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Original article

Characteristics of two mountain lion *Puma concolor* populations in Texas, USA

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Influential factors associated with population dynamics of mountain lions *Puma concolor* include exploitation rates, prey availability, habitat structure and social structure. Throughout most of North America, mountain lion harvest is regulated by state or provincial quotas or is protected by federal laws. In Texas, however, they are not classified as a game or fur-bearing animal so their harvest is not regulated. To better understand the differences between population characteristics of mountain lions in west Texas (WTX) and south Texas (STX), we initiated two ecological studies. We captured, radio-marked and monitored mountain lions to ascertain survival, mortality factors, density, reproduction and population structure. We captured and monitored 19 and 21 mountain lions in the STX and WTX study sites, respectively. Average densities (No/100 km^2) were different between our two study sites (STX = 0.269, WTX = 0.427) and were considerably lower than in previous studies. Mortality factors also differed between the two areas; in STX the causes were predominantly hunter harvest compared to trapping in WTX. Seasonal survival rates of mountain lions were lower during the general hunting season (STX = 0.783, WTX = 0.750) than during the non-hunting season (STX = 0.962, WTX = 0.931). Because population characteristics differed between the two genetically separated populations (Walker et al. 2000), resource managers should consider evaluating regional, rather than statewide management plans for mountain lions in Texas.

Key words: cougar, density, mountain lion, population dynamics, Puma concolor, reproduction, survival, Texas

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Characteristics of mountain lion *Puma concolor* populations have been studied throughout much of their current range in the United States, including the Pacific Northwest (Lambert et al. 2006), the north and central Rocky Mountains (Hornocker 1969, 1970, Seidensticker et al. 1973, Shaw 1980, Hemker et al. 1984, Smith et al. 1986, Anderson et al. 1992, Ross & Jalkotzy 1992, Lindzey et al. 1994, Cunningham et al. 1995, Spreadbury et al. 1996, Logan & Sweanor 2001), California (Beier 1993), Arizona (Cashman et al. 1992, Cunningham et al. 2001), New Mexico (Logan & Sweanor 2001) and southern Florida (Maehr et al. 1991, Buergelt et al. 2002, Taylor et al. 2002).

Influential factors associated with population dynamics of mountain lions include exploitation rates (Harveson et al. 1999, Cunningham et al. 2001, Anderson & Lindzey 2005), prey availability (Hemker et al. 1984, Ross & Jalkotzy 1992, Logan & Sweanor 2001, Rosas-Rosas et al. 2003), habitat structure (Ross & Jalkotzy 1992, Beier 1993, Spreadbury et al. 1996, Sweanor et al. 2000, Stoner et al. 2006) and social structure (Hornocker 1969, Logan & Sweanor 2001, Pierce et al. 2000, Stoner et al. 2006). Most information on mountain lion population dynamics is derived from study sites, in which harvest restrictions are placed on specific management units or at regional or state levels.

In Texas, mountain lions are classified as nongame animals with no restrictions on harvest (Russ 1996). Research on mountain lion populations in Texas has been sporadic with few studies resulting in published data (Harveson et al. 1996, 1999, 2000, Pittman et al. 2000, Walker et al. 2000). Aside from a statewide monitoring program of reported mountain lion sightings and mortalities, all information on mountain lion population ecology derives from studies conducted on state or federal lands in the Trans-Pecos Region of western Texas, where mountain lions are protected from harvest (McBride 1976, Harveson et al. 1997, Guzman 1998, Pittman et al. 2000). Baseline ecological characteristics are needed to establish a state-wide management plan for mountain lions in Texas. We compared the characteristics of two mountain lion populations in Texas with different harvest pressure. Our objectives were to compare population characteristics including: population structure, density, reproduction, survival and mortality factors.

