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Effects of Environmental Enrichment on Reproduction

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Although there have been few demonstrations of a direct empirical relationship between environmental enrichment and reproductive success in captive animals, indirect and anecdotal evidence indicates the importance of physical and temporal complexity for reproduction. We discuss three major mechanisms through which environmental enrichment that specifically increases the complexity of an animal's surroundings may influence reproductive physiology and behavior: developmental processes, modulation of stress and arousal, and modification of social interactions. In complex environments developing animals learn that performing active behavior produces appropriate functional outcomes. Learning to control their environment influences their ability to adapt to novel situations, which may profoundly influence their reproductive behavior as adults in breeding situations. Chronic stress may compromise reproductive physiology and behavior; enrichment reduces stress by providing increased opportunity for behavioral coping responses. However, some degree of acute stress may be beneficial for reproduction by maintaining an animal's level of responsiveness to socio-sexual stimuli necessary for sexual arousal and reproductive activation. Finally, environmental enrichment may influence reproductive success by stabilizing social groups, reducing aggression and increasing affiliative and play behaviors. It is concluded that multi-variate multi-institutional behavioral research in zoos will play an increasingly important role in the successful captive propagation of many species by closely examining relationships between environmental variables and reproductive potential of individual animals.

Key words: rearing, stress, arousal, environmental complexity, social behavior

INTRODUCTION

In a 1965 paper on reproduction of zoo animals, Heini Hediger pointed out that we have come a long way in providing the species-specific "biological elements" to the environments of captive wild animals that enable them to breed. He noted that in Darwin's time it was thought that there was a special "sterility factor" associated with captivity that prevented many mammals and birds from reproducing. Indeed, as

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of 1951, there had been no successful captive births of species such as Indian rhino (*Rhinoceros unicornis*), okapi (*Okapia johnstoni*), gorilla (*Gorilla gorilla*), cheetah (*Acinonyx jubatus*), and flamingo (*Phoenicopterus ruber*). Within a decade, however, several zoos had been successful in breeding these species as a result of heightened awareness of the importance of external factors on the reproductive behavior of captive wild animals. For most zoo animal species, we now readily recognize the importance of providing environments with certain basic requirements for reproduction, such as nutrition, ambient climate, social groups, and substrates for courtship, nesting, parturition, and maternal/paternal behaviors. The field of zoo biology seeks, in part, to understand the many biological processes that intervene between an animal's environment and its reproductive outcome, processes that may be physiological, psychological, and/or social in nature. Observational research on the behavior of animals in zoos is one of the primary means of examining these processes. Through behavioral research we gain information needed to design and maintain captive environments that promote animal well-being and reproduction. In addition, animals are increasingly being bred and reared in captivity for release into free-ranging wild habitats. The survival and reproduction of such animals is dependent on behavioral research to assess the influence of very specific aspects of captive environments on the development and performance of natural behaviors [Shepherdson, 1993].

The relatively new, but rapidly expanding, field of environmental enrichment aims to provide environments of greater physical, temporal, and social complexity that affords animal more of the behavioral opportunities found in the wild. In so doing, enrichment may improve the reproductive potential of individual animals. Although many environmental factors have been demonstrated to be of critical importance to reproduction, such as the size and composition of social groups for gorillas [Beck and Power, 1988], the reproduction-enhancing effects of manipulations aimed at increasing the physical and temporal complexity of captive environments are less well documented. In this paper, we use the term *environmental enrichment* in considering only the effects of environmental manipulations that provide greater physical and temporal complexity, excluding manipulations of social groupings.

To date, few studies have successfully demonstrated a direct empirical relationship between enrichment of the physical environment and reproductive success. However, a considerable body of literature exists in the areas of developmental psychobiology, behavioral biology of stress, and reproductive physiology that points to the important role that enrichment may play in furthering the success of captive breeding for many species. This paper will discuss some of the mechanisms through which environmental enrichment may improve the general well-being of individual animals, which in turn influences their potential for reproduction. For an animal to reproduce under captive conditions, it needs to be responsive to the social, physical, and psychological stimuli in its surroundings that are appropriate for courtship, copulation, incubation, parturition, parental, and other reproductive behaviors. A goal of environmental enrichment is to provide physical environments that promote and maintain an animal's responsiveness to such stimuli. For the sake of discussion, we suggest that the physical environment may influence responsiveness to the socio-sexual stimuli involved in reproduction, separately and in aggregate, through (1) developmental processes, (2) modulation of stress and arousal, and (3) modification of social interactions.

