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Ecological and reproductive constraints of body size in the gigantic *Argentavis magnificens* (Aves, Theratornithidae) from the Miocene of Argentina

Paul PALMQVIST[1] and Sergio F. VIZCAÍNO[2]

Abstract. Several estimates of ecological and reproductive parameters are offered for the giant *Argentavis magnificens* (Teratornithidae), from upper Miocene localities in Argentina. Using the allometric relationship between home range and body mass observed in modern birds of prey, the home range of this extinct raptor is estimated in 542 km^2. This implies that an adult individual soaring at an altitude of 120 m would travel around 2,168 km searching for its prey, a task that needs nearly three days flying 12 hours per day at 68 km/h. Such estimate suggests it behaved as vultures rather than eagles. The amount of meat ingested daily by an adult individual is estimated in 5-10 kg. Clutch size is predicted in 0.78 eggs per year for a bird this large, with an estimate for egg mass above 1000 g, suggesting one hatchling every two years. The scaling of incubation, nestling and post-fledging periods in modern raptors provide for *A. magnificens* figures of 64, 230 and 190 days, respectively; the estimate of the time needed for acquiring adult plumage is 12.6 years. Annual mortality rate of this species was probably less than 2%. All these figures provide an emerging picture about *A. magnificens* as a scavenger with a very low population density and a strikingly slow turnover rate, whose individuals had very high metabolic requirements, thus needing to scan a large home range searching for food, and invested too much energy cost and time in reproduction.

Resumen. TAMAÑO CORPORAL Y LIMITACIONES ECOLÓGICAS Y REPRODUCTIVAS DE *ARGENTAVIS MAGNIFICENS* (AVES, TERATORNITHIDAE) DEL MIOCENO DE ARGENTINA. Se realizan estimaciones de parámetros ecológicos y reproductivos de *Argentavis magnificens* (Teratornithidae), del Mioceno superior de Argentina. Usando relaciones alométricas en aves modernas, se estimó el tamaño del territorio en 542 km^2. Esto implica que un individuo solitario planeando a una altitud de 120 m debería recorrer 2168 km para encontrar una presa, lo que le demandaría aproximadamente 3 días volando a 68 km/h. Tales valores sugieren un comportamiento más similar al de los buitres que al de las águilas modernas. Se estima en 5 a 10 kg la cantidad de carne ingerida diariamente por un adulto. El tamaño de la puesta se infiere en 0,78 huevos por año, la masa de cada huevo en 1000 g y la frecuencia de puesta cada dos años. Los tiempos de incubación, anidamiento y crianza se estiman en 64, 230 y 190 días, respectivamente, y el período necesario para adquirir el plumaje adulto en 12,6 años. La tasa de mortalidad fue probablemente inferior al 2%. La consideración de estos valores en conjunto sugiere que *A. magnificens* fue un ave carroñera, con una baja densidad poblacional, una remarcablemente baja tasa de renovación y unos requerimientos metabólicos muy altos, por lo que necesitaba prospectar un territorio bastante amplio en busca de su alimento, invirtiendo un alto costo energético y tiempo en la reproducción.

Key words. Palaeoecology. Body size. Aves. Teratornithidae. *Argentavis magnificens.* Miocene. Argentina.

Palabras clave. Paleoecología. Tamaño corporal. Aves. Teratornithidae. *Argentavis magnificens*. Mioceno. Argentina.

Introduction

In an article recently published, Vizcaíno and Fariña (1999) reanalyse the fossil evidence available of the giant bird *Argentavis magnificens* Campbell and Tonni (Aves: Ciconiiformes: Teratornithidae), known from three Upper Miocene localities in central and northwestern Argentina. Although there is some variability in the estimates of body mass offered for *A. magnificens*, with a range of values comprised between 65 and 120 kg (Campbell and Tonni, 1980, 1981, 1983; Campbell and Marcus, 1992; Campbell, 1995; Vizcaíno and Fariña, 1999), most authors agree that the mean size of this species would have been around 80 kg, with a wingspan of 6.5-7.0 m (the largest extant volant birds range in mass 8-14 kg, with wingspans of 3.0-3.5 m). Given that *A. magnificens* was the world's largest known flying bird, with a body mass at least five times heavier than that of the related California condor, *Gymnogyps californi-*