Material and methods

Study area

Data were collected from two ecoregions in Texas: the Rio Grande Plains of southern Texas and the Trans-Pecos Mountains and Basins of western Texas (Fig. 1). The southern Texas (STX) population was studied on private lands on which harvest was unrestricted. The western Texas (WTX) mountain lion population was studied on the Big Bend Ranch State Park, in which they are protected from harvest due to park regulations. In STX, we collected data from a 2,683-km^2 study site consisting of privately owned lands along the Nueces River between Cotulla, Tilden, Freer and Encinal, Texas. Elevation ranged from 90 to 208 m a.s.l. (Gabriel et al. 1994) and precipitation averaged 64 cm. Soil composition

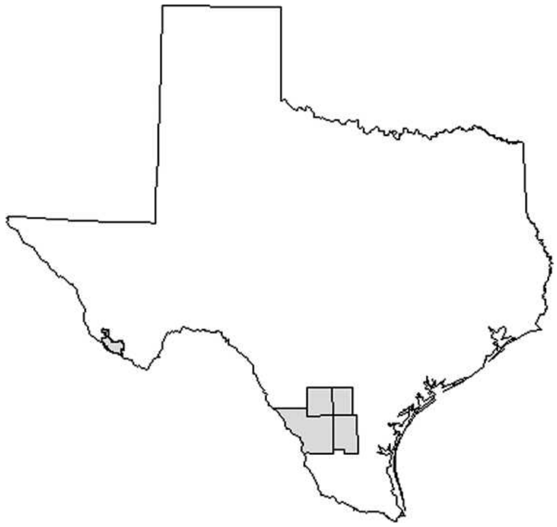

Figure 1. Approximate location of study sites in western Texas (WTX; the Big Bend Ranch State Park) and southern Texas (STX; La Salle, McMullen, Webb and Duval counties).

varied with clay and silty soils occurring more frequently along riparian habitats, and sandy soils becoming more common away from the Nueces River. Upland habitats on the STX study site included mesquite *Prosopis glandulosa*, whitebrush *Aloysia gratisima* and mixed-brush shrublands. Riparian habitats included riparian woodlands dominated by Mexican ash *Fraxinus berlandieriana* and huisache *Acacia farnesiana*, and the riparian floodplain was dominated by gulf cordgrass *Spartina spartinae* and spiny aster *Aster spinosa* (Harveson 1997, Harveson et al. 1997).

In WTX, data were collected from the Big Bend Ranch State Park which encompassed 1,210 km^2. The Big Bend Ranch State Park is owned and operated by Texas Parks and Wildlife Department and is bordered by the Rio Grande to the south and west, the Big Bend National Park to the east and private lands to the north. Elevations were typical of the Trans-Pecos ecoregion and varied from 700 to 1,565 m. Average annual precipitation for the region ranged from 27.5 to 40.8 cm, with most rainfall occurring during July-October. Soils on the study site were primarily sandy and gravelly. Deeper soils were more common in lower elevations (draws and canyons; Milner 2003). Vegetation communities varied considerably including desert riparian, juniper *Juniperus pinchotii,* sotol *Dasylirion leiophyllum* and desert scrub. Typical vegetation in the desert riparian communities included giant cane *Arrundo donax*, salt cedar *Tamarisk* spp. and cottonwood *Populus ari-*

zonica. Plants indicative of the desert scrub included creosotebush *Larrea tridentata*, ocotillo *Fouquieria splendens* and lechuguilla *Agave lechuguilla* (Henklein 2003).

Capture and handling

Mountain lions were captured using leg-hold snares (Logan et al. 1999) and trained dogs (Hornocker et al. 1965) from March 1994 to March 1997 for STX and from December 1992 to August 1997 for WTX. Trapping and handling procedures were approved by Animal Care and Use Committees at Texas A&M University-Kingsville, Texas A&M University, as well as by Texas Parks and Wildlife Department (permit SPR-0592-525). Captured mountain lions were immobilized with 11 mg/kg ketamine hydrochloride and 1.8 mg xylazine hydrochloride/kg estimated body mass (Logan et al. 1986). Mortality-sensitive radio-collars (Telonics Inc., Mesa, Arizona, USA) were affixed to captured mountain lions. Radio-collared mountain lions were located weekly from the ground or air for STX and every two weeks for WTX.

Population structure

Mountain lions were aged according to Ashman et al. (1983) and were compared to known-aged mountain lions using tooth wear and colouration and pelage characteristic. Sex and age composition of the two populations were derived from the captured mountain lions and from verified mountain lion mortalities within the study site (Harveson 1997). Mountain lions were then classified as adults (A; $\geq$ 3 years), subadults (S; 1-3 years) or kittens (K; $\leq$ 1 years), based on movement patterns from telemetry monitoring (subadults were independent whereas kittens were dependent; Harveson 1997, Pittman et al. 2000).

