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TECHNICAL REPORT

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The historical development of juvenile mortality and adult longevity in zoo-kept carnivores

Marco Roller[1] | **Dennis W. H. Müller**[2] | **Mads F. Bertelsen**[3] | **Laurie Bingaman Lackey**[4] | **Jean-Michel Hatt**[5] | **Marcus Clauss**[5]

[1]Zoological Garden Karlsruhe, Karlsruhe, Germany

[2]Zoological Garden Halle (Saale), Halle (Saale), Germany

[3]Copenhagen Zoo, Frederiksberg, Denmark

[4]World Association of Zoos and Aquariums (WAZA), Barcelona, Spain

[5]Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Zurich, Switzerland

Correspondence
Marcus Clauss, Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstr. 260, 8057 Zurich, Switzerland.
Email: mclauss@vetclinics.uzh.ch

Abstract

Zoos need to evaluate their aim of high husbandry standards. One way of approaching this is to use the demographic data that has been collected by participating zoos for decades, assessing historical change over time to identify the presence or absence of progress. Using the example of carnivores, with data covering seven decades (1950–2019), 13 carnivore families, and 95 species, we show that juvenile mortality has decreased, and adult longevity increased, over this interval. While no reason for complacency, the results indicate that the commitment of zoos to continuously improve is having measurable consequences.

KEYWORDS
Carnivora, husbandry, progress, survival, zoo

1 | INTRODUCTION

Zoos are institutions where humans interact with a large variety of species kept for display and species conservation. Over the centuries, the value of zoos has expanded to include recreational, educational, and scientific purposes. Their conservation aims focus on both ex situ programs in terms of conserving individual species as such (Conde et al., 2011), and in situ actions in terms of contributing to habitat (and hence, indirectly species) conservation (Gusset & Dick, 2011; Tribe & Booth, 2003). These activities are performed with an increasing focus on animal welfare (Hosey et al., 2013).

There are several narratives about the aim of animal welfare. They include "proximal cause narratives," arguing that it is only justified, or socially acceptable, to pursue the zoological institution's other aims if animal welfare is not compromised and is state-of-the-art (Gray, 2017). While this narrative is plausible and valid, it tends to overshadow the "ultimate cause narrative" that optimal animal welfare is an aim of zoological institutions for its own sake, because of the self-concept of zoo professionals, and their vision that it is possible to create an ideal environment, providing a meaningful yet anxiety-free life for individual animals that foregoes the many causes of fear and harm they are exposed to in natural habitats (Clauss & Schiffmann, 2021). Creating such conditions on a species-specific basis is a learning process, and zoos need to know if they are making progress.

In their dedication to professional animal husbandry, zoos have long instigated record-keeping systems that facilitate tracking individual animals and evaluating life stage-specific mortality (Carisch et al., 2017; Müller et al., 2011; Tidière et al., 2016; Young et al., 2012). This also allows assessing progress in husbandry practices: one would expect uncontrolled, life stage-specific mortality (e.g., neonatal mortality) to decrease over time, if husbandry standards have improved over the years, as has been demonstrated in individual species like okapi (*Okapia johnstoni*) (EAZWV Summer School Participants & Clauss, 2008), orangutans (*Pongo* sp.) (Wich et al., 2009) or chimpanzees (*Pan troglodytes*) (Havercamp et al., 2019).

Here, we test whether several metrics—neonate/juvenile mortality and the proportion of 1-year-old animals that reach 50% of the species' reported maximum longevity—changed in 95 zoo-kept species of the order Carnivora over the past seven decades. We chose Carnivora because their neonate mortality in zoos has received particular attention in the literature (Clubb & Mason, 2003; Kroshko et al., 2016). Our expectation was, based on the global commitment of the zoo community to continuously improve husbandry systems, that age-specific mortality would decrease, and longevity hence increase over time. We did not aim to explore the detailed effects in different species or the sexes; however, because of large overall differences in husbandry requirements between families (where, e.g., pinnipeds differ from nonaquatic Carnivora), we included the families as factors in the analyses.

2 | MATERIALS AND METHODS

We obtained records for all carnivore species from Species360, an online database platform that is used by more than 1200 zoos worldwide to manage their animal data, with known dates of birth and death, from which the subsequent data were calculated (Species360 Research Data Agreement # 2019-Q3-RR3). The reporting of animal data into the repository is mandatory for zoos accredited by the European Association of Zoos and Aquaria (EAZA) but not others like the American Association of Zoos and Aquaria. It must be noted that while it is very unlikely that adult animals that are alive at member zoos are not entered into the system due to their visibility, there is no independent control of whether newborns are consistently entered. In the experience of one of the coauthors (LBL), the practice of not entering newborn animals until they survived to about 1 month of age was more common in earlier decades of the last century than it is now. This would result in an underestimation of positive developments in neonate mortality. The data we worked with did not contain indications of the cause of death; this means that we could not differentiate between individuals that died or were euthanized due to disease, and individuals that were euthanized ("culled") only for management reasons.

