

Conservation Science in Fire-Prone Natural Areas

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Abstract. To understand and protect wildlife within southern California natural areas will require consideration of both the effects of fire on wildlife and the consequences of habitat fragmentation on remaining wildlands. Fire effects on wildlife can be direct, resulting in increased mortality and population declines for some species, and indirect, resulting in habitat changes which influence wildlife populations over time. In unfragmented areas, the regional consequences of these effects may not be substantial, although the size and spatial configuration of the burn, and the intensity of the fire will influence the ultimate outcome. In fragmented areas, on the other hand, fire effects on wildlife can interact with fragmentation effects to substantially impact native biota. Specifically, the effects of fire can interact with extinction mechanisms, connectivity loss, and edge effects to influence wildlife persistence and recovery after fire. These interactions between fire and fragmentation will significantly affect conservation efforts in fire-prone natural areas. Several management strategies can be implemented and information needs can be addressed to help mitigate some of these concerns.

Keywords: Conservation; fire; habitat fragmentation; Santa Monica Mountains; wildlife.

Introduction

For millions of years, southern California has been subjected to a variety of dramatic natural forces that have helped to shape its landscapes and affect its natural communities. Now human activities are also exerting dramatic influences on natural areas and impacting remaining native biota. To understand and protect increasingly rare examples of natural habitat in southern California, will require consideration of these major influences. In particular, knowledge of the effects of fire on the ecosystem, including its effects on vegetation and wildlife, must be incorporated into an understand-

ing of the consequences of habitat loss, habitat fragmentation, and development encroachment on wildland areas.

In recent years, these two issues have often been approached separately by resource managers and conservation biologists. Although significant and important work has been conducted in both areas, much less has occurred linking these two fields, particularly for conservation and management applications. But, as again demonstrated in the fall of 1993, fires will continue to be a dominant force in southern California wildlands, and significant habitat loss and fragmentation related to development has and will continue to occur. As a result, there is a tremendous need to examine these effects together to properly manage and conserve remaining biota.

This paper examines these issues from the perspective of both a natural resource manager and an applied scientist attempting to address these issues on an ongoing basis. Although this perspective reflects many specific concerns of the National Park Service in the Santa Monica Mountains National Recreation Area, it also represents general concerns encountered by all those attempting to manage natural open space in coastal southern California or other rapidly developing, fire-prone natural areas.

The specific objectives of this paper are threefold. First, I provide a general overview of the effects of fire on wildlife in southern California and discuss some variables which can complicate this general picture. This overview draws from numerous published studies, focusing primarily on vertebrate species in southern California ecosystems, as the effects of fire on vegetation are addressed in several other papers included in this volume. Second, I discuss some consequences of habitat fragmentation on wildlife, specifically linking these ideas to the discussion of wildlife fire effects, and their implications for wildlife conservation and resource management in southern California. Finally, I conclude

with some thoughts on management recommendations and critical information needs, partly based on experiences from the Santa Monica Mountains National Recreation Area.

The Effects of Fire on Wildlife in Southern California

The effects of fire on wildlife can be divided into two broad categories: direct effects that occur during the fire and later, indirect effects that occur following the fire (Quinn 1979, Lyon et al. 1978, Barro and Conard 1991, Patton 1992). Both effects can significantly influence the long-term ecological dynamics of a community by directly altering local wildlife population levels and by dramatically changing habitats in areas that have burned. A number of published studies exist which address various aspects of these issues, many based on research conducted in southern California.

Direct effects on wildlife during a fire

Because so many fires happen unexpectedly, detailed, quantitative studies of the direct effects of fire on wildlife are somewhat limited, particularly for large-scale wildfires. In addition, most research in this area has focused on small animals, including small mammals, reptiles, and some birds. Despite these limitations, a substantial amount is known about how fires directly affect local wildlife species.

For relatively small vertebrates, fires can and do cause substantial mortality and can result in local declines or extinctions (Wirtz 1974, McClure 1981, Peek 1986, Patton 1992). This is particularly true for species that live above ground and tend to retreat to brush or nests for safety — species such as brush rabbits, woodrats, some reptiles, and sedentary chaparral birds. For example, dusky-footed woodrats (*Neotoma fuscipes*) can be markedly impacted by fire. This species, which inhabits thick chaparral vegetation, has been observed to become disoriented during fires, haphazardly retreating to woody nests or to roads and trails to escape oncoming flames (Quinn 1979). Of course, these strategies are often ineffective and may be fatal, resulting in extensive woodrat mortality within a burned area.

