, Grünwaldt et al. 1994, Richman and Johnson 1995, Fraser and Gordon 1997).

The central part of Argentina (35-40° S 62-66° W) is occupied by semi-arid shrublands, where grasses and shrubs are the dominant life forms (Distel and Bóo 1996). During the first half of the XX century the region was grazed by sheep, and since then it has been grazed by cattle. Studies on the botanical composition of diets show that cattle feed on grasses and forbs only, except for the consumption of *Prosopis*' pods in summer and fall (Boo et al. 1993, Bontti et al. 1999). However, no information is available on the diets of other livestock species, particularly goats. If shrubs are important components of goat diets, then the implementation of a mixed species grazing (cattle and goat) may result in an increased potential carrying capacity of a landscape. The aim of the present study was to determine diet selection by goats on a semi-arid shrubland in central Argentina. We hypothesized that goats behave as mixed feeders (eat grasses and shrubs) in the studied ecosystem.

Materials and Methods

The study site is located in the southern part of the Caldenal rangelands in central Argentina (35-40° S, 62-66° W), which cover an area of approximately 4 000 000 ha. A general description of the region has been provided by INTA et al. (1980), and a more detailed description of the vegetation dynamics by Distel and Bóo (1996). The climate is temperate and semi-arid. Mean monthly temperatures ranges from a low of 7°C in July to a high of 24 °C in January, with an annual mean of 15 °C. Mean annual rainfall is 344 mm (105 mm in summer, 71 mm in fall, 59 mm in winter, and 109 mm in spring). During the study period the winter of 1995 was dry (40% of the average), the spring of 1995 was wet (135% of the average, although the beginning of the spring was dry), and the summer of 1996 was wet (125% of the average). The dominant soils are Calciustolls (Soil Survey Staff 1996). Soils are sandy in slopes, sandy-loam in uplands, and loamy in lowlands. The potential vegetation physiognomy is open woodland in lowlands, shrubland in slopes, and grasslands with isolated shrubs or trees in uplands (INTA et al. 1980). The most abundant woody species are *Prosopis caldenia*, *P. flexuosa*, *Larrea divaricata*, *Condalia microphylla*, and *Chuquiraga erinacea*. The herbaceous layer is dominated by the soft perennial bunchgrasses *Poa ligularis*, *Stipa clarazii*, *Piptochaetium napostaense*, and *S. tenuis*. However, at present the prevailing vegetation physiognomy is shrubland in all topographic positions, and coarse perennial bunchgrasses and annual forbs are frequently dominant species in the herbaceous layer. Coarse grasses are mainly represented by *S. tenuissima*, *S. gynerioides*, *S. trichotoma*, *S. speciosa*, *S. brachychaeta*, and *S. ambigua*; whereas forbs are mainly represented by the exotic species *Medicago minima* and *Erodium cicutarium*. The phenology of the main woody and herbaceous species has been described by Distel and Peláez (1985). *Prosopis* spp. are warm-season caducifolius species; *L. divaricata*, *C. microphylla*, and *C. erinacea* are evergreen species; whereas all dominant herbaceous are cool-season species.

Diet selection by goats was determined in a 2-ha pasture of an upland shrubland. Selection of the pasture was based on amounts and variety of the most common grasses and shrub species in the study site. Variety and abundance of the available forage allowed animals to express dietary preference. Moreover, the size of the pasture was minimized to precisely estimate food items availability. Ten adult, female, crossbred Angora - Spanish goats (experimental units), familiarized with the vegetation of the study site, were kept on the pasture from July 07 to July 14, 1995 (winter); from November 16 to November 23, 1995 (spring), and from February 9 to February 15, 1996 (summer). These periods account for all the phenological variations of the herbaceous and woody plants (Distel and Peláez 1985). In between periods of observation goats were kept outside the pasture, on an area with similar vegetation, in order to prevent overutilization of the pasture.

