



## Original Investigation

## Diets of three sympatric Neotropical small cats: Food niche overlap and interspecies differences in prey consumption

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## ABSTRACT

Dietary investigations of sympatric felids are means for understanding how closely related species deal with food resources in a potentially competitive scenario. The diets of the oncilla *Leopardus tigrinus*, the jaguarundi *Puma yagouaroundi* and the ocelot *Leopardus pardalis* were studied through the analysis of scats in Araucaria Pine Forest with Natural Grasslands of southern Brazil. Small mammals comprised the bulk of the diets of the three felids, followed by birds and reptiles. The smallest food-niche overlap index was 0.84, indicating that these felids shared an important portion of their food resources. Inter-species differences were detected in the consumption of the most frequent rodent prey; *L. tigrinus* was the only species that consumed all the most frequent rodent prey differently from the rate expected from their abundances. Although these findings suggest competitive interactions, with the oncilla being the most subordinate species, further experimental investigations are necessary to elucidate more precisely how these syntopic felids coexist. The effects of sample size and its influences on the evaluation of the diets of the felids, especially of the ocelot, are discussed. We compare our data to a previous study in the same area, to account for the possible influences of biased sampling and uneven distribution of food resources on the diet of the ocelot. The opportunistic feeding behavior and the abundance of their primary prey (cricetid rodents) seem to allow these small cats to be resilient despite severe anthropogenic disturbance in the study area. We further suggest guidelines for future studies in the study region, in order to understand the dynamics of mammalian carnivores demography.

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## Introduction

All felid species share specializations for capturing and killing live prey (Sunquist and Sunquist 2002). Where felids live in sympatry, such as in most of the Neotropical domain, the species differ among themselves especially in their body size and size-related traits (Kiltie 1984). As ecologists have often acknowledged, this body-size differentiation among sympatric felids enables differential food exploitation, and hence potentially reduces intra-guild competition (Rosenzweig 1966; Davies et al. 2007).

The oncilla *Leopardus tigrinus* (Schreber, 1775), the jaguarundi *Puma yagouaroundi* (Geoffroy, 1803) and the ocelot *Leopardus pardalis* (Linnaeus, 1758) are small Neotropical cats with a wide range of geographic overlap in the South American continent (Sunquist and Sunquist 2002). These species have discrete body weight distribution: oncilla 1.8–3.4 kg; jaguarundi 3.8–6.5 kg and ocelot 8–16 kg (Sunquist and Sunquist 2002).

Empirically, the discrete distribution of the body sizes of these species will hardly imply diet segregation, because for instance, small mammals comprise the bulk of the diets of most small Neotropical cats (Emmons 1987; Konecny 1989; Ludlow and Sunquist 1989; Facure and Giarretta 1996; Wang 2002; Bianchi and Mendes 2007; Abreu et al. 2008). Because small mammals are also the most abundant mammalian prey in tropical forests (Solari and Rodrigues 1997), one can presume that these predators hunt opportunistically (Jaksic 1989). However, beyond the random influence of encounter rates on food acquisition, different felid species living in sympatry can capture their prey selectively, as for instance, to minimize the negative effects of intra-guild competition (Durant 1998; Pierce et al. 2000; Ray and Sunquist 2001; Novack et al. 2005; Hayward and Kerley 2008).

To our knowledge, there are no previous studies concerning the food-niche characteristics of these felids in a syntopic context. The objectives of this study were to (1) describe comparatively the diets of the oncilla, the jaguarundi and the ocelot and to (2) compare the frequency of some small mammal species in the diet of the three felids with their relative abundance in the habitat. Further, we contrast our data with a previous study that described the diet of ocelots in the same area (see Abreu et al. 2008), and dis-

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cuss possible mechanisms that allow the coexistence of these three species.

## Material and methods

This study was carried out in the Devonian Scarp of the state of Paraná, Southern Brazil (25°20'–25°29' S and 49°39'–49°42' W). The local climate is subtropical, mesothermic, and constantly humid with mild summers. The mean annual temperature varies from 14°C in the winter to 21°C in the summer, and the mean annual rainfall averages 1600 mm with no marked seasonal incidence throughout the year (SEMA 2004). The terrain in the Paraná Devonian Scarp is rugged, and altitudes range from around 900 m to 1142 m above the sea level (Maack 1981).