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[1] Departamento de Ecología y Geología (Área de Paleontología), Facultad de Ciencias, Universidad de Málaga. Campus Universitario de Teatinos. 29071 Málaga, Spain.
Paul.Palmqvist@uma.es

[2] Departamento Científico Paleontología de Vertebrados, Museo de La Plata, Paseo del Bosque s/n, 1900 La Plata, Argentina (CONICET).
vizcaino@museo.fcnym.unlp.edu.ar

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anus (Shaw), which is the largest New World vulture, Vizcaíno and Fariña (1999) concentrate on the flight capabilities and palaeogeographic distribution of this extinct bird.

According to the calculations of Vizcaíno and Fariña (1999), *A. magnificens* had to reach a speed of 40 km / h to take off. Campbell and Tonni (1983) have argued that the anatomical features of the pelvis and the hindlimb of teratorns, including *A. magnificens*, indicate that they probably were not good runners. However, given that the critical speed to take off is wing speed relative to the air, it could be attained by running against the wind, as many large extant birds do. Vizcaíno and Fariña (1999) also suggested that the pampas were only part of a wide home range or territory of *A. magnificens* that included areas with mountain ranges to nest and were taking off would have been much easier. The wing shape was inferred as more similar to that of large extant birds that soar relatively slowly on thermals over land than to that of large pelagic birds that soar over water (Campbell and Tonni, 1983; Vizcaíno and Fariña, 1999). This high wing loading would have allowed it to fly in moderate to strong winds that must have been prohibitive for the largest known contemporary thermal soarers. The high wing loading would have been ill suited to flight under poor thermal conditions, but it would have been useful in slope soaring on uprising air current against hillsides. Vizcaíno and Fariña (1999) also showed that flapping flight was not impossible for the wing muscles of such a 80-kg bird, not especially for long term flights but to be used in short bursts during take off and landing, as well as for sudden manoeuvres in the air.

Apart from biomechanical constraints on flapping / soaring flight in a bird this large, which are discussed in depth by Alexander (1992, 1998), Pennycuick (1996), Rayner (1996) and Vizcaíno and Fariña (1999), body size must have also involved severe limitations in the ecology and reproductive behaviour of *A. magnificens*. A huge amount of empirical evidence has been collected during the last decades indicating that body size is closely related to the autecology and function of organisms, including many aspects of their physiology, metabolism, growth and behaviour, plus a plethora of related phenomena in their life histories, evolution, and several synecological properties, such as population density, community size structure and predator-prey relationships (Peters, 1983; Calder, 1984; Damuth, 1981, 1982, 1987, 1991; Palmqvist *et al.*, 1996a). Due to these reasons, body size is probably the best predictive tool for unravelling many issues related to the palaeoautecology of an extinct species like *A. magnificens*, such as its home range, daily food requirements and annual mortality, as well as several breeding parameters, including clutch size, egg size, incubation, nestling and fledging periods, and time required for acquiring adult plumage.

Territory size and feeding in *Argentavis*

Birds of prey hold home ranges whose surface is adjusted for providing them their feeding requirements, which is largely determined by prey availability. A part of this home range, from several hundred meters to a few kilometers around the nest, is used as the territory, and most birds of prey defend them against their own kind (Newton, 1979). Data compiled for extant birds of prey by Palmqvist *et al.* (1996a) from different sources in Cramp and Simmons (1980) showed that territory size (T, in km^2) is interspecifically related in Falconiformes to mean adult body mass (M, in g) by the 0.787 power (Table 1); according to the standard error of the slope, the latter value does not differ significantly from 0.75. Given that territory size is the reciprocal of optimal population density (i.e., number of pairs per km^2), this relationship is then very close to the one expected according to Damuth's rule, which predicts that population density is allometrically related to body size by the power -0.75 (Damuth, 1981, 1987).

Using the equation shown in Table 1, adjusted for modern hawks and eagles, an estimate of 542 km^2 is obtained for the size of the territory held by *A. magnificens* (i.e. approximately 23 x 23 km). Although some caution must be observed with this estimate, obtained by extrapolations, because teratornithids belong to the order Ciconiiformes and the data used in the analysis are derived from species of a different avian order, such figure is clearly very large, since it implies that an adult individual could not easily roam daily a territory this large in search of its prey: the widest territory recorded in a living bird of prey is that of the golden eagle, *Aquila chrysaetos* (Linnaeus) (mean adult body mass of 4.3 kg), in xeric localities of southern Spain, with occasional estimates in excess of 250 km^2 (Cramp and Simmons, 1980), although the average territory size of this species is 61 km^2 (Palmqvist *et al.*, 1996a).