DEVELOPMENTAL PROCESSES

The complexity of the captive rearing environment can have far-reaching effects on the developing animal, including changes in behavior, physiology, and brain morphology. In laboratory experiments, rats reared in a so-called ''enriched'' environment, consisting of group housing in a large cage with daily exposure to novel objects and additional environments to explore, have a higher cerebral cortex weight, increased number of glial cells, and increased dendritic branching in the visual cortex, compared to rats reared alone in small cages with no changes in stimulation [for a review, see Uphouse, 1980]. Enriched rats also exhibit higher motoric activity and increased exploration. More detailed behavioral analyses by Renner and Rosenzweig [1986] have revealed that rats reared under enriched conditions demonstrate greater behavioral diversity and complexity while exploring objects. These qualitative differences in investigatory behavior reflect functional differences in learning that may exert a significant influence on an animal's ability to behave adaptively when faced with a novel situation or threat, such as a predator [Renner, 1988].

In physically complex surroundings, a developing animal is more likely to learn that it can exert ''control'' over its environment. The animal learns that it can adjust its behavior so as to produce a desired change in the stimulation it is receiving from its surroundings. ''Control'' is a psychological construct meaning that the animal has developed contingencies between performance of a behavior and its functional outcome. The importance to a developing animal of having control over its environment has been demonstrated experimentally by Joffe et al. [1973]. Rats reared in an environment in which they could control changes in lighting and presentations of food and water by lever presses (the contingent group) were compared with a control group housed in identical cages in which lever presses were possible but changes in lighting, food and water were based on (yoked to) the lever presses made by the contingent group of rats. Both groups thus received equal amounts of light, food, and water, but only the contingent group had control over them. When tested at 60 days of age in a novel, large, bare arena, the contingent group rats were more active, and explored more, than rats from the noncontingent group. They also demonstrated less emotionality in a novel situation (as indicated by the number of defecations). Mineka et al. [1986] reared rhesus monkeys (*Macaca mulatta*) in three different environments: one in which they could control access to food, water, and treats; a second one, identical to the first but with rewards delivered randomly; and a third in which there were no rewards (daily feedings were given). When tested between ages 6 and 10 months, the monkeys with control over rewards were bolder in the presence of a fear-provoking toy, were more eager to enter a novel room, explored it more, and adapted more quickly to stressful separation from peers than the monkeys reared without control.

A wild animal example of the consequences of experience with physical complexity is provided by black-footed ferrets (*Mustela nigripes*) that are captive-reared for reintroduction into the wild in Wyoming. Captive-born ferrets reared in large, seminatural outdoor cages with live prey and real burrows in which they could dig had more than a threefold higher survival rate upon release than those reared in indoor cages with live prey and artificial, pipe burrows in which they could not dig [Vargas, 1993]. In the wild, the ferrets reared in the most complex environment seemed better able to use and remain in good burrows, resulting in lower predation rates, than ferrets reared without experience with real burrows [A. Vargas, personal communication].

These and other experiments show how early experience with physically complex environments may result in adult individuals better able to adapt behaviorally to new situations. The absence of early learning about contingencies between behavior and its outcome may produce an adult animal that is less likely to investigate actively and learn about novel situations, and more likely to respond to change with excessive emotionality. While failure to respond actively to environmental changes may not be deleterious for an animal accustomed to a monotonous, stimulus-poor environment, many events involved with reproducing require active behavioral responses. Introductions to mates, mating, and bearing and caring for young, may be both novel and stressful, and animals reared in less enriched environments may not cope as well with these situations. This may be one reason why breeding introductions in zoos are often difficult. It may also help explain the observation in some species, that wild-born and -reared animals have greater reproductive success in captivity than captive-born individuals (e.g., great apes, some ungulates).