The Paraná Devonian Scarp contains interfaces of two distinct landscapes: natural grasslands (Campos Gerais) and Araucaria Pine Forest (Mixed Ombrophilous Forest). The forested regions are associated with streams, hillsides and valleys, with the Paraná Pine *Araucaria angustifolia* as a characteristic element (Maack 1981). Many locally important species of trees have been intensively logged and are currently rare (Maack 1981). Natural Grasslands are dominated by Gramineae species, herbs, scattered shrubs, and sparsely distributed trees. These natural grasslands have been extensively converted to grazing fields and alternating crops, and are currently restricted to small fragments and undergoing alteration with the expansion of dispersing exotic *Pinus* species.

Scats were collected from three different localities within the Paraná Devonian Scarp: Bugre District, São Luis do Purunã District, and Santa Rita Ranch. We considered all these localities as a single sampling area, because their close proximity precluded assumption of sample independence (5–10 km between sites). We walked an average of 12 km per locality every month from April 2006 through March 2007, in order to search for carnivores' fecal samples in forest fragments, natural grasslands, and pasture fields. Fecal samples were collected, stored, and taken to the laboratory for identification and analysis.

Scats were identified exclusively by microscopic analysis of the cuticle patterns of the guard hairs (Quadros and Monteiro-Filho 2006). We compared guard-hair cuticle patterns of specimens in reference collection (MHNCI) with those found in the scats. A total of 363 scats was collected during the study, but only 108 (30%) could be identified unambiguously to one of the three felid species investigated, resulting in 36 oncilla scats, 51 jaguarundi scats, and 21 ocelot scats. Most of these scats were collected during drier periods (86% collected between March and November), because the steady rains during the summer removed or degraded a high proportion of the dropped scats.

The scats collected were washed and dehydrated, and food items were separated in the following categories: hair, bones, teeth, nails, feathers, and scales. Food items were identified to the lowest possible taxonomic level through comparison with voucher specimens in local collections (Coleção Mastozoológica do Departamento de Zoologia da Universidade Federal do Paraná, CCMZ-DZUP; Coleção de Mamíferos do Museu de História Natural do Capão da Imbuia, MHNCI; and Museu de Zoologia da Pontifícia Universidade Católica do Paraná, MZ.PUC.PR). Mammal species were identified to family, genus, or species levels, depending on the quality of the diagnostic structures. Feathers of birds were frequently unidentifiable even at ordinal level, and therefore all the specimens were identified as Birds. Reptiles were identified by comparing scales and jaw fragments.

To investigate the cumulative behavior of each individual prey item as a function of sample size, we randomly selected five scats, analyzed the FO (see below) of the food items, selected five more and analyzed the food items, and so on until all the scats had been

analyzed (Azevedo 2008). This iterative process allows the identification of a minimum number of items necessary to represent the most frequent prey taxa.

We estimated the minimum number of individuals consumed (MNI) by counting the teeth of mammals. We assumed birds and reptiles to have MNI equal to 1, because the feathers and scales encountered in scats were scarce and indistinguishable (see Ray and Sunquist 2001). Food items were represented as frequency of occurrence (FO) (the percentage of scats in which one food item was found) and percentage of occurrence (PO) (the percentage of one item in relation to the total MNI). Levin's standardized niche breadth and Pianka's food overlap indexes were calculated for the three species using the software Ecological Methodology (Krebs 1999).

Abreu et al. (2008) described the diet of ocelots within the same sampling area as the present study. Therefore we performed G-tests for goodness-of-fit to investigate if differences in the use of prey-size categories would appear by including the data from Abreu et al. (2008). Prey categories were arranged in size classes according to prey mean body mass ( $\leq 100$  g; 101–1000 g;  $> 1000$  g), as described in species accounts in the current literature (Reis et al. 2006; Bonvicino et al. 2008).