Density

Population density was estimated as the known number of mountain lions in the two respective study areas. We defined the effective area (e.g. the area from which we extrapolated density) as the composite home range (100% minimum convex polygon) of all adult radio-marked mountain lions during the course of the study (e.g. STX during 1994-1997 and WTX during 1992-1997). The composite home range for STX and WTX was 4,592 km^2 and 2,765 km^2, respectively. In addition to radio-collared mountain lions, we included non-radioed subadult and adult mountain lions that were harvested on the study sites during the research period (Harveson 1997). Only mortalities that fell within the composite home range or trapping area were used in density calculations. Density estimates were calculated for each study site on 1 September for 1994, 1995 and 1996, with the assumption that mountain lions were residents and alive in the study area at the beginning of the respective year.

Reproduction

We estimated mean litter size for females in the WTX and STX study sites. We determined presence of litters by investigating sites on which radio-telemetry indicated that a radio-collared female was exhibiting localized movements. Visual observations and searches for mountain lion tracks were used to determine the presence of family groups and litter size (Harveson 1997).

Survival

We used radio-telemetry collected from radio-collared mountain lions in STX during 1994-1997 and WTX during 1992-1997 to estimate survival rates. Due to small sample sizes for kittens, only telemetry data from subadult and adult mountain lion locations were used in analysis. In Texas, the general hunting seasons for upland game birds and large mammals span from September to February. Seasons were defined as hunting (September-February) and non-hunting (March-August), due to the variability of mortality risk to mountain lions during the general hunting season. Survival rates were estimated for each study area using a known-fate model framework in program MARK (White & Burnham 1999). Season and sex were used as predictor variables for survival.

For each area, four models were constructed based on sex and season, and the combinations of them were evaluated using program MARK (White & Burnham 1999). Models were evaluated based on Akaike's Information Criterion (AIC_c), and the highest ranking model was selected to estimate survival (Burnham & Anderson 1998). We also compared mortality factors between the two study sites.

Results

Population structure and density

In STX, we caught 19 mountain lions (two adult females (AF), six adult males (AM), one subadult female (SF), six kitten females (KF) and four kitten

Table 1. Estimated densities and sex ratios for mountain lion populations in southern Texas (STX; during 1994-1996) and western Texas (WTX; during1993-1997) based on radio-collared mountain lions and verified non-radio-collared mountain lions.

		Radio-collared				Non-radio-collared						Total		
		Adult		Subadult		Adult			Subadult			Sex ratio		Density
Area	Year	M	F	M	F	M	F	U	M	F	U	N	(M:F)	(N/100 km^2)
STX	1994	2	1	1	2	1	6	0	0	0	1	14	0.44:1	0.305
	1995	4	3	2	1	1	2	0	0	0	0	13	1.17:1	0.283
	1996	4	2	2	1	1	0	0	0	0	0	10	2.33:1	0.218
WTX	1993	2	2	2	0	0	1	0	2	1	0	10	1.50:1	0.362
	1994	4	5	2	0	1	0	0	0	0	0	12	1.40:1	0.434
	1995	7	3	1	1	0	1	2	0	0	1	16	1.60:1	0.579
	1996	2	4	0	0	2	2	0	2	1	1	14	0.86:1	0.506
	1997	1	2	0	0	1	1	1	0	0	1	7	0.67:1	0.253

males (KM)). We captured eight male (14 times) and three female (three times) mountain lions using foot snares for an initial trap success (excluding recaptures) of 459 trap-nights/capture. Trained hounds were used 37 times and resulted in 12 mountain lions being treed 21 times; the target animal was successfully treed on 13 occasions. Two litters of radio-collared mountain lions were captured by hand. Sex ratios (M:F) were variable among years and ranged from 0.44:1 in 1994 to 2.33:1 in 1996 (Table 1). Mountain lion densities showed little variation in STX and ranged from 0.218 to 0.305 mountain lions/100 km^2 and averaged 0.269 mountain lions/100 km^2.