The average biomass per unit area (kg DM per ha) of each species in the pasture was estimated immediately before introducing the animals in each observation period. The biomass of shrub per unit area was estimated by measuring biomass per unit cover and cover per unit area. Biomass per unit cover was measured by harvesting the leaves and measuring the cover up to 1.65 m high of a quarter to half plant on 5 individuals of each species, whereas cover per unit area was measured through the line intercept technique (Bonham 1989) on 15 transects (20-m long) placed randomly on the pasture. Foliar biomass and cover up to 1.65 m high were considered because preliminary observations showed that goats consumed leaves only and up to this height. The herbaceous biomass per unit area was estimated by stratifying the pasture in patches of soft grasses, coarse grasses and *Baccharis ulicina* (lignified herb), harvesting the biomass on 20 plots (0.25 by 1 m) placed at random in each patch type, and pondering the estimated biomass by patch cover. Patch cover was visually estimated on 98 plots (204 m² each) that represented 100% of the pasture. Both shrub and herbaceous biomass were oven dried at 60 °C until constant weight.

During the last day of each period, all animals were observed every 5 min from 8:30 to 10:30 and from 15:00 to 17:00, and the botanical species that each animal was consuming was recorded (Altmann 1974). The order in which individuals were observed was established at random. A total of 480 observations (48 times x 10 goats) were taken in each data collection period. At the same time, 10 individual samples of fresh feces were collected for microhistological analyses (Spark and

Malechek 1968). Forty microscope fields were observed on each of five slides for each sample. Preliminary results showed that this sampling intensity allowed 10% ($p < 0.05$) precision in the estimation of the mean for individual species with more than 3.5% contribution to the total sample composition. Finally, the botanical composition of the diet was determined by the microhistological technique, complemented with data from direct observation. For example, the microhistological technique did not allow for the differentiation between *P. caldenia* and *P. flexuosa*. However, goats were never observed to feed on *P. flexuosa*. Therefore, it was assumed that the epidermis fragments observed through the microscope referred to *P. caldenia*.

The selectivity of goats for each species in the pasture was determined by calculating the Ivlev's selectivity index (SI) (Ivlev 1961):

$$SI = \frac{\% \text{ diet} - \% \text{ available in pasture}}{\% \text{ diet} + \% \text{ available in pasture}} \times 10$$

The SI varies from -10 (highly avoided species) to +10 (highly preferred species).

The significance of the difference in dietary contribution of grasses and shrubs in each season was determined by Paired t-test.

Results

Table 1 shows for each species the percentage in the pasture, the percentage in goat diet and the Ivlev's SI in winter, spring, and summer. Coarse grasses represented most (> 80 %) of total biomass on the pasture in all seasons; however, they were always highly avoided (SI=-10) by goats. *Baccharis ulicina*, an herbaceous species, was also highly avoided by goats in all seasons. On the contrary, soft grasses represented a low proportion (0.5% to 4%) of the biomass available, but they were always selected (SI > 0) by goats and contributed the most to their diet (except in summer). On the other hand, woody species represented 32%, 40%, and 74% of goat diets in winter, spring, and summer, respectively. However, there were only two species selected by goats: *P. caldenia*, which was highly selected in spring and summer, and *C. microphylla*, which was highly selected in winter and summer. The rest of the woody species were highly avoided by goats in all seasons. The difference between grasses and shrubs in goat diet was highly significant ($p < 0.01$) in all seasons (Table 2).