In order to estimate the relative abundances of some small mammal species in the habitat, we applied trapping efforts systematically from September 2006 through August 2007 (seven months concurrently with the collection of fecal samples). We used 100 Sherman live traps (50 traps with dimensions of 12 cm  $\times$  14 cm  $\times$  30 cm and 50 traps with 8 cm  $\times$  9 cm  $\times$  18 cm) per night. Each month, one locality was sampled during four nights of trapping, for a total of 400 trap-nights per month and 4800 trap-nights after 12 months of sampling. In each locality, we distributed the traps in two ways: (1) five parallel rows spaced every 10 meters, each row containing 10 traps spaced every five meters; and (2) one linear trail containing 50 traps spaced every ten meters. All traps were baited with banana and bacon. We checked all the traps each subsequent morning, to replace the bait and carry out the post-capture procedures. Individuals captured were weighed, sexed, identified to species level, and released. Chi-square tests were applied to detect differences between the relative abundance of small mammals in the diet of the felids and their relative abundance in the traps. We only included the small mammal species with a frequency in the traps  $\geq 5$ , to generate adequate numbers for calculating the expected frequency. We further calculated a simultaneous Bonferroni confidence interval to detect which prey taxa accounted for the statistical differences (Byers et al. 1984). All tests were considered significant if  $p < 0.05$ .

## Results

We found 19 prey items altogether in the diet of the three felids, which were represented by a minimum number of 276 prey individuals (MNI) (Table 1). Rodents of the family Cricetidae were both the most frequent and most abundant items for the oncilla (FO = 86.1%; PO = 82.3%), the jaguarundi (FO = 96%; PO = 77.6%), and the ocelot (FO = 100%; PO = 92.4%). Birds were also frequent, except in the diet of the ocelot (Table 1). Plant material was sporadically ingested by all three felids, but was excluded from the analysis because there were only small amounts of grass leaves, and we assumed that this material was accidentally ingested despite the possibility of its digestive usefulness. The evaluation of the cumulative frequency of occurrence of the most important (PO  $\geq 5\%$ ) prey items revealed that the relative contribution of these prey types was represented in 30 scats for the oncilla, 35 scats for the jaguarundi and 15 scats for the ocelot (but see Discussion).

The oncilla had the widest Levin's standardized niche, followed by the jaguarundi and the ocelot (Table 2). The food-niche over-

**Table 1**  
Diet composition of three sympatric felids in southern Brazil from 36 scats of oncilla, 51 scats of jaguarundi, and 21 scats of ocelot. FO% = frequency of occurrence; PO% = percentage of occurrence; MNI = minimum number of individuals consumed.

Food item	Oncilla			Jaguarundi			Ocelot		
	FO%	PO%	MNI	FO%	PO%	MNI	FO%	PO%	MNI
<i>Akodon</i> sp.	30.5	16.4	14	41.1	18.4	23	52.4	34.8	23
<i>Juliomys pictipes</i> (Osgood, 1933)	5.5	2.3	2	1.9	0.8	1			
<i>Oligoryzomys flavescens</i> (Waterhouse, 1837)	38.9	17.6	15	35.3	17.6	22	28.6	12.1	8
<i>Oligoryzomys nigripes</i> (Olfers, 1818)	8.3	3.5	3	11.7	5.6	7	4.8	1.5	1
<i>Oligoryzomys</i> sp.				1.9	0.8	1	4.8	1.5	1
<i>Sooretamys angouya</i> (Fischer, 1814)	27.7	14.1	12	15.6	6.4	8	28.6	9.1	6
<i>Euryoryzomys russatus</i> (Wagner, 1848)	16.7	8.2	7	7.8	3.2	4	19	6.1	4
<i>Brucepattersonius iheringi</i> (Thomas, 1896)				1.9	0.8	1	4.8	1.5	1
<i>Thaptomys nigrita</i> (Lichtenstein, 1829)				3.9	1.6	2	14.3	6.1	4
<i>Nectomys squamipes</i> (Brants, 1827)							4.8	1.5	1
Unidentified Cricetidae	41.7	20	17	45.1	21.6	27	42.9	18.2	12
Unidentified Echimyidae	2.7	1.2	1	1.9	0.8	1			
<i>Monodelphis</i> sp.	5.5	2.3	2	5.8	2.4	3	4.8	1.5	1
<i>Gracilinanus</i> sp.				5.8	2.4	3			
Unidentified Armadillo (Dasypodidae)				1.9	0.8	1			
Unidentified Mammals	2.7	1.2	1	5.8	2.4	3			
Unidentified Birds	27.7	11.8	10	25.5	10.4	13	9.5	3	2
<i>Tropidurus</i> sp.				1.9	0.8	1			
Unidentified Reptiles	2.7	1.2	1	7.8	3.2	4	9.5	3	2
Total		100	85		100	125		100	66

**Table 2**  
Levin's standardized niche breadths ( $B_{st}$ ) and Pianka's overlap indexes of three sympatric felids in southern Brazil.