In WTX, we caught 21 mountain lions (six adult females (AF), seven adult males (AM), two subadult males (SM), two kitten females (KF) and four kitten males (KM)). We captured seven male (11 times) and six female (eight times) mountain lions for an initial trap success of 366 trap-nights/capture. An additional six male and two female mountain lions were captured with trained hounds. One litter of a radio-collared female was captured by hand but was not radio-marked. Sex ratios (M:F) were variable among years and ranged from 0.67:1 in 1997 to 1.60:1 in 1995 (see Table 1). Mountain lion densities varied in WTX and ranged from 0.253 to 0.579 mountain lions/100 km^2 and averaged 0.427 mountain lions/100 km^2.

Reproduction

We recorded a minimum of 13 mountain lion litters in STX with a mean litter size of 1.77 (N = 13, SD = 0.83). We also documented 13 litters in WTX with a mean litter size of 1.54 (N = 13, SD = 0.52).

Survival

Mountain lion survival was estimated for radio-collared subadults and adults in STX (N = 14; 9M, 5F) and WTX (N = 12; 7M, 5F). Mountain lions captured as kittens were included in analysis once they became subadults. Of the four models evaluated, the season-only model ranked highest for STX and second highest for WTX (Table 2). We used this model for both areas for comparison purposes, and

Table 2. Candidate models and selection results for estimated survival for mountain lions[a] in southern Texas (STX) and western Texas (WTX).

Study area	Candidate model	No of parameters	Δi^b	Akaike weight (w_i)	Evidence ratio (w_1/w_i)
STX	S_{Season}	2	0.000	0.39	1.00
	$S_{Season, Sex}$	3	0.072	0.37	1.05
	$S_{All\ equal}$	1	1.696	0.17	2.29
	S_{Sex}	2	3.370	0.07	5.57
WTX	$S_{Season, Sex}$	3	0.000	0.54	1.00
	S_{Season}	2	1.347	0.27	2.00
	$S_{All\ equal}$	1	3.092	0.11	4.91
	S_{Sex}	2	4.037	0.07	7.71

[a] Subadult and adult mountain lions were combined for analysis.
[b] STX minimum AIC_c = 36.823; WTX minimum AIC_c = 53.404.

Table 3. Seasonal survival estimates of mountain lions in southern Texas (STX; during1994-1997) and western Texas (WTX; during 1992-1997).

Study area	Season[a]	Survival	SE	95% LCI	95% UCI
STX	Non-hunting	0.962	0.038	0.772	0.995
	Hunting	0.783	0.086	0.572	0.907
WTX	Non-hunting	0.931	0.047	0.762	0.98
	Hunting	0.750	0.077	0.570	0.870

[a] The non-hunting season was from September to February and the hunting season from March to May.

because our sample size was not big enough for the season by sex model which ranked first for WTX. The estimates were similar for lions in both study areas, with survival being higher during the non-hunting season than during the hunting season (Table 3). Our results indicated considerable variation in mountain lion survival between hunting and non-hunting seasons; with differences between seasonal survival estimates (STX = 0.179, WTX = 0.181) exhibiting confidence interval overlap, but showing obvious biological relevance.

Mortality factors

Mortality factors differed substantially between the two mountain lion populations (Fig. 2). Of the 19 mountain lions captured in STX, one died as a result of research related capture. Of the 18 radio-collared mountain lions, nine were alive at the end of the study. Mortality causes during the study for nine radio-collared cats included hunting (N = 5), professional trapping (N = 2), natural (N = 1) and unknown (N = 1) causes.

In the WTX population, 21 mountain lions were captured. Three cats died as a result of research-related capture. Two kittens were released without collaring, so their subsequent status was unknown. Of the 16 remaining radio-collared cats, 15 died from predator control (trapping); the other one was shot by a hunter (Guzman 1998, Pittman et al. 2000). All predator control and hunting mortalities occurred outside of the park boundaries (Pittman et al. 2000).

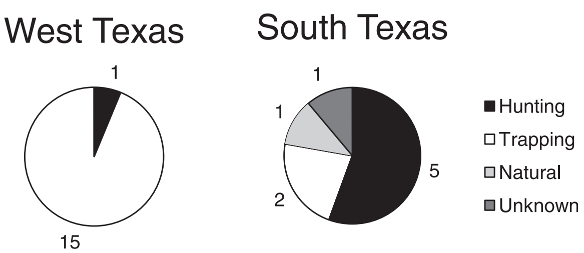

Figure 2. Mortality causes of radio-collared mountain lions in western Texas (during 1993-1997), and southern Texas (during 1994-1996) excluding research-related capture mortalities.