Despite these potential local population impacts for small vertebrates, most researchers agree that at the regional population level, mortality effects are very small if not negligible (Quinn 1979, Patton 1992, Wirtz 1977). This is because the species that are most affected are able to rapidly re-colonize burned areas through recruitment and immigration from surrounding areas as the habitat recovers following the fire. Thus,

while local extinctions may occur for some species, at the landscape level these impacts are generally regarded as insignificant.

Many small animals are able to survive fire by burrowing or seeking refuge in unburned patches or other safe areas (e.g., within rock outcrops). For example, in underground burrows or under rocks, survival has been documented for small mammals and reptiles just 10 to 20 cm below the soil surface (Howard et al. 1959, Lawrence 1966, Quinn 1990). In these locations, animals can be insulated from surface heat as high as 500° C (Wirtz 1977). Lawrence (1966) conducted field experiments which demonstrated that, for rodents, survival can occur within burrows because vapor pressures remain low enough to facilitate evaporative cooling from lung surfaces. In another study, 75% of Heermann's kangaroo rats (*Dipodomys heermanni*) were estimated to survive within an experimental burn by retreating to their burrows (Quinn 1979).

Small vertebrates can also survive fires by retreating to unburned refugia within and around the burn (Quinn 1986). For example, some lizards survive fires by escaping within rock outcrops (Kahn 1960) and some bird species have been observed escaping fires by retreating to unburned islands and other safe areas during fires (McClure 1981). In general, although there is a potential for significant local mortality for some species of small animals, a number of species are capable of retreating from oncoming flames, even if they remain within the immediate burn area.

Much less is known about the direct effects of fire on larger vertebrates. Where studies have been conducted, however, mortality has generally been found to be quite low (Barro and Conard 1991). In general, larger animals such as mule deer (*Odocoileus hemionus*), bobcats (*Felis rufus*), coyotes (*Canis latrans*), and gray foxes (*Urocyon cinereoargenteus*) are capable of escaping fires by fleeing (Peek 1986, Patton 1992). For example, in an extensive study of Columbian black-tailed deer (*Odocoileus hemionus columbianus*) in northern California, deer were observed moving ahead of a fire and were seldom injured (Taber and Dasmann 1957). In addition, carcasses and other evidence of large animal mortality immediately following fires are relatively rare.

Overall, the direct effects of a fire are not considered substantial for most larger animals at the regional level. In addition, although fire impacts can be fairly dramatic for smaller species in localized areas and sometimes result in local extinctions, even small species can escape fires by burrowing and seeking refuge in safe areas. For those species which do suffer fire-induced mortality, the population-level effects over the

long-term are not generally considered significant. These species tend to have high reproductive capacities and can readily recolonize recovering habitat from surrounding unburned sites.

*Indirect effects on wildlife following a fire —
postfire succession*

In addition to the potential direct effects of fires on wildlife, fires also dramatically modify the available habitat within burned areas (Peek 1986, Patton 1992). In particular, the habitat composition, structure, and resource availability for wildlife may be drastically altered for a wide variety of species and these effects may persist for several years following the fire. However, just as burned vegetation proceeds through a predictable postfire succession sequence, so too do wildlife communities. As the habitat changes and wildlife species recolonize burned areas, the community eventually begins to appear and function much as it did prior to the initial burn.

Much of the empirical work on postfire wildlife recolonization and succession has come from studies of small mammals. A number of important studies have examined this issue in some detail and have led to a fairly complete understanding of the general pattern of postfire small mammal succession in southern California chaparral (e.g., Wirtz 1982, Wirtz et al. 1988, Quinn 1990). In general, in the first few months to few years following a fire, small mammal communities change in predictable ways, which primarily reflect the fire survival abilities and habitat preferences of the small mammal species that occur in the area.