The largest eagles, whose visual acuity is equivalent to that of a person equipped with a 8x binoculars, fly searching for their prey at heights comprised between 60 and 120 m, while raptors of smaller size usually fly at lower altitudes, typically 20-60 m (Cramp and Simmons, 1980). Soaring at 120 m above the ground *A. magnificens* could scan a maximum land strip of around 250 m, which implies that it would require four passings to cover each km^2 of the territory, thus needing to fly a distance of approximately 2,168 km per day for scanning the whole surface of its territory. The soaring velocity of the largest modern raptors is 30 to 50 km per hour. Such speed is maintained with minimum power requirements, and is allometrically scaled to body mass by the 0.15 power (Peters, 1983). Given that a 10 kg vulture reaches an optimal velocity of 50 km / h, this implies that *A. magnificens* could soar at around 68 km / h, thus needing approximately 32 hours for the task of searching the whole surface of its territory (*i.e.*, nearly three days for travelling a foraging distance of more than two thousand kilometers, considering 12 hours per day devoted to soaring flight, which is the maximum period observed in modern raptors). On the other hand, the energy expenditure of *A. magnificens* would have been greater than that of the largest living birds of prey, since transport costs rise with body mass (Peters, 1983). Therefore, the strikingly large estimate obtained for the territory size that should be hold by a bird of prey this large allows to discard the possibility that the predatory behaviour of *A. magnificens* was similar to that of modern eagles, which catch and consume their own prey whole, as it has been proposed previously (Campbell and Tonni, 1981).

The speed mentioned above is the air speed, but this can be greatly affected by the wind, changing the final time to cover some distance on the ground. Campbell and Tonni (1983) argued that the constant westerlies blowing over that part of South America during the Miocene would have been important for *A. magnificens* to take off. With the available data, the influence of wind on the final time to scan an area can be estimated in the way an aircraft pilot can do it using the following equation:

$$V_g = V_a.\cos\{\mathrm{asin}[V_w / V_a.\sin(2.\pi.A_w / 360)]\} + V_w.\cos(A_w / 360)$$

in which V_g is the ground speed, V_a is the air speed, V_w is the wind speed, and A_w is the wind angle.

We have recalculated the time to cover an squared territory, assuming a wind speed of 40 km / h blowing constantly from different angles in relation to the flight direction. This speed, the minimum speed needed to generate lift, is normal for Southern Patagonia today, an environment comparable to that proposed by Campbell and Tonni (1983) as the habitat of *A. magnificens*. The figures obtained range from 38 h 35 min 8.5 s (i.e. 3 days and 2 h 30 min 20.5 s) when the wind blows completely laterally (90º) to 46 h 37 min 26 s (i.e. 3 days and 10 h 35 min 2 s) with the wind blowing in the direction of flight most of the time (i.e directly from the back in one way and from the front in the other). That implies that it would be strategically more convenient to fly most of the time on a South-North than on an East-West axis. In this way the animal would save almost one day of work to cover the same area.

It is worthwhile to address that these are still conservative hypotheses. In our analysis we have assumed that the animal flew indefinitely at the same level and did not loose time gaining height soaring in circles in ascending warm air columns (i.e. thermals). We reckon that this is not true, but we cannot know the speed of the rising air within the thermal, how frequent they were, and other aerodynamic features of *A. magnificens* needed to make this calculations. Hence, the overall time needed to go over the whole territory searching for preys must have been close to (or even in excess of) four days.