Discussion

Much of the published research documenting mountain lion population characteristics in the United States has occurred in Florida and the western United States with only a few studies in the southwestern states (Arizona = Cunningham et al. 2001, New Mexico = Logan & Sweanor 2001 and Texas = Harveson et al. 1997, 1999, 2000, Pittman et al. 2000 and Walker et al. 2000). Logan & Sweanor (2001) provided one of the most comprehensive studies on mountain lions in the San Andres Mountains, New Mexico, during 1985-1995, and the proximity of this study site, to our west Texas study site makes it an ideal choice for comparison purposes. Additionally, Cunningham et al. (1995 and 2001) published information on mountain lions in Arizona with similar mortality factors as in our Texas populations. For comparison purposes, we have focused our discussion on these previous studies in the southwestern United States, due to the proximity and similarities in habitat and population pressures.

Population structure

Sex and age ratios from our study sites varied considerably, due to small sample sizes. Logan & Sweanor (2001:73-74) reported that resident females outnumbered males on average 1:1.4 (M:F) and 1:1.6 for each of their study sites, with the highest difference of 1:1.8 and 1:1.7, respectively. This skewed sex ratio has been reported in other studies (e.g. Lindzey et al. 1994, Spreadbury et al. 1996). In WTX the sex structure of adult captured mountain lions was 1:1; however, for STX the adult segment was skewed heavily toward males (3:1). This disproportionate number of males in the capture sample was likely a result of high mortality of females. In STX, eight female and three male mountain lions that were not part of our radio-marked sample were harvested from our composite range during the study.

Anderson & Lindzey (2005) evaluated age and sex structure for hunted mountain lions in Wyoming. They found that subadults were the most vulnerable age class, followed by adult males and finally adult females as the least vulnerable to be harvested. If Anderson & Lindzey's (2005) suppositions hold true in southern Texas, the high number of harvested females (N = 9) may imply that this population suffered from high hunting pressure. This could also explain the lack of subadults detected during this study, where only one female and two males were noted in the STX and WTX studies, respectively.

Density

The reported mountain lion densities in our study sites are some of the lowest densities reported for North America. Few studies have documented density estimates similar to ours (0.27-0.43 mountain lions/100 km^2). Lambert et al. (2006) estimated 0.36-0.67 mountain lions/100 km^2 in the Pacific Northwest, and Hemker et al. (1984) and Lindzey et al. (1994) reported densities of 0.3-0.50 mountain lions/100 km^2 (during 1979-1981) and 0.37 mountain lions/100 km^2 (during 1979-1987), respectively, from the same study area in southern Utah. Most estimates of mountain lion density are an order of magnitude greater than ours, including Logan & Sweanor's (2001) which ranged from 0.8 to 2.1 mountain lions/100 km^2.

Several factors may account for the disparity between our density estimates and those reported in previous studies. First, we used a minimum known number alive, whereas other studies have employed different techniques. Thus, our density estimates are admittedly conservative. However, in both study sites, field researchers felt that 75-90% of the adult segment of the populations were trapped and radio-marked. This was supported by intensive field observations coupled with telemetry monitoring, where most sign found could be attributed to radio-marked mountain lions.

Another factor that may contribute to the low density estimates is the high levels of human-related mortality reported in our study. This is especially true for our WTX study site, where 16 of 19 mortalities were attributed to human-related harvest (trapping = 15 and hunting = 1). Additionally, for our STX study site, nine of 19 mountain lions died during our monitoring period, and seven of the nine deaths were human-related (trapping = 2 and hunting = 5).

Reproduction

Mountain lion studies throughout North America have documented an average litter size of 2-3 kittens (Logan & Sweanor 2001). Our estimates of litter size (STX = 1.77, WTX = 1.54) were inherently biased low because many litters were not documented until they were 6-9 months old, thus allowing for undocumented mortality of kittens. Furthermore, Harveson (1997) and Guzman (1998) reported short average birth intervals (STX = 12 months and WTX = 18 months); however, their sample sizes were small (STX = 2 and WTX = 4).