	$B_{st}$	Pianka's overlap indexes		
		Oncilla	Jaguarundi	Ocelot
Oncilla	0.59	1.00	0.95	0.84
Jaguarundi	0.43	0.95	1.00	0.87
Ocelot	0.38	0.84	0.87	1.00

lap according to Pianka's index was the highest for oncilla vs jaguarundi, followed by oncilla vs ocelot and ocelot vs jaguarundi (Table 2).

Among the small mammal species, only those that had five or more trapped individuals and a percentage of occurrence equal to or greater than 5% in the diet of the felids were compared to investigate prey selection (see Table 1 for the prey POs and Table 3 for the species captured). *Didelphis aurita* (Wied-Neuwied, 1826) and *Philander frenatus* (Olfers, 1818) were frequently trapped, but they were not consumed by the felids in our sample. All three felid species consumed the most abundant rodent prey species (*Akodon* sp., *Oligoryzomys flavescens*, *Sooretamys angouya* and *Euryoryzomys russatus*) differently from what would be expected by

chance: oncilla (chi-square = 48.8; d.f. = 3;  $p < 0.05$ ), jaguarundi (chi-square = 47.3; d.f. = 3;  $p < 0.05$ ), and ocelot (chi-square = 13.1; d.f. = 3;  $p < 0.05$ ) (see Table 4 for the species that influenced these differences).

Considering the prey items reported by Abreu et al. (2008), the ocelot was the only cat that preyed upon items larger than 1000 g significantly (comparing ocelot vs jaguarundi:  $G = 18.38$ ; d.f. = 1;  $p < 0.05$ ). This reflects the consumption of howler monkeys, armadillos, and porcupines by the ocelot in the Bugre District. The oncilla did not consume prey > 1000 g.

## Discussion

Similarly to this study, the previous dietary investigations have shown that small vertebrates (below 1000 g), especially mammals, comprise the bulk of the prey array of the Neotropical felids up to the size of the ocelot (Emmons 1987; Konecny 1989; Ludlow and Sunquist 1989; Facure and Giarretta 1996; Wang 2002; Bianchi and Mendes 2007; Abreu et al. 2008). In contrast, the larger-bodied jaguars [*Panthera onca* (Linnaeus, 1758)] and cougars [*Puma concolor* (Linnaeus, 1771)] rely mostly on the larger mammals, thus exploiting, and possibly competing for, different food resources from the smaller felids (Aranda and Sanchez-Cordero 1996; Chinchilla 1997; Novack et al. 2005; Moreno et al. 2006).

This pattern is consistent with the carnivore community structure theory, in which sympatric felids tend to be distributed over a gradient of body size, and hence are able to exploit a corresponding gradient of prey size (Rosenzweig 1966; Kiltie 1984; Hayward et al. 2006a,b), except for group hunting lions (Hayward and Kerley 2008). However, since rodents are the most abundant mammalian prey in tropical forests (Solari and Rodrigues 1997), the overlapping in the prey size range of the ocelot and all the

**Table 3**  
Small mammal species captured from Sherman traps in three localities of the Paraná Devonian Scarp from September 2006 through August 2007.

Species	Number of individuals captured	Percentage of individuals captured
<i>Didelphis aurita</i>	13	12.1
<i>Monodelphis iheringi</i>	1	0.9
<i>Philander frenatus</i>	8	7.4
<i>Akodon montensis</i> <sup>a</sup>	41	38.3
<i>Brucepattersonius iheringi</i>	2	1.8
<i>Nectomys squamipes</i>	1	0.9
<i>Juliomys pictipes</i>	1	0.9
<i>Oecomys catherinae</i>	1	0.9
<i>Oligoryzomys flavescens</i> <sup>a</sup>	10	9.3
<i>Sooretamys angouya</i> <sup>a</sup>	5	4.6
<i>Euryoryzomys russatus</i> <sup>a</sup>	23	21.4
<i>Rattus rattus</i>	1	0.9
TOTAL	107	100

<sup>a</sup> Species that were compared with their frequency in the scats of the three felids.