The relationship between the amount of meat ingested daily by captive raptors (which is an indicator of their basal metabolic requirements; data from Kendeigh, 1970; Kirkwood, 1981) and body mass is allometric and positive, with a value of 0.721 for the exponent (i.e., close to 0.75, as predicted by Kleiber's law for metabolic requirements and size; Kleiber, 1932, 1975). After the equation provided in Table 1, a bird the size of *A. magnificens* would have needed 2,404 g of meat per day to survive. Given that the basal metabolic requirements are ca. 25-50% of the daily field expenditure (Peters, 1983), this estimate implies that an adult individual must have consumed around 5-10 kg of meat per day; such quantity would have even increased substantially during the breeding season, because estimates for Rüppell's vultures (Houston, 1976) indicate that food requirements rise up to three times during the breeding season. Despite this important constraint on the palaeobiology of *A. magnificens*, there are however important metabolic advantages derived of the large body size reached by this bird of prey: given that mass-specific metabolic rates decline as the inverse of the fourth root of body mass (Damuth, 1981, 1987; Peters 1983), this raptor presumably could survive much longer on its energy stores than could smaller ones, thus taking longer to starve. In addition, it would have been less adversely affected by low temperatures in metabolic-cost terms, its body temperature probably changed more slowly than that of smaller species experiencing the same thermal gradient, and a given energy supply would have supported a much greater biomass of *A. magnificens* than of smaller raptors.

Breeding behaviour of *Argentavis*

There are three main trends in the breeding behaviour of birds of prey related to body size (Newton, 1979): the larger the species, the later the age at which breeding begins, the longer each successful attempt takes, and the fewer young produced with each attempt. As a result, large, long-lived species have relatively small eggs in relation to body size, single-egg clutches, protracted breeding cycles, and deferred maturity. Such trends reflect the greater advantage that large species gain from reducing the risk and energy expended in any one breeding attempt in the interests of improved survival for future attempts, and a generally greater difficulty that large species have in obtaining food and/or in digesting and processing it, because metabolic rate slows with increase in body size. All these limitations must have posed several constraints on the reproductive behaviour of *A. magnificens*.

Usual clutch size (*N*, in number of eggs per year) is allometrically related to body mass in raptors by the power -0.273 (Table 1), which provides for *A. magnificens* an estimate of 0.78 clutched eggs per year, a figure suggesting one (or occasionally two) hatchling every two years. Egg mass is scaled to female weight in modern birds of prey by the 0.662 exponent, thus predicting a figure slightly larger than 1000 g in the case of *A. magnificens*. The mass of each individual egg, expressed as a percentage of female weight, is negatively correlated to body size of adults by the power -0.332, which gives an estimate of only 1.36% for *A. magnificens*. Incubation and nestling periods are positively related to body mass by the 0.137 and 0.354 powers, which provide estimates of 64 and 230 days, respectively; post-fledging period of chicks is scaled to female size by the exponent 0.370, indicating 190 days for a bird as large as *A. magnificens*. Finally, the estimate of the time needed for acquiring adult plumage, which is related in extant raptors to body mass by the 0.360 power, is 12.6 years. These figures suggest that the adults elapsed 484 days (i.e. approximately 16 months) between laying the eggs and emancipation of the young, which probably implies that the egg was incubated during the winter season and blooming happened in spring, being the chick nourished in the nest until mid autumn. Such a prolonged reproductive season indicates clearly that breeding took place every two years, in agreement with the low estimate obtained for clutch size.

Death is caused in modern birds of prey by starvation, diseases, parasites, predation (mostly by other raptors or owls) or accidents. Annual mortality rates scale allometrically with adult body mass by the -0.565 power (Table 1), which gives an estimate of only 1.91% for a bird as large as *A. magnificens*.

Discussion

Our data suggest that *A. magnificens* was a bird of prey with both low population density and mortality turnover rate, whose individuals had very high feeding requirements and thus required a strikingly large territory, investing too much energy cost and time in reproduction.

Larger animals tend to have fewer individuals in each species, which represents a risk for the long term viability of their populations (Alexander, 1998). As indicated above, larger extant raptors have long breeding cycles and small clutches, due to three reasons (Newton, 1979): (i) large, long-lived species gain comparatively less by investing heavily in any one

Table 1. Least squares allometric curves describing the relationship between adult body mass (M, in g) and several ecological/breeding parameters (Y) measured in extant raptors ($Y = aM^b$)[1]. / *Curvas alométricas por mínimos cuadrados que describen la relación entre la masa corporal de los ejemplares adultos (M, en g) y diversos parámetros ecológicos y reproductivos (Y) estimados en aves de presa actuales ($Y = aM^b$)[1].*