MODULATION OF STRESS AND AROUSAL

The term *stress* has a negative connotation because of its well-established deleterious effects on health, well-being, and reproduction. Stress can inhibit reproductive function through a variety of mechanisms which appear to be species-specific [Moberg, 1985]. Hediger [1964] describes situations in which captive animals have injured themselves or failed to breed because of the inability to escape from the presence or sight of caretakers or visitors. It is generally considered important to maintain zoo animals in a "stress-free" environment. However, what is "stressful" differs between species and between individuals. Also, stress may have beneficial arousal-inducing effects on reproduction; environmental enrichment may modulate the direction of this effect.

Stress refers to the complex of physiological, homeostatic, and behavioral responses elicited by aversive physical or psychological stimuli (stressors). The physiological and behavioral impact of a stressor is highly dependent on (1) the subjective perceptions of the individual, and (2) the individual's behavioral response style. There appear to be at least two different patterns of response to a perceived aversive situation: (1) an active "fight–flight" pattern characterized by increased activity, increased sympathetic adrenal–medullary activation and related increases in cardiac output and arterial pressure; and (2) a more passive "conservation-withdrawal" pattern characterized by decreased environment-directed activities, increased adrenocortical activation and suppressed reproductive function [Engel, 1967; Henry and Stephens, 1977; Koolhaas et al., 1985; Suomi, 1987]. Any individual may exhibit both types of response pattern, and the pattern more likely to occur is dependent on rearing experience and genetic background [Gentsch et al., 1981; Mormede et al., 1984; Suomi, 1987].

Prolonged stress can have significant effects on reproductive function. Changes in stress hormones of the hypothalamic–pituitary–adrenal axis may result in a reduction of steroid hormone levels, which translates into a reduction of libido or sexual activity, or suppression of reproductive physiological function. For example, stress-related increases in glucocorticoid secretion act directly at the testicular level in socially living male olive baboons (*Papio anubis*) to decrease testosterone secretion [e.g., Sapolsky, 1987]. In low-ranking marmosets (*Saguinus fuscicollis*) social stress caused by harassment or overcrowding may lead to hormonal suppression of fertility [e.g., Epple, 1978]. Transportation stress in cows reduces ovulation rate [Edwards et al., 1987]. Potentially stressful disturbances of pregnant mammals as a result of husbandry procedures, such as relocation or removal from a social group, may affect the viability and hormonally mediated development of the young, their emotionality, or even their later sexual behavior. For example, Ward [1972] has shown that as adults, the male offspring of female rats stressed daily in the last week of gestation showed reductions in attempted copulations and ejaculation responses as adults.

While prolonged or chronic stress may have inhibitory effects on reproduction, short-term stress-induced activation of the sympathetic adrenomedullary system, releasing catecholamines norepinephrine (NE) and epinephrine (E), may be involved in sexual activation. There is evidence in many species that acute "stress" may facilitate or even be necessary for reproductive activation. In rats, dogs, chimpanzees, and humans, stress-induced sexual arousal is well documented (e.g., "the Coolidge effect," tail-pinch and footshock-induced copulation in rats, masochism in humans [Antelman and Caggiula, 1980]). In particular, NE has been implicated as an arousal component of estrus induction in at least two induced ovulators—the prairie vole and the rabbit [Carter et al., 1986; Ramirez and Beyer, 1988]; in rats and guinea pigs, the preovulatory surge of luteinizing hormone (LH) is also preceded by augmented NE neurotransmission in the hypothalamus and preoptic area [Hansen et al., 1980; Fernandez-Guasti et al., 1985; Vincent and Feder, 1988]. Sapolsky [1986] provides evidence that acute social stress induces a rise in testosterone in dominant male baboons that is mediated by the sympathetic nervous system; increased testosterone probably confers a reproductive advantage in these males by accentuating aggressive tendencies during competition over mates [Sapolsky, 1986].