Discussion

The high quality of the soft grasses (Cairnie and Monesiglio 1967, Abiusso 1974, Magoja 1974, Lutz and Graff 1980) may explain why they were highly selected by goats throughout the year. However, their relatively higher quality and (or) quantity in winter and spring than in summer may explain why they contributed mostly to the diet of goats in the first two seasons. Species in this group are cool-season grasses (except for *Pappophorum* spp., a warm-season grass), which maintain high quality (low fiber, and high protein and digestibility) from the start of the growing season in fall up to the onset of stem elongation in spring (normally October). But the winter and the beginning of the spring of 1995 were so dry that grasses did not flower. This may contribute to explain the high representation of soft grasses in the diet of goats in middle spring (the spring data collection period was from November 16 to November 23, 1995), when they are in the reproductive stage and present low quality in years with normal precipitations. Moreover, in years with normal precipitation *M. minima* and *E. cicutarium* (annual forbs) are abundant in spring (Fresnillo Fedorenko 1991), and they may make an important contribution to goat diets under these

Table 1. Botanical composition of pasture, botanical composition of goat diets, and Ivlev 's Selectivity Index (SI), in winter, spring, and summer. Values are mean \pm 1 S.E.

Species	Winter 1995			Spring 1995			Summer 1996		
	% Pasture	% Diet	SI	% Pasture	% Diet	SI	% Pasture	% Diet	SI
Soft Grasses									
<i>Piptocarhetium napostaense</i>	2.9 \pm 0.33	38.5 \pm 1.47	9	0.3 \pm 0.04	38.4 \pm 2.54	10	0.2 \pm 0.02	16.2 \pm 1.51	10
<i>Poa sp.</i>	0.2 \pm 0.07	11.4 \pm 0.98	10	0.04 \pm 0.01	4.7 \pm 0.59	10	0.03 \pm 0.01	3.3 \pm 0.47	10
<i>Stipa tenuis</i>	0.7 \pm 0.16	9.7 \pm 0.82	9	0.1 \pm 0.02	6.7 \pm 0.69	10	0.1 \pm 0.01	1.5 \pm 0.25	9
<i>Pappophorum sp.</i>	0.1 \pm 0.06	0.03 \pm 0.03	-5	0.2 \pm 0.08	2.9 \pm 0.45	9	0.1 \pm 0.004	1.1 \pm 0.18	8
<i>Stipa clarazii</i>	0.3 \pm 0.28	1.1 \pm 0.43	6	0.3 \pm 0.08	0.9 \pm 0.27	5	0.07 \pm 0.04	0.1 \pm 0.13	2
Coarse Grasses									
<i>Stipa gynerioides</i>			-10	43.6 \pm 3.70		-10	38.9 \pm 6.93		-10
<i>Stipa tenuissima</i>			-10	11.0 \pm 1.55		-10	13.8 \pm 0.46		-10
<i>Stipa trichotoma</i>			-10	26.9 \pm 4.62		-10	29.4 \pm 3.79		-10
Unidentified grasses		7.7 \pm 0.60		6.7 \pm 0.69			3.7 \pm 0.38		
Subtotal grasses	85.4	68.4		82.5	60.3		82.6	25.9	
Lignified Herbs									
<i>Baccharis ulicina</i>	6.3 \pm 0.66		-10	6.1 \pm 0.98		-10	7.1 \pm 0.43		-10
Shrubs									
<i>Prosopis caldenia</i>				1.0 \pm 0.36	32.8 \pm 3.71	9	0.9 \pm 0.32	48.6 \pm 2.05	10
<i>Condalia microphylla</i>	2.2 \pm 0.68	22.4 \pm 2.62	8	2.5 \pm 0.77	0.9 \pm 0.24	-5	2.3 \pm 0.69	18.6 \pm 1.97	8
<i>Prosopis flexuosa</i>				1.0 \pm 0.32		-10	0.9 \pm 0.29		-10
<i>Larrea divaricata</i>	1.8 \pm 0.53		-10	2.0 \pm 0.59		-10	1.8 \pm 0.54		-10
<i>Prosopidastrum globosum</i>	0.7 \pm 0.12		-10	0.8 \pm 0.13		-10	0.7 \pm 0.12		-10
<i>Chuquiraga erinacea</i>	3.6 \pm 0.72		-10	4.1 \pm 0.81		-10	3.7 \pm 0.73		-10
Unidentified shrubs		9.2 \pm 0.49		6.0 \pm 0.62			6.9 \pm 0.62		
Subtotal shrubs	8.3	31.6		11.4	39.7		10.3	74.1	