Parameter (Y)	log(a) (±s.e.)	b (±s.e.)	s.e.e.	r	F	p	N	Prediction for *Argentavis* ($p < 0.05$ interval)
territory size (km^2)	-2.590 (+0.929)	0.787 (+0.133)	0.616	0.820	34.9	<0.001	19	542 (162, 1812)
meat ingested daily (g)	-0.359 (+0.072)	0.721 (+0.230)	0.282	0.931	304.4	<0.001	48	2,404 (1,917, 3,287)
usual clutch size (N)	2.839 (+0.254)	-0.273 (+0.037)	0.335	0.678	55.4	<0.001	67	0.78 (0.41, 1.51)
egg mass(g)	-0.515 (+0.113)	0.662 (+0.016)	0.149	0.981	1659.0	<0.001	67	1,052 (786, 1,409)
Egg mass as % of female mass	4.058 (+0.115)	-0.332 (+0.017)	0.151	0.928	402.2	<0.001	67	1.36 (1.01, 1.83)
Incubation period (days)	2.619 (+0.084)	0.137 (+0.012)	0.104	0.826	131.0	<0.001	63	64.4 (55.5, 79.0)
Nestling period (days)	1.442 (+0.149)	0.354 (+0.021)	0.186	0.904	273.0	<0.001	63	230.1 (164.6, 331.3)
post-fledging period (days)	1.070 (+0.396)	0.370 (+0.058)	0.407	0.707	41.0	<0.001	43	190.0 (85.6, 422.0)
Adult plumage (years)	-1.528 (+0.242)	0.360 (+0.035)	0.292	0.821	107.5	<0.001	54	12.6 (9.4, 16.9)
annual adult mortality (%)	7.024 (+0.617)	-0.565 (+0.093)	0.295	0.870	32.3	<0.001	14	1.91 (1.42, 2.56)

[1] Data obtained from Kendeigh (1970), Newton (1979), Cramp and Simmons (1980), Kirkwood (1981) and Palmqvist *et al.* (1996b). The equation for territory size was obtained with data from predator species; vultures and insectivores were excluded, because these species show comparatively smaller territories than those of birds of prey of similar size (Palmqvist *et al.*, 1996a). Abbreviations: log(a): Y-intercept, b: slope, s.e.e.: standard error of estimate, r: Pearson correlation coefficient, F: F-test, p: probability, N: number of cases.