Data were processed separately by decades. For neonate and juvenile mortality, the percentage of all animals that died within their first day of life, the first 10 days of life, the first 30 days of life, the first 100 days of life, and the first year of life was calculated for each cohort (born in the respective decade). While first-day, first-month, and first-year mortalities are common points of interest in the zoo community (L. Bingaman Lackey, pers. obs.), the additional time points of 10 and 100 days were chosen to more closely track the development in the earlier parts of the first year. Addressing species-specific setpoints, such as age at weaning, age at sexual maturity, or age at dispersal, would be relevant in future studies. For adult longevity, the proportion of a cohort (born in the respective decade and having reached the age of one year) that reached at least 50% of the maximum lifespan of the species was calculated. Depending on the maximum lifespan of the respective species, the current decade may have needed to be excluded for species that do not reach half of their maximum lifespan within a decade. We use this proxy to describe adult longevity for two reasons: (i) We use the 50% cut-off because a simple "average" calculation would be impossible for many cohorts due to the long longevity of the species in question. (ii) We do not use absolute values (like maximum lifespan, average lifespan, or the age at which a certain % of the population are still alive) because these absolute measures do not allow a comparison of different species. For example, these measures are all expected to be higher in species of a higher body mass, that is, large species typically on average "get older" (Lemaître et al., 2014). Therefore, it is important in comparative studies to express the achieved ages on a comparable background—one of which is the % of the maximum lifespan recorded in a species (Müller et al., 2011). Thus, a species that achieves, on average, 50% of its possible maximum lifespan lives comparatively "longer" than a species that achieves, on average, only 30% of its possible maximum lifespan.

As maximum lifespan, data from the AnAge database (de Magalhães & Costa, 2009) was used, except in cases where our data set indicated a higher value under the condition that it did not represent a single extreme value remote from the rest of the population, but that the value represented a maximum that was the final point of an uninterrupted sequence of lifespans from the population mean to the data in question. For both evaluations, only species were included that had at least 25 births (for juvenile mortality) or 25 animals of 1 year of age (for lifespan). First, evaluations were performed on a species level. Then, these cohorts were used to calculate averages for the 13 carnivore families presented in the remaining data set.

The decade-specific data collections on mortality and lifespan for the carnivore families were subjected to statistical evaluation using linear models (and testing of the residuals for normal distribution) in R. First, models were evaluated that also contained a covariate to assess autocorrelation (i.e., the corresponding value of the preceding year; this reduced sample size to those years having a preceding year). Then, models without the autocorrelation covariate were performed. All models included, as independent variables, the decade, the carnivore family, and the "family × decade" interaction to test whether differences in temporal development across families existed. The significance level was set to .05. Graphics for individual species are provided in Online Supporting Information.

3 | RESULTS

Generally, there was autocorrelation in the data sets, with values of the preceding decade significant for Day 30 mortality, Day 100 mortality, Day 365 (first year) mortality, and close to significance for adult longevity (Tables 1–6). For all neonate and juvenile mortalities, there was a significant effect of decade, carnivore family, and a significant decade × family interaction, indicating differences between carnivore families in the progress made in neonate/juvenile mortality reduction (Tables 1–5). By contrast, the decade × family interaction was not significant for adult longevity, indicating that improvements of this measure were consistent across carnivore families (Table 6).

When displayed at the family level, a pattern emerges that juvenile mortality in zoo populations differed between carnivore

TABLE 1 Neonate mortality in zoo-kept carnivore families at the day of birth (Day 0 mortality) over decades

	df	*F*	*p*	*p* normality residuals
Model (*n* = 66)	Day 0 mortality = Decade × Family + VPreviousDecade			.480
Decade	1	161.876	<.001	
Family	12	24.743	<.001	
Decade × Family	12	1.850	.073	
Value previous decade	1	1.782	.190	
Model (*n* = 79)	Day 0 mortality = Decade × Family			.419
Decade	1	140.308	<.001	
Family	12	20.768	<.001	
Decade × Family	12	2.030	.039	

TABLE 2 Neonate mortality in zoo-kept carnivore families after 10 days (Day 10 mortality) over decades

	df	*F*	*p*	*p* normality residuals
Model (*n* = 66)	Day 10 mortality = Decade × Family + VPreviousDecade			.691
Decade	1	203.077	<.001	
Family	12	7.188	<.001	
Decade × Family	12	3.302	.002	
Value previous decade	1	1.127	.295	
Model (*n* = 79)	Day 10 mortality = Decade × Family			.451
Decade	1	118.842	<.001	
Family	12	2.916	.004	
Decade × Family	12	2.871	.004	

TABLE 3 First month-mortality mortality in zoo-kept carnivore families (Day 30 mortality) over decades

	df	*F*	*p*	*p* normality residuals
Model (*n* = 66)	Day 30 mortality = Decade × Family + VPreviousDecade			.482
Decade	1	177.849	<.001	
Family	12	4.813	<.001	
Decade × Family	12	3.182	.003	
Value previous decade	1	6.534	.015	
Model (*n* = 79)	Day 30 mortality = Decade × Family			.285
Decade	1	169.925	<.001	
Family	12	3.265	.001	
Decade × Family	12	3.673	<.001	

TABLE 4 100 day-mortality in zoo-kept carnivore families (Day 100 mortality) over decades

	df	*F*	*p*	*p* normality residuals
Model (*n* = 66)	Day 100 mortality = Decade × Family + VPreviousDecade			.813
Decade	1	191.808	<.001	
Family	12	4.344	<.001	
Decade × Family	12	3.248	.003	
Value previous decade	1	7.445	.009	
Model (*n* = 79)	