Table 2. Within season comparison of dietary contribution of grasses and shrubs

Food item	Dietary contribution (%)		
	Winter 1995	Spring 1995	Summer 1996
Grasses	68.4	60.3	25.9
Shrubs	31.6	39.7	74.1
<i>P</i>	0.0002	0.0133	0.0000

conditions. Studies on diet selection have shown a significant consumption of forbs by goats when they are readily available (Bryant et al. 1979, Barroso et al. 1995). On the other hand, coarse grasses are characterized by low levels of protein and high levels of fiber and lignin (Moretto and Distel 1997). Also, the reduced grazing pressure on coarse grasses enables them to accumulate senescent biomass, which decomposes slowly and further reduces the plants' nutritional value to grazers (A.S. Moretto and R.A. Distel unpublished data). These factors may account for their high avoidance by goats, which present a relatively limited capacity for the digestion of cell wall (Hofmann 1988, 1989).

Woody species were always present in the diet of goats, although the highest contribution was in summer, when soft grasses were less available and low in quality. Like for grasses, goats showed a high selectivity for certain woody species, which was probably related to the level of antiherbivore defenses. Numerous evidence pointed out the importance of chemical (reviewed by Bryant et al. 1991) and physical (reviewed by Myers and Bazely 1991) defenses on herbivore preference for woody plants. Examples of antiherbivore defenses in the four species highly avoided by goats are a high level of phenolic resins in *L. divaricata* (Rhoades 1977), high level of total phenols in *P. flexuosa* (Pisani and Distel 1998), small and coriaceous leaves with apical spines in *C. erinacea*, and

leafless and spinescent stems in *Prosopidastrum globosum* (M.J. Pisani personal observation). On the other hand, although *P. caldenia* and *C. microphylla* are also spinescent and high in total phenols (Pisani and Distel 1998), they were highly selected by goats. However, the same class of secondary compound can differ in biological activity (Zucker 1983), and species may also differ in the class of secondary compound (e.g., phenols, terpenoids, alkaloids), which may account for the observed pattern of selectivity.

Previous studies (B6o et al. 1993, Bontti et al. 1999) showed that the diet of cattle (predominant domestic livestock in the region) is mainly composed by grasses and forbs on semi-arid shrublands in central Argentina. The only consumption of woody species is represented by the pods of *Prosopis* spp in late summer and fall. On the other hand, our results showed that woody plants can represent an important part of the diet of goats in the same ecosystem. Together, these results suggest that a mixed species grazing (cattle and goat) may result in an increased potential carrying capacity. Moreover, since goats can destroy small trees and saplings by browsing and debarking them (Wood 1987), they may represent an opportunity for the biological control of woody plants encroachment in central Argentina rangelands. Testing of these hypotheses will require diet selection measurements replicated in space and time.

Acknowledgements. This research was supported by the Universidad Nacional del Sur, the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) de la República Argentina, and the Agencia Nacional de Promoción Científica y Tecnológica (ANPCyT) de la República Argentina. A fellowship from CONICET to J.M. Pisani is also acknowledged.