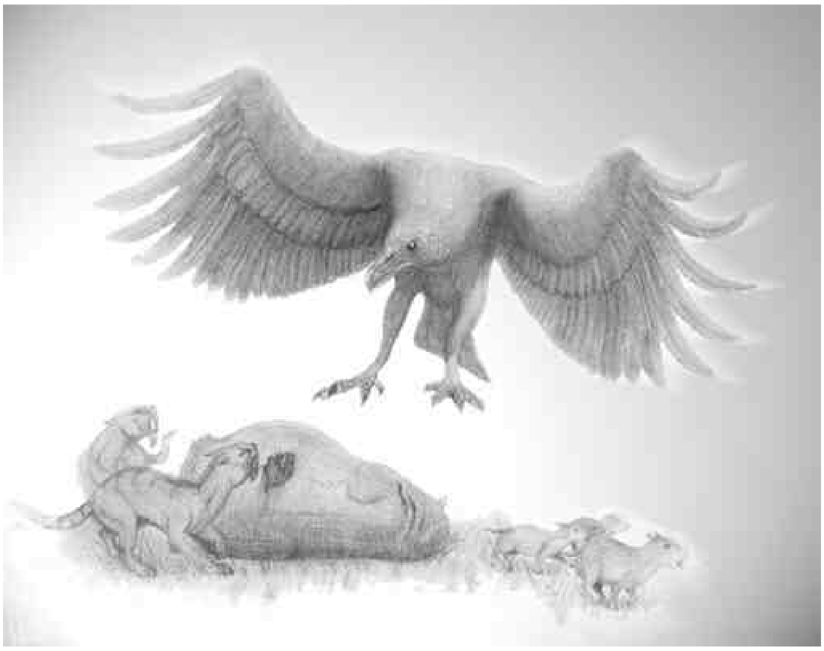

Figura 1. Reconstruction of kleptoparasitism (i.e. aggressive scavenging) by the giant bird *Argentavis magnificens* on the prey (a large ungulate carcass) of thylacosmilid sabre-tooths. Although modern vultures do not steal the prey from large carnivores, *A. magnificens* might have used its large size for intimidating these marsupial predators and taking their food, as often do spotted hyaenas (*Crocuta crocuta* Kaup) with the prey of wild dogs (*Lycaon pictus* Brookes). Given the high energetic cost of hunting (twenty-five times the basal metabolic rate for wild dogs; Gorman *et al.*, 1998), the loss of prey to kleptoparasites would have had a large impact on the amount of time that thylacosmilids devoted to hunting activities in order to achieve their energy balance. Drawn by Néstor Toledo. / *Reconstrucción del comportamiento cleptoparásito (carroñeo agresivo) del ave gigante* Argentavis magnificens *sobre las presas (cadáveres de grandes ungulados) de los tilacosmílidos con dientes de sable. Aunque los buitres modernos no roban las presas de los grandes carnívoros,* A. magnificens *pudo haber usado su gran tamaño para intimidar a estos predadores marsupiales y tomar su comida, como suelen hacer las hienas manchadas* (Crocuta crocuta *Kaup) con las presas de los perros salvajes (*Lycaon pictus *Brookes). Dado el alto costo energético de la caza (unas veinticinco veces la tasa metabólica basal en los perros salvajes; Gorman et al., 1998), la pérdida de las presas robadas por los cleptoparásitos pudo tener un gran impacto sobre la cantidad de tiempo que los tilacosmílidos dedicarían a las actividades de caza con vistas a satisfacer su balance energético. Dibujo de Néstor Toledo.*

breeding attempt, and natural selection favours a low reproductive effort in any one season in the interests of better chances to breed in several future seasons, which also favours deferment of maturity, giving time for useful experience to be gained; (ii) the metabolic rate in birds slows with increase in body size, and so the lower breeding rates of the largest raptors are due partly to their slower metabolism, a given amount of food taking longer to digest and convert to egg or body tissue, which accounts for the relatively smaller eggs, longer laying intervals, and longer growth periods of the larger species; and, finally, (iii) large size confers not only a longer potential lifespan, but also a greater immunity from predation and an increased ability to survive temporary food shortages. Hence, other things being equal, the larger the bird, the more consistently is its population likely to remain close to the level that the environment will support (i.e. the carrying capacity of the ecosystem); under these conditions, reproduction generally will be difficult, and vacancies in the breeding population will be few at any given time. For large species, then, selection pressure will favour the production of well-nurtured juveniles released from prolonged parental care with the greatest chance of competing successfully with others of their species (i.e. *k*-selection). Due to these reasons, population turnover is generally low in large species, with more overlap between generations and a more stable age structure, all of which tend to dampen fluctuations in numbers. There are also trends to be a relatively large non-breeding population, consisting mainly or entirely of immatures, and less than half the total population breeds in any one year, producing only a small number of young. All these trends seem to have been carried to an extreme in *A. magnificens.*

In certain large condors and tropical eagles, each breeding cycle lasts more than one year, and successful pairs breed no more than once in two years. These raptors resemble in their population dynamics certain seabirds with small clutches, long breeding cycles, and deferred maturity. In both groups, single-egg clutches are frequent and, when two eggs are laid, often only one young is raised. Long post-fledging periods, in which the juveniles are fed near the nest, occur in some tropical seabirds; moreover, the only other flying birds whose complete breeding cycles are known to last more than one year are some albatrosses and frigate birds, with periods of up to ten years to reach maturity. This evidence offers reliability for the figures presented above concerning the breeding parameters of *A. magnificens*.