Survival and mortality factors

In comparing our findings to other mountain lion studies in the desert southwest, we noted that survival and mortality factors were comparable when considering timing and location of different population pressures. Logan & Sweanor (2001) reported mean annual survival rates of 0.91 for adult males and 0.82 for adult females from an unexploited population in New Mexico, whereas we observed overall survival rates of 0.75 (STX) and 0.70 (WTX) from exploited populations in Texas. These differences were primarily due to different mortality factors. The relatively low mortality observed in New Mexico was driven primarily by intra-specific strife, and the relatively high mortality, which we observed, was dominated by human causes (i.e. hunting and trapping). Survival rates from an exploited mountain lion population in Arizona (Cunningham et al. 2001) were lower (0.58 for adult males and 0.67 for adult females) than the combined survival rates, which we observed, but mortality factors were similar between the studies. If we extrapolate our non-hunting season survival rates to annual rates and compare them to the sex-averaged survival rate from New Mexico and Arizona, respectively, we noted similarities based on differences in population pressures among areas (Fig. 3).

Although the Big Bend Ranch State Park provided protection for radio-collared mountain lions, survival rates for the WTX population was lower than for the STX population. This suggests that the protected area within the park was too small (1,210 km^2) to fully protect this mountain lion population. In WTX, a number of mountain lions captured within the park boundaries were subsequently trapped or hunted legally in areas surrounding the park (N = 16). Collared mountain lion mortalities in STX were represented primarily from hunting (56%) and what seems to be opportunistic trapping (22%).

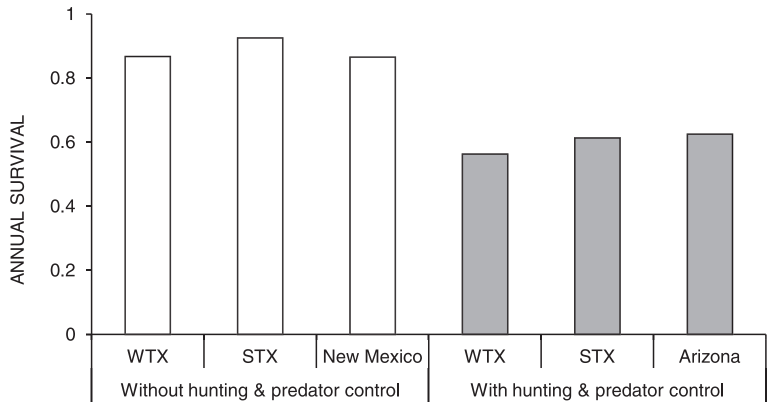

Figure 3. Comparison of mountain lion survival rates for populations with (Arizona; Cunningham et al. 2001) and without (New Mexico; Logan & Sweanor 2001) hunting and predator control to seasonal rates in western Texas (WTX) and southern Texas (STX). Seasonal rates for the Texas populations were extrapolated to annual rates and sex-specific rates for Arizona and New Mexico were averaged for comparison purposes.

This is not the case for WTX, where the main cause of death (94%) was attributed to predator control.

Management implications

Using tissue samples from our captured lions, Walker et al. (2000) demonstrated that the two populations were not geographically connected. The STX population had less genetic variation than the WTX population (Walker et al. 2000). Such a reduced gene flow between STX and WTX suggests that Mexico could serve as a source population for STX. Based on their analysis, Walker et al. (2000) argued that the STX and WTX mountain lion populations should be treated as independent management units for the implementation of monitoring and harvest strategies. Furthermore, Pena (2002) evaluated the attitudes of Texans regarding the management of mountain lions in Texas. She suggested that the majority of urban and rural Texans supported a defined season (open hunting season with specific dates) as opposed to an open (current status) or a closed season (no hunting season; Pena 2002). These studies coupled with the documented differences in density, survival and mortality factors from our study suggest that mountain lions should be managed on a regional level in Texas.

Future research should examine the impacts of these demographic parameters for both mountain lion populations. The demographic parameters estimated in our paper could be used to construct population models for the southern Texas and western Texas ecoregions. These models could provide insight into the viability of each population and assist managers by evaluating various management scenarios, and their predicted impacts on these populations.

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