References

- Altmann, J. 1974. Observational study of behavior: sampling methods. *Behavior* 49:227-267.
- Abiusso, N.G. 1974. Niveles proteicos y valores de digestibilidad (DIVMS) de tres gramíneas invernales nativas de La Pampa. *Rev. Inv. Agrop.* 12:1-10.
- Barroso, F.G., C.L. Alados and J. Boza. 1995. Food selection by domestic goats in Mediterranean arid shrublands. *J. Arid Environm.* 31:205-217.
- Belovski, G.E., O.J. Schmitz, J.B. Slade and T.J. Dawson. 1991. Effects of spines and thorns on Australian arid zone herbivores of different body masses. *Oecologia* 88:521-528.
- Bonham, C.D. 1989. *Measurements for Terrestrial Vegetation*. John Wiley and Sons, New York. 338 pp.
- Bontti, E.E., R.M. B6o, L.I. Lindstr6m and O.R. Elía. 1999. Botanical composition of cattle and vizcacha diets in central Argentina. *J. Range Manage.* 52:370-377.
- B6o, R.M., L.I. Lindstr6m, O.R. Elia and M.D. Mayor. 1993. Botanical composition and seasonal trends of cattle diets in central Argentina. *J. Range Manage.* 46:479-482.
- Bryant, F.C., M.M. Kothmann and L.B. Merrill. 1979. Diet of sheep, Angora goats and white-tailed deer under excellent range conditions. *J. Range Manage.* 32:412-417.
- Bryant, J.P., F.D. Provenza, J. Pastor, P.B. Reichardt, T.P. Clausen and J.T. Du Toit. 1991. Interactions between woody plants and browsing mammals mediated by secondary metabolites. *Ann. Rev. Ecol. Syst.* 22:431-446.
- Cairnie, A.G. and J.C. Monesigho. 1967. Composición química de especies forrajeras nativas e introducidas en la región semiárida pampeana. *Rev. Inv. Agrop.* 4:207-221.
- Cheeke, P.R. 1994. A review of the functional and evolutionary roles of the liver in the detoxification of poisonous plants, with special reference to Pyrrolizidine Alkaloids. *Vet. Human Toxicol.* 36:240-247.
- Cheeke, P.R. and R.T. Palo. 1995. Plant toxins and mammalian herbivores: co-evolutionary relationships and antinutritional effects. Pp. 437-456. In: Journet, M., E. Grenet, M.H. Farce, M. Th6riez and C. Demarquilly (eds.). *Recent Developments in the Nutrition of Herbivores*. INRA Editions, Paris, France.
- Cooper, M. and N. Owen-Smith. 1986. Effects of plant spinescence on large mammalian herbivores. *Oecologia* 68:446-455.
- Distel, R.A. and D.V. Pel6ez. 1985. Fenología de algunas especies del Distrito del Cald6n (*Prosopis caldenia* Burk.). *IDIA Sept. -Dic.*:35-40.
- Distel, R.A. and F.D. Provenza. 1991. Experience early in life affects voluntary intake of blackbrush by goats. *J. Chem. Ecol.* 17:431-450.