Based on various empirical studies of small mammal postfire succession, it is possible to construct a very generalized ten-year postfire sequence which illustrates these points. In the first one to three years following a southern California chaparral fire, species capable of surviving the fire in the burned area as well as species more adapted to the relatively open habitat conditions found after the burn may predominate. Examples of such species include kangaroo rats (*Dipodomys* spp.), which burrow during fires and prefer more open habitats, and other species, such as deer mice (*Peromyscus maniculatus*) and California voles (*Microtus californicus*), which benefit by more open chaparral. Over the next two to five years, as shrub species recover more fully, habitat generalist species may dominate. For example, California mice (*Peromyscus californicus*) and pocket mice (*Perognathus* spp.), which tend to occur in both open areas and within more densely vegetated cover, may increase in frequency. Finally, after five to ten years, as dense shrub cover returns to the landscape, chaparral-requiring species such as brush mice (*Peromyscus*

boylii) and woodrats (*Neotoma* spp.) become most prevalent. At the same time, those species which previously took advantage of the more open areas (e.g. the voles and kangaroo rats) may become rare or absent from the postfire community.

Similar patterns of postfire bird succession have also been observed (Wirtz 1982, Peek 1986), with different species dominating at different times over the sequence of habitat changes. For bird species, increased dispersal and movement ability may help explain observed patterns of more rapid postfire succession relative to small mammals.

For large mammal species, postfire use of burned areas also reflects habitat conditions and resource availability, in addition to species-specific adaptations and habitat preferences. In general, most large mammals return fairly quickly to burned areas (e.g., within months) (McClure 1981) and often take advantage of the modified site conditions resulting from the fire. For example, rapid growth of herbaceous plant species following fires provides abundant and high quality forage for herbivores (Peek 1986, Komarek 1985). This flush of resources can attract and facilitate population increases for herbivores, such as deer, in burned areas, which are known to rapidly recolonize and occupy burned areas in large numbers (Taber and Dasmann 1957, Bleich and Holl 1982, Tiller et al. 1986). In addition, the abundance of prey following fires facilitates recolonization and occupation by predators, such as coyotes, which have been observed returning to burned areas within weeks after a fire (Wirtz 1977, McClure 1981). In general, because of higher resource levels and modified habitat characteristics favorable to a wide variety of species, large mammals may actually be more abundant in the first three to eight years following a fire than before it.

Overall, following initial dramatic habitat changes resulting from a fire, a predictable succession of wildlife recolonization and occupation occurs which reflects patterns of vegetation succession, wildlife species habitat preferences, and species-specific survival probabilities during fires. Although wildlife abundance and species composition may vary through this succession, diversity and richness is little changed over the postfire period.

Fire has been and continues to be a natural process in fire-prone natural areas of southern California. Not surprisingly, the species within these communities have evolved a variety of individual mechanisms to respond to fires and to even take advantage of the ecological opportunities available following fire events. Although the indirect effects of fire on wildlife can be dramatic, the overall consequences should be viewed within the context of this natural process and not as a negative impact.

Variables complicating fire effects on wildlife

The descriptions above provide fairly broad and simplified overviews of the effects of fire on wildlife communities. The ultimate results of a burn, however, will be influenced by a variety of additional complicating variables. Two of these variables, the size and spatial configuration of the burn and the intensity of the fire, can have dramatic effects on how wildlife communities respond to and recover from a fire.

Fire size and spatial configuration can substantially alter postfire wildlife recovery patterns (Peek 1986, Quinn 1979). Although some individual animals are able to survive within a burn area immediately after a fire, most must recolonize the site from the periphery of the burn or from unburned refugia in the burned area. In addition, wildlife species that are capable of surviving the direct effects of the fire often depend on the cover and resources available at unburned edges, both within and around the burn. These dependencies have been observed for a variety of species, including rabbits and other small mammals, various birds, and particularly for larger mammals such as deer, coyotes, and other predators (McClure 1981, Quinn 1986, Quinn 1990).

It follows from these observations that a larger, more contiguous burn may result in fewer recolonization sources and less cover and resources available for wildlife. This will alter the recovery patterns for local species by affecting the availability of dispersal opportunities and limiting critical resources needed to maintain populations within recently burned sites. In addition, a larger, more contiguous fire would be expected to provide fewer escape opportunities for wildlife, thus increasing the amount of direct mortality resulting from the burn. Overall, one might expect to find a greater probability for local extinctions in larger burns and a more prolonged succession (i.e., a slower recovery) for some wildlife species (Quinn 1986).