**Table 4**

Simultaneous Bonferroni confidence intervals used to evaluate small mammal consumption by three sympatric felids in southern Brazil.

	Actual proportion of use ( $p_i$ )	Expected proportion of use	Bonferroni confidence interval for $p_i$
Oncilla			
<i>Akodon</i> sp.	0.291	0.518	$0.128 \leq p_i \leq 0.453^*$
<i>O. flavescens</i>	0.312	0.126	$0.147 \leq p_i \leq 0.477^*$
<i>S. angouya</i>	0.250	0.063	$0.095 \leq p_i \leq 0.405^*$
<i>E. russatus</i>	0.145	0.291	$0.020 \leq p_i \leq 0.270^*$
Jaguarundi			
<i>Akodon</i> sp.	0.403	0.518	$0.240 \leq p_i \leq 0.565$
<i>O. flavescens</i>	0.385	0.126	$0.226 \leq p_i \leq 0.546^*$
<i>S. angouya</i>	0.140	0.063	$0.027 \leq p_i \leq 0.252$
<i>E. russatus</i>	0.070	0.291	$0.000 \leq p_i \leq 0.152^*$
Ocelot			
<i>Akodon</i> sp.	0.589	0.518	$0.393 \leq p_i \leq 0.785$
<i>O. flavescens</i>	0.154	0.126	$0.010 \leq p_i \leq 0.298$
<i>S. angouya</i>	0.154	0.063	$0.010 \leq p_i \leq 0.298$
<i>E. russatus</i>	0.102	0.291	$0.000 \leq p_i \leq 0.223^*$

\* Significant difference.

other smaller Neotropical felids will lead to a predictable sharing of food resources. This was the case in this study, given the food profiles and the high Pianka's niche overlap indexes observed, which indicated no clear food-niche partition among these co-existing felids. The abundance of their primary prey item (cricetid rodents) could possibly allow them to coexist without competing for food (see [Carvalho and Gomes 2004](#)), although periods of food shortage might increase the food-niche overlap, and hence, the competition among the three species ([Carvalho and Gomes 2004](#)).

The data we presented regarding the abundance of small mammal prey should be interpreted with caution because individuals were sampled based on the ability of only one trapping technique (Sherman traps), which is able to catch a limited group of species (see [Umetsu et al. 2006](#)). Distinct behavior and food habits among the small mammal species make clear the need for different sampling methods to avoid biased conclusions. Yet, traps and cats exhibit different capture performances, what hamper conclusions concerning the actual availability of prey to cats. Therefore, our data regarding prey selection is best interpreted as a conjecture supported by a statistical test and corroborated by ecological predictions, rather than conclusive statements (see below).

Aware of its limitations, the statistical tests that concerned the consumption of terrestrial small mammals suggests a differential usage of rodent prey by the felids. The ocelot (the largest species) was the most opportunistic predator, consuming the majority of its prey types according to their abundance in the habitat. The jaguarundi opportunistically consumed two rodent prey species (*Akodon* sp. and *Sooretamys angouya*), while the oncilla (the smallest species) consumed all these rodent species differently from the proportions expected by their abundance (as shown in [Table 4](#)). Despite our explanatory limitations given the lack of data on activity patterns and use of space of these syntopic felids, the set of possible causal explanations for these results might be complex and not mutually exclusive. For instance, predators and prey may increase their encounter rates because of synchronicity in activity patterns within an overlapping use of space ([Linnell and Strand 2000](#); but see [Hayward and Slotow 2009](#)). In such a circumstance, the dominant species is able to select habitat in which its prey live, whereas subordinate species would be forced to select a habitat patch where the dominant species is absent ([Caro and Stoner 2003](#)). In the Neotropics, the dominant jaguars were reported to constrain the consumption of capybaras [*Hydrochaeris hydrochaeris* (Linnaeus, 1766)] by the subordinate cougars, even when capybaras were among the most available prey at the site ([Scognamiglio et al. 2003](#)). Because the oncilla did not consume rodent prey according to their availability, ecological avoidance as a product of competition could have taken place in the Paraná Devonian Scarp ([Futuyma](#)

and [Moreno 1988](#); [Pianka 1994](#)), as suggested by the evidence of [Di Bitetti et al. \(2010\)](#) in northeastern Argentina.