- Distel, R.A. and R.M. Boo. 1996. Vegetation states and transitions in temperate semi-arid rangelands of Argentina. Pp. 117-118. In: West, N. (ed.). Rangelands in a Sustainable Biosphere. Society for Range Management, Denver, USA.
- Fraser, M.D. and I.J. Gordon. 1997. The diet of goats, red deer and South American camelids feeding on three contrasting Scottish upland vegetation communities. *J. Appl. Ecol.* 34:668-686.
- Freeland, W.J. and D.H. Janzen. 1974. Strategies in herbivory by mammals: The role of plant secondary compounds. *Am. Nat.* 108:269-289.
- Fresnillo Fedorenko, D.E. 1991. Estrategias ecológicas de *Medicago minima* (L.) Grufb. var. mínima y *Erodium cicutarium* (L) L'Herit., dos anuales de valor forrajero en el Caldenal. Tesis de Magíster en Producción Vegetal. Universidad Nacional del Sur, Bahía Blanca, Argentina.
- Granwaldt, E.G., A.R. Pedrani and A.I. Vich. 1994. Goat grazing in the arid piedmont of Argentina. *Small Rumin. Res.* 13:211-216.
- Hofmann, R.R. 1988. Anatomy of the gastro-intestinal tract. Pp. 14-43. In: Church, D.C. (ed.). The Ruminant Animal. Prentice Hall, Englewood Cliffs.
- Hofmann, R.R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. *Oecologia* 78:443-457.
- Instituto Nacional de Tecnología Agropecuaria, Provincia de La Pampa y Universidad Nacional de La Pampa. 1980. Inventario Integrado de los Recursos Naturales de la Provincia de La Pampa. INTA, Buenos Aires, Argentina. 493 pp.
- Ivlev, V.S. 1961. Experimental Ecology of the Feeding of Fishes. Yale Univ. Press, New Haven, USA.
- Lutz, E.E. and A.B. Graff. 1980. Efecto de la quema controlada sobre la pastura natural, en un monte de la region semiárida pampeana. *Rev. Inv. Agrop.* 15:1-15.
- Magoja, J.L. 1974. La composición mineral y su variación estacional en tres forrajeras nativas de La Pampa: *Stipa tenuis* Phil., *Poa ligularis* Nees ex Steudel y *Piptochaetium napostaense* (Speg.) Hacker Ap. Stuckert. *Rev. Inv. Agrop.* 12:27-47.
- McArthur, C., A.E. Hagerman and C.T. Robbins. 1991. Physiological strategies of mammalian herbivores against plant defenses. Pp. 103-114. In: Palo, R.T. and C.T. Robbins (eds.). Plant Defenses Against Mammalian Herbivory. CRC Press. Boca Raton, USA.
- Moreno, A.S. and R.A. Distel. 1997. Competitive interactions between palatable and unpalatable grasses native to a temperate semi-arid grassland of Argentina. *Plant Ecol.* 130:155-161.
- Myers, J.H. and D. Bazely. 1991. Thorns, spines, prickles, and hairs: Are they stimulated by herbivory and do they deter herbivores? Pp. 325-344. In: Tallamy, D.W. and M.J. Raupp (eds.). Phytochemical Induction by Herbivores. John Wiley and Sons, New York, USA.
- Pisani, J.M. and R.A. Distel. 1998. Inter- and intraspecific variation in production of spines and phenols in *Prosopis caldenia* and *Prosopis flexuosa*. *J. Chem. Ecol.* 24:23-36.
- Ricardi, C. and A. Shimada. 1992. A note on diet selection by goats on a semi-arid temperate rangeland throughout the year. *Appl. Anim. Behav. Sci.* 33:239-247.
- Richman, L.M. and D.E. Johnson. 1995. Diet selection by goats in the sagebrush steppe of eastern Oregon. *Small Rumin. Res.* 18:7-17.
- Riggs, R.A., P.J. Urness and T.A. Hall. 1988. Diets and weight responses of Spanish goats used to control Gambel Oak. *Small Rumin. Res.* 1:259-271.
- Rhoades, D.F. 1977. The antiherbivore chemistry of *Larrea*. Pp. 135-175. In: Mabry, T.J., J.H. Hunziker and D.R. Difeo (eds.). Creosote bush. Dowden, Hutchinson and Ross, Stroudsburg, USA.
- Silanikove, N., N. Gilboa, A. Perevolotski and Z. Nitsan. 1996. Goat fed tannin-containing leaves do not exhibit toxic syndromes. *Small Rumin. Res.* 21:195-201.
- Soil Survey Staff. 1996. Keys to Soil Taxonomy, 7th edition. USDA Natural Resource Conservation Service, Washington, D.C., USA.
- Sparks, D.R. and J.C. Malecheck. 1968. Estimating percentage dry weight in diets using a microscopic technique. *J. Range Manage.* 21:264-265.
- Wood, G.M. 1987. Animals for biological brush control. *Agron. J.* 79:319-321.
- Zucker, W.V. 1983. Tannins: does structure determine function? An ecological perspective. *Am. Nat.* 121:335-365.

Received: Agosto 1, 2000

Accepted: Septiembre 18, 2000