In addition, a very intense, fast moving fire would be expected to result in increased direct mortality within a burn area (Lawrence 1966, Peek 1986, Wirtz et al. 1988). In this situation, fleeing is more difficult, burrowing is less effective, and unburned refugia may be less likely to occur. This may be particularly relevant to Santa Ana wind-driven fires which occur in very dry, old chaparral — fires similar to those that occurred throughout southern California in the fall of 1993.

Very few studies have directly addressed the complicating factors of fire size, configuration, and intensity on wildlife populations (Wirtz et al. 1988, Quinn 1979, 1986). In fact, most wildlife studies have focused on prescribed burns which not only provide very controlled circumstances, but also tend to be

smaller and leave substantial amounts of unburned edge. In these cases, mortality has been found to be relatively low and recovery rates fairly rapid. It is likely, though, that this is not always the general rule. The critical role of unburned refugia and the interacting influences of fire size, shape, and intensity may significantly alter the abilities of wildlife communities to respond to and recover from fire, particularly in large, intense wildfires during Santa Ana conditions.

Overall, while many vegetation species seem to be fairly well-adapted to a variety of fire intensities and sizes (fire frequencies may be a significant exception to this rule, see vegetation articles from this volume), these variables may be critical for postfire wildlife successional patterns and recovery rates. From studies of both the direct and indirect effects of fire on wildlife, the mechanisms of wildlife survival and recovery suggest that burn size and shape, and fire intensity will strongly affect postfire recovery patterns. Specifically, larger, more complete, and more intense fires may result in slower recovery and higher local extinction probabilities for a number of wildlife species.

Habitat Fragmentation and Fire: Implications for Wildlife

In addition to fire effects, a second critical issue influencing the ecology of southern California wildlands are the effects of human-induced landscape fragmentation on wildlife distribution and abundance. Throughout southern California, rapid development is encroaching upon and subdividing remaining natural areas. The effects of fragmentation on wildlife are many and varied, and can profoundly affect the capability of remaining wildlands to support wildlife populations (Wilcox 1980, Simberloff and Abele 1982, Shaffer 1990). For the purposes of this paper, I focus on three specific fragmentation concerns — including extinction mechanisms, the loss of connectivity, and the influence of edge effects — which can directly interact with fire to affect wildlife distribution, abundance, and persistence. By linking these concerns to fire effects on wildlife, substantial implications are illustrated for wildlife conservation efforts in southern California and other fire-prone natural areas.

Extinction mechanisms

Island biogeographic theory predicts, and empirical research has demonstrated, that as habitats are subdivided, local extinctions may occur (Willis 1974, Diamond 1975, Diamond and May 1981, Diamond 1984). This is because small, isolated habitat fragments are less capable of supporting as many species as larger, more contiguous areas. Several mechanisms have been

identified which may contribute to this increased extinction rate, most related to the fact that small areas support smaller populations, and smaller populations do not persist as long as larger populations (Wilcox and Murphy 1985).

Important mechanisms which may operate to increase extinction risks for species in fragmented habitats include demographic stochasticity, inbreeding depression, and environmental stochasticity and catastrophes (Shaffer 1981, Soulé and Simberloff 1986). Specifically, small populations are more likely to go extinct due to random variation in demographic parameters over time. For example, biased sex ratios within generations may critically impact the persistence of a small population. Small populations are also more prone to inbreeding, increasing the amount of genetic homogenization and the chances that certain genetic problems will become fixed in the population. Finally, random environmental changes and natural catastrophes that reduce populations sizes are more likely to drive smaller populations extinct than larger populations.

These mechanisms will preferentially impact extinction-prone species (Terborgh 1974). For example, species which depend on large areas for survival or have specific habitat needs will more likely suffer greater impacts in fragmented systems. In addition, if local extinctions do occur, recolonization is less likely because isolated habitats often do not occur close enough to one another or to source habitats to receive any recolonists (Wilcox and Murphy 1985).