The estimates of territory size and metabolic requirements of *A. magnificens* are more realistic if we envisage it as a scavenger rather than as a predator. It is difficult to obtain reliable estimates of territory sizes in vultures, since many species show gregarious behaviour, loosely colonial nesting, and use communal home ranges, usually with no evidence of restricted feeding areas used; all this implies that no obvious territory is held (and defended) in most cases. New World vultures and condors usually nest in cliffs well apart from one another, but all they roost communally and feed in groups. However, data on population densities and the scarce evidence available for those species which maintain individual home ranges (Cramp and Simmons, 1980), such as the lapped-facet vulture (*Torgos tracheliotus* Forster; mass of adults around 7 kg, territory size of 43 km^2) and the Egyptian vulture (*Neophron percnopterus* Linnaeus; 2 kg, 12 km^2), indicate that vultures hold, on average, a territory size two or three times smaller than that of an eagle of the same size (Palmqvist *et al.*, 1996a). This provides an estimate of approximately 180-260 km^2 for a bird the size of *A. magnificens*, a figure that can be considered more realistic than the previous one, as it is actually covered by modern birds of prey. On the other hand, vultures often fly at larger altitudes than eagles when searching for food, typically at 100-200 m in the case of griffon vultures (*Gyps fulvus* Hablizl), but up to some thousand metres in other species (Cramp and Simmons, 1980). Vultures can see objects 4-8 cm diameter from heights of 1000 m. Although they are usually attracted to carcasses by sight, most vultures often watch the movements of other neighbouring birds on ground or in air, which facilitates the search for food at higher altitudes, thus allowing them to scan a wider surface than that of eagles and travelling their territory in a shorter time.

There is a potential candidate for supplying large enough food as that required by a 80 kg vulture during late Miocene times in Argentina. Palmqvist *et al.* (1996b), Arribas and Palmqvist (1999) and Palmqvist and Arribas (2001) have proposed for a fossil fauna in the Old World (the lower Pleistocene assemblage of large mammals from Venta Micena, Orce, Spain) a similar ecological relationship between the sabre-toothed felids *Homotherium latidens* (Owen) and *Megantereon whitei* (Broom), and the giant, strictly scavenging hyaena *Pachycrocuta brevirostris* (Aymard). Indeed, in the Miocene South American fauna to which *A. magnificens* belonged, the marsupial sabre-tooth *Achlysictis lelongii* Ameghino (Borhyaenoidea, Thylacosmilidae) is found. This top predator reached approximately the body size of a modern puma, *Puma concolor* (Linnaeus), showing a highly specialised craniodental design, similar to that of the most advanced machairodontines (e.g. *Smilodon* and *Megantereon*) and nimravines (e.g. *Barbourofelis*), which includes: (i) a well developed, curved backwards symphyseal region in the mandible, which protected the extremely elongated upper canines from lateral bending; (ii) a lowered glenoid fossa, a reduced height of the coronoid process, a laterally shifted angular process, and a shortened zygomatic arch, features which allow a wide gape; and (iii) a lowered and ventrally extended mastoid process, which is enormous relative to modern felids, thus indicating that the neck muscles were correspondingly large, which suggests that a head-depressing motion was involved in the penetration of the canines inside the body of the prey.

Sabre-toothed predators were able to hunt very large prey relative to their own size, and they left on the carcasses of the ungulates hunted large amounts of flesh and all nutrients within bone, which could be subsequently scavenged by other carnivores (Arribas and Palmqvist, 1999; Palmqvist *et al.*, 2003). Therefore, those marsupial predators were also likely to have left only partially eaten carcasses of large herbivores, as the notoungulate *Pisanodon nazari* (Cabrera and Kraglievich), the litoptern *Promacrauchenia* sp., the ground sloths *Plesiomegatherium* sp. and *Elassotherium altirostre* Cabrera, and even the glyptodonts *Aspidocalyptus castroi* Cabrera, *Hoplophractus tapinocephalus* Cabrera, *Coscinocercus marcalaini* Cabrera, *Coscinocercus brachyurus* Cabrera and *Plohophorus araucanus* Ameghino. Given the extremely slicing condition of thylacosmilid teeth, the carcasses of such prey must have provided rather huge amounts of flesh and intact, marrow-rich bones to scavengers, thus opening a new ecological niche that allowed the evolution of a vulture as large as *A. magnificens* in South America during late Miocene times (figure 1).

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Comisión organizadora
Silvio Casadío
Edsel Brussa
Claudia Montalvo
Ana Parras
Miguel Griffin
Ricardo Melchor
Marcelo Zárate

Edificio Central de la Universidad Nacional de La Pampa
Salón Azul, primer piso
Coronel Gil 353, Santa Rosa, La Pampa
Teléfono: 02954-436787, int. 13
apa2003@exactas.unlpam.edu.ar