This apparent contradiction in the effects of stress on reproduction suggests that animals might need to experience some level of environmental novelty or uncertainty (i.e., stress) on a regular basis to be able to optimize individual vigilance and responsiveness to environmental changes [Dantzer and Mormede, 1983; Wiepkema and Koolhaas, 1993]. Many types of acute stressors result in increased general "arousal" that may be physiologically and psychologically beneficial to an animal. Arousal is attended by increased locomotory behavior, increased glucocorticoid secretion from the adrenal cortex, and increased catecholamine secretion from the adrenal medulla [Cannon, 1914; review, Glavin, 1985; Natelson et al., 1987]. A large body of theoretical and empirical animal research has been concerned with the concept of arousal, due largely to the fact that behavioral performance of animals in experimental test situations has long been observed to vary with their general level of activation or arousal [Berlyne, 1960; Hennessy and Levine, 1979]. At low levels of arousal, behavioral performance is suboptimal. Lengthy exposure to stimulation-deprived conditions results in decreased stimulation-seeking or exploratory behavior, lethargy, and slower habituation to novel surroundings in rats, pigs, monkeys, and humans [Butler, 1957; Inglis, 1975]. High levels of arousal may correspond to uncontrolled "fight–flight", or response inhibition and behavioral suppression. However, intermediate levels of arousal are associated with enhanced alertness, exploratory and/or locomotory behavior, faster learning rates, and improved immune response [Weiss et al., 1989]. Physiologically, experiments with rats have demonstrated that periodic acute exposure to a stressor leads to an augmented norepinephrine response to novel stimulation [Kvetnansky et al., 1984; Konarska et al., 1989].

Whether an animal's reproduction is suppressed or stimulated by stress may depend on the animal's ability to *cope* with the stressor, and thus, its duration and intensity. Coping refers to an active psychological *process* that occurs to alter initially threatening or aversive environmental conditions having stress as a major component [Levine, 1983]. Coping is modulated by the complexity of the animal's environment and the response options it provides the animal; if the animal has control over its environment it is able to perform an active behavioral response to reduce the impact of the stressor (e.g., hiding, fleeing, attacking). In general, when an animal cannot respond to a stressor by performing an active behavior; i.e., when it lacks control over its environment, predicting the occurrence of the stimulation becomes more important in an animal's ability to cope with it [for reviews, see Weinberg and Levine, 1980; Abbott et al., 1984]. There are complex interactions between the controllability and predictability components of coping responses [for reviews, see Overmeier et al., 1980; Mineka and Henderson, 1985]. The effectiveness of predictive information in coping with aversive stimulation may be modulated by control over the situation [Davis and Levine, 1982], or there may be preferences for predictability, depending on the type of stressor [Badia et al., 1979].

The evidence that environmental enrichment promotes reproduction by reducing stress is mostly implied rather than empirical, for such studies are only starting to be carried out in zoos. In a survey of maternal behavior of female captive gorillas, Miller-Schroeder and Paterson [1989] conclude that the larger and more complex the enclosure, especially with respect to sight barriers, privacy refuges and dens that allow escape from conspecifics and the public, the better the female's chances of rearing her infants normally. There is experimental evidence that enrichment has stress-reducing effects by giving animals greater control and/or prediction over their environment. Increasing the physical complexity of the environment provides opportunities for responding with an appropriate behavioral response (e.g., hiding or fleeing) or, perhaps, by diverting attention away from the stressor [Carlstead et al., 1993a]. Rats or pigs subjected to a frustrating experimental situation that was stress inducing were able to inhibit pituitary–adrenal stress responses (i.e., increased glucocorticoid secretion) if provided with enrichment in the form of opportunities to perform behaviors such as chain-pulling, drinking, or wheel-running [Heyback and Vernikos-Danellis, 1979; Dantzer and Mormede, 1981]. Adding manipulable devices to the otherwise barren cages of laboratory-housed adult rhesus monkeys lowered basal plasma cortisol concentrations and decreased abnormal behaviors [Line et al., 1991]. Similar adapation was observed in captive leopard cats (*Felis bengalensis*) moved to a chronically stressful environment in which large cat species (*Panthera*) were housed nearby (i.e., potential predators to leopard cats); providing a variety of hiding places reduced chronically elevated cortisol concentrations to baseline levels and reduced stereotypic pacing [Carlstead et al., 1993a]. Failure to lower stress-induced activation of the hypothalamic-pituitary-adrenal axis may eventually compromise reproductive function, as indicated in a different experiment, with domestic laboratory cats. Carlstead et al. [1993b] found that the stressors an unpredictable caretaking routine responsible for chronic cortisol elevation also reduced pituitary sensitivity to gonadotropin-releasing hormone (GnRH). Such examples demonstrate that environmental enrichment may have an important influence on an animal's ability to modulate physiological stress responses, which may potentially lead to a behaviorally or hormonally mediated inhibition of reproductive function.