For all of these reasons, as development isolates remaining wildlands in southern California, local extinctions are expected. Empirical results from studies of chaparral fragments in San Diego County support this contention (Soulé et al. 1988, Bolger et al. 1991, Soulé et al. 1992). In particular, during the mid-1980s, 37 isolated canyons of varying size and isolation age were surveyed for chaparral birds and small mammals. The basic results from these studies were that smaller fragments supported fewer species, presumably because many sites were too small to support viable populations of species; older fragments had fewer species, as more species disappeared over time; and species went extinct in a predictable order over time, presumably because some species were more prone to extinction than others. These results were true for both small mammals and chaparral birds (Soulé et al. 1992), and similar results have been demonstrated in other fragmented systems, as well (e.g., Galli et al. 1976, Whitcomb et al. 1981).

These fragmentation consequences may be particularly relevant to fireprone natural areas, especially as these regions become increasingly subdivided by de-

velopment. As discussed above, fire can act as an extinction mechanism, leading to the local disappearance of certain species from a burned area. In a "natural," unfragmented system, the long-term population impacts of such extinction events may be inconsequential because of the availability of nearby unburned habitat to serve as a recolonization source. However, if fire-induced extinctions occur in fragmented habitats, local populations may be eliminated entirely if the burn encompasses the entire habitat fragment.

In addition, because local population sizes are already relatively small in habitat fragments, fire-associated mortality may actually push population levels below viability thresholds for some species. These reduced populations will be further subjected to various extinction mechanisms, increasing the chances of their removal from the habitat fragment (Gilpin and Soulé 1986). If the affected fragment is not close enough to recolonization sources, local extinctions can be permanent.

Loss of connectivity

Another important consequence of habitat fragmentation and development encroachment is the loss of connectivity within formerly continuous habitats (Noss 1987, 1991, Saunders and Hobbs 1991). Habitat fragmentation within a region can reduce connectivity by isolating habitats from one another. For many species, this removes options for movement between remaining habitat patches. In addition, within a natural area, development encroachment may impact or make impassable formerly available interconnections, thus reducing the options available for wildlife to move unimpeded across the landscape (Harris and Gallagher 1989). For example, while some developments may not actually isolate a particular habitat area, they may include roads or other obstacles which remove wildlife movement options. These types of connectivity losses, both within and between patches, may critically affect how wildlife species respond to fires.

If fire-induced mortality results in local extinctions, the recolonization potential for the area depends on its proximity to other occupied habitats. For example, when a fire burns through an area, postfire recovery for many species depends on their ability to return to the burned landscape from surrounding unburned areas. In a fragmented system, individual patches may be too far apart to allow species movements to occur between patches. If this is the case, a local extinction caused by a fire can be permanent, with little or no chance for the species to return to the patch from which it was removed.

In addition, many species rely on their ability to flee oncoming flames to escape fire. This strategy depends on having escape routes within habitat areas which can be used by fleeing wildlife to retreat to safe areas. Loss of connectivity can remove these options, constraining both the ability of wildlife to find escape routes and the availability of safe, unburned refugia. As a result, fire-induced mortality may increase and postfire recovery opportunities may be lost. This will likely affect the long-term persistence of wildlife species in remaining fire-prone natural areas. Thus, the combined effects of fire and fragmentation will work together to increase the chances for species declines in fragmented areas.

The influence of edge effects

Habitat fragmentation also greatly increases the amount of exposure between natural habitats and adjacent developed areas (Schonewald-Cox and Bayless 1986, Scott 1995). This exposure can facilitate the movement of impacts from developed areas into nearby natural systems (Janzen 1983, Lovejoy et al. 1986, Saunders et al. 1991, Kelly and Rotenberry 1993). Such intrusive impacts or edge effects may result from a variety of mechanisms. For example, direct habitat alteration may occur near edges due to the proximity of human activities (Schonewald-Cox 1988), or edge-adapted predators and competitors may impact "interior" species near human-modified edges (Soulé et al. 1992, Paton 1994). These impacts can potentially have significant effects on conservation efforts in fragmented landscapes.

The movement of these types of impacts into natural areas can be facilitated by disturbance events (Orians 1986, Fox and Fox 1986, MacDonald et al. 1988, Buechner and Sauvajot in press). For example, recent research has indicated that, while intact chaparral ecosystems may be quite resistant to many community-level edge effects, if disturbances occur, invasion of edge-related impacts may be greatly facilitated (Sauvajot and Buechner 1993, Buechner and Sauvajot in press, Sauvajot unpublished data). This is most likely because edge-associated impacts are also disturbance-associated (e.g., alien plants, various types of human-commensal species, direct habitat alteration from increased human access, etc.). Thus, a more disturbed area may be susceptible to greater impacts from edge effects.