Larger prey (>1000 g), although less frequent than smaller ones, have often been reported in the diet of ocelots throughout the Neotropics ([Emmons 1987](#); [Ludlow and Sunquist 1989](#); [Wang 2002](#); [Bianchi and Mendes 2007](#); [Abreu et al. 2008](#)). Anecdotal data have reported the sporadic consumption of prey larger than 1000 g for the jaguarundi ([Sunquist and Sunquist 2002](#); [Wang 2002](#)), and we also report here the consumption of one (otherwise unidentified) armadillo. The oncilla did not consume prey larger than 1000 g in this study, and to the best of our knowledge, no study has reported the consumption of prey of this size by the oncilla. Because smaller prey tend to be more abundant than larger ones ([Jaksic 1989](#)), the ocelot seems to consume prey according to their abundance in a given habitat, best fitting within the definition of an opportunistic predator, instead of maximizing energy intake through selecting for a preferred prey size ([Griffiths 1975](#); [Jaksic 1989](#)). This is also expected based on the optimal foraging theory, in which the catchability of small prey offers lower risks of injury to the predator ([Pianka 1994](#)).

Apart from mammals, birds and lizards have been reported in the diets of all the three felids (this study; [Facure and Giaretta 1996](#); [Sunquist and Sunquist 2002](#); [Villa-Meza et al. 2002](#); [Wang 2002](#)), which can provide them with an additional food supply. Although this supposition has not been statistically tested against prey abundance, the geographical taxonomic variation of the prey types recorded in the diet of these cats indicates their dietary flexibility ([Konecny 1989](#); [Manzani and Monteiro-Filho 1989](#); [Sunquist and Sunquist 2002](#); [Wang 2002](#)). Neotropical felids are therefore more likely to be specialists on hunting of available and profitable live prey, rather than exhibiting taxon-specific preferences (but see [Hayward and Kerley 2005](#); [Hayward et al. 2006a,b](#), for the African large cat's taxon-specific prey preferences).

Although an increase in the sample sizes for *L. tigrinus* and *P. yagouarundi* could add no previously recorded prey items, it would scarcely alter their niche breadths because the most frequently used items would far outweigh the values for any new prey items in the analysis ([Krebs 1999](#)). In contrast, the case of the ocelot was different. The data of [Abreu et al. \(2008\)](#) showed a frequent consumption of larger mammals (>1000 g) by the ocelot in the Bugre District. This variation might have occurred due to (1) bias in the data of [Abreu et al. \(2008\)](#), and/or (2) unrepresentative sample size in our data. The former case is possible because most of the scats analyzed by [Abreu et al. \(2008\)](#) were likely dropped by a single adult male ocelot, in a latrine situated within a more-structured micro-habitat (R.F. Moro-Rios *pers. comm.*). These sampling effects must be taken into account, because all food-niche analyses are sensitive



to it. For instance, the upper limit of the prey size range increased from the 116 g of *Sooretamys angouya* (mean weight from Bonvicino et al. 2008) to the 16,000 g of *Mazama guazoubira* (G. Fischer, 1814) (Abreu et al. 2008). Also, we could only detect any statistically significant difference of the prey-size class usage among the felid species after comparing our data with that in Abreu et al. (2008).

Other important prey types such as birds and many cricetid rodents were neither measured for abundance in the habitat nor identifiable at a lower taxonomic level in the diet analyses. Therefore, methods for more precise taxonomic identification of prey items would be desirable to test patterns of prey use at the species, rather than the functional level of prey types (see Greene and Jaksic 1983).

Finally, it seems that the above-mentioned opportunistic feeding behavior of these cats and the abundance of their primary prey item are allowing them to coexist and to tolerate severe anthropogenic disturbances. Future studies addressing seasonal variations in prey availability, and their influence on the feeding habits and use of space and time of the small felids could shed light upon the mechanisms involved in modeling communities of both prey and predators. In turn, such studies would help to predict when displacement takes place, and how it affects their demography.

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