There is more direct, albeit anecdotal, evidence that environmental stimulation that increases activity and arousal may benefit reproductive function in a variety of species by promoting optimal neuroendocrine states required for adequate physiological and behavioral responsiveness. Translocation of female pigs [Paredis, 1982] or domestic cats [Wildt, 1980] has been reported to have a synchronizing effect on estrous cycles. Introducing unfamiliar partners, and enhancing the cage space of gorillas has often been reported to stimulate breeding [O'Donoghue, 1982; Maple, 1983]. One of the most interesting features of anecdotal accounts of cheetah breeding is the preponderance of evidence that acutely arousing or stressful events facilitate mating. A pair of cheetahs attempted their first mating after they became excited when given live chickens for the first time [Davis, 1964]. Allowing cheetahs to view or kill live prey, or transferring them to new quarters, or a new zoo, are manipulations reported to be useful in facilitating breeding [Seager and Demorest, 1978]. D.E. Wildt [personal communication] reports that cheetahs will breed naturally after anesthesia, electroejaculation, and/or laparoscopy. A female at Fossil Rim Wildlife Center mated with a previously isolated male 5 days after she was removed and subjected to a veterinary exam [Stearns, 1991]. Arousing aggressive interactions upon introduction to a mate are correlated with successful breeding [Manton, 1970; Benzon and Smith, 1974].

Many of the above-mentioned situations that facilitate sexual arousal are examples of "fortuitous" enrichment. However, there is increasing consensus that some level of "stress," particularly short-lasting acute stress, should be incorporated into environmental enrichment programs as a means of providing animals with experience necessary for competently responding to environmental change [Dantzer and Mormede, 1983; Beck, 1991; Wiepkema and Koolhaas, 1993]. While there is no single way of determining whether a given zoo animal is maintained at an optimum level of intermittent arousal, attentive zoo staff essentially do so by providing enrichment that eliminates lethargy and signs of chronic stress but avoids overagitation or excitability. This requires close behavioral monitoring of the effects of enrichment on each individual under one's care. Providing a complex varying environment is more likely to allow an animal to experience intermittent exposure to novel and uncertain situations that are stress inducing, but such environments also allow the animal to cope with the stress by responding with an appropriate active behavior.

MODIFICATION OF SOCIAL INTERACTIONS

Characteristics of the physical environment can have important qualitative and quantitative effects on the dynamics of social interaction. These in turn are likely to influence reproductive success. In particular, undesirably high levels of aggressive behavior may disrupt or prevent the establishment of stable social groups necessary for reproduction. Environmentally-induced abnormal behaviors can also inhibit the development of normal social interactions.

One of the most fundamental environmental factors for socially housed captive animals is cage size, and the interrelated variable, population density. Reduced cage size for example, has been correlated with increased aggression in bush babies (*Galago galago*) [Nash and Chiltern, 1986], reduced reproduction in cotton-topped tamarins (*Saguinus oedipus oedipus*) [Snowdon et al., 1984], and decreased pack stability in wolves (*Canis lupus*) [Sullivan and Paquet, 1977]. However, the effects of cage size, and shape, on social behavior are rarely simple. They tend to be highly species and context specific. As a case in point, Erwin [1986] describes how doubling the space available for a group of pigtailed macaques (*Macaca nemestrina*) by providing a second room resulted, unexpectedly, in increased aggression because it allowed females to remove themselves from the aggression-mediating influence of males.

Chamove [1989] has suggested that much physical enrichment can be seen as analogous to increasing the psychological space available to animals. One way of achieving this is to increase environmental complexity by dividing space with locomotor and visual barriers, in other words to provide cover or seclusion. Estep and Baker [1991] found that the provision of cover to stumptailed macaques (*Macaca arctoides*) significantly reduced aggression and the ability of the dominant male to monopolize copulations. Similarly, Erwin et al. [1976] showed that provision of escape areas to stable groups of pigtailed macaques could reduce aggression. The frequency of affiliative behaviors was increased in a pair of giant pandas (*Ailuropoda melanoleuca*) after a complex climbing structure with multiple resting platforms was installed in their enclosure [Kleiman and Peters, 1990]. However, as with cage size, the effect of cover is highly species and situation specific. More research, on a wider range of species, is needed.

The quantity, quality, and distribution of food resources also can have a great influence on captive social dynamics, as indeed it does in the wild. Anderson and Chamove [1984] found that aggression in a stumptailed macaque group was reduced in the presence of food scattered into a woodchip litter substrate. Similar results were reported by Boccia [1989] for pigtailed macaques, and by Bloomsmith et al. [1988] for chimpanzees (*Pan troglodytes*). Provision of puzzle feeders may also have the potential for beneficial affects on social behavior, such as reduced abnormal behavior and higher levels of affiliative interactions. However, the context within which these are used is critical. Maki et al. [1989] documented increased aggression and competition as a consequence of providing a single puzzle feeder to a group of chimpanzees.

Adding novelty and manipulable objects to an enclosure may also have an important role to play in the establishment of stable, balanced, social interactions. Macedonia [1987] recorded increased activity, including play, in sifakas (*Propithecus verreauxi*) and Markowitz [1982] describes many cases in which enrichment with manipulable objects has resulted in a greater range and diversity of positive social interaction in a number of species. Moodie and Chamove [1990] documented increased levels of affiliative interactions in captive groups of tamarins after exposure to brief, novel, threatening events. This is, perhaps, another example of the beneficial behavioral effects of short-term acute stress.

Clearly, enrichment techniques can be used to modify social interactions to optimize the chances of reproduction in captivity. Many of these effects, however, are subtle and highly species specific. As the results of more studies become available, it may become easier to predict the most effective strategies.

DISCUSSION

Behavioral research on environmental enrichment has taught us that increasing the degree of control that captive animals have over their environments benefits well-being. We know that increasing the physical and temporal complexity of captive environments can facilitate normal development and coping with stress, reduces abnormal behaviors, increases activity and behavioral diversity, and promotes appropriate social interactions. Several enrichment techniques are known to be effective in producing behavioral benefits: providing structures to increase use of space; providing visual barriers for hiding, privacy, and camouflage; providing substrates for natural digging, scentmarking, grooming, nesting, and resting behaviors; giving animals control of microclimate through provision of heaters, light, shade, and shelter; increasing visual exploration through lookouts and perches; multiple feedings of diverse and varied foods; increasing food-handling time by feeding unprocessed foods (e.g., browse, whole fruits, carcasses); requiring work for food, such as searching for hidden food, manipulation of food-containing objects, and problem solving; unexpected additions of toys or novel objects; training for husbandry manipulations; improving relationships with human caretakers; and changing environment through addition and removal of scents, sounds, furniture, and plants.

However, there is still much to be gained from behavioral research that focuses on a more direct understanding of the relationship between environmental variables and behavioral and physiological *reproductive parameters* in captive animals. Certainly, more studies are needed that look at the effects of environmental enrichment on exploratory behavior, general arousal and responsiveness to challenging stimulation [e.g., Ogden et al., 1990; Shepherdson et al., 1993]. Studies of the direct effects of enrichment on sexual activation, sperm quality and quantity, and sensitivity to gonadotropins and other stimulatory hormones would be a worthwhile area of investigation. Increased knowledge is also greatly needed concerning the influence of individual differences in behavior and temperament on reproduction. In particular, studies of the effects of environmental manipulations on behavior are needed that consider the *long-term consequences* for the development, health, well-being, and reproduction of the animal. This requires multivariate analyses on a multi-institutional level designed to investigate the relationships between behavior and specific environmental stimuli, health, husbandry, and reproductive results. The few behavior studies carried out across multiple institutions have provided valuable information concerning environmental influences on reproductive success [e.g., Mellen, 1991]. Many husbandry surveys have also been carried out in which data on aspects of animal housing and management have been collected from many institutions. When subjected to statistical analyses, such surveys permit conclusions to be drawn about the relative importance of various husbandry procedures for reproductive success, as they have for red pandas [Roberts, 1989] and lowland gorillas [Miller-Schroeder and Paterson, 1989]. Analysis of populations of animals distributed over a number of idiosyncratic institutions is an important current and future direction for behavioral research in zoos that promises to validate and refine the role of environmental enrichment programs in the captive propagation of wild species.

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