In natural systems in southern California, fires have been and continue to be an important component of overall ecosystem function. At the same time, fires have historically served as a mechanism of "natural" disturbance, with vegetation and wildlife communities having evolved various adaptations accordingly. However, in human-dominated, fragmented landscapes, fre-

quent fires near fragment edges may facilitate the invasion of edge-associated impacts into natural areas. In particular, the openings and disturbed areas created after fires can accelerate invasions by disturbance-associated exotic plants, increase the entry of development-associated species into natural areas, and facilitate other types of human-caused habitat alteration due to the proliferation of social trails and off-road vehicle access routes. These impacts can be exacerbated by increased fire frequencies associated with nearby human development. In fact, substantial anecdotal evidence suggests that human-caused fires are more frequent in fragmented habitats.

This combination of frequent human-caused fires and disturbance-facilitated impact invasions along the urban-wildland interface may significantly alter the distribution and abundance of native wildlife in fragmented systems. In addition, large, intense fires which are potentially more damaging to native biota may also be more effective at facilitating intrusive edge effects. Very little research has addressed these issues, however, the consequences of these interactions between fire and edge effects may substantially affect wildlife conservation and management efforts in fire-prone natural areas.

Concluding Remarks

In order to understand, protect, and conserve natural resource values in fire-prone natural areas, it is critical to link knowledge of fire effects on wildlife with information on the consequences of habitat fragmentation. Although substantial information is available for both, very little research has linked these two critical issues. As habitats continue to be fragmented and fires continue to occur, creating this linkage will become more important to preserve increasingly rare examples of southern California natural communities.

Several areas of concern exist which suggest that wildlife persistence and recovery may be substantially altered in fragmented areas following fire, based on existing knowledge of fires and fragmentation. First, the combined extinction effects of fire and fragmentation may result in the local disappearance of some species in fragmented areas that have burned. In addition, the loss of habitat connectivity due to fragmentation and development encroachment may limit the ability of some wildlife species to respond to and recover from fires. Finally, frequent human-caused fires in fragmented areas may facilitate the movement of intrusive edge effects into natural systems, impacting native biota. Each of these effects is exacerbated with the occurrence of large, intense fires like those of fall 1993 in southern California.

Management strategies and information needs

Several management strategies are available to help mitigate some of the problems associated with fire and fragmentation. In the Santa Monica Mountains National Recreation Area, the National Park Service is working cooperatively with a number of agencies and the public to attempt to implement these strategies to protect resource values in southern California.

First and foremost, large blocks of significant natural habitat should be identified and protected. By protecting large core areas, fragmentation impacts can be minimized and fire recovery and succession mechanisms can operate under more "natural" conditions. Second, ecologically sensitive prescribed burning should be conducted to promote a shifting mosaic of postfire successional communities. This will not only support a wider variety of native species, it can also reduce the probability of large-scale, catastrophic wildfires from occurring. Such wildfires, because of their size and intensity, can result in greater wildlife impacts over the long run, particularly in fragmented areas. Finally, agencies, organizations, and the public should work together to identify and facilitate the completion of high priority research projects and studies which address pressing fire management information needs.

Specifically in the areas of fire, fragmentation, and wildlife conservation, a number of issues would benefit from additional research and studies. For example, the effects of fire on wildlife under different fire sizes, shapes and intensities is an area where very little research has been conducted but is critical for management needs. Very little information is available on how surrounding human-modified landscapes influence postfire recovery patterns in natural areas, even as most natural areas in southern California are being encroached upon or surrounded by development. Very little research has been done on the significance of human-caused wildfires as potential extinction mechanisms and edge effect facilitators in fragmented habitats. In all cases, results of such research should directly address the implications for fire management planning, prescribed burning, and reserve design in fire-prone natural areas.

Acknowledgments. I wish to thank Drs. Jon Keeley, Ron Quinn, Tom Scott, and Bill Wirtz for helpful discussions and information critical to the development of this paper. Rose Rumball-Petre, and Jim Benedict provided helpful comments on earlier drafts of this manuscript. Support for this research was provided in part by the National Park Service, Santa Monica Mountains National Recreation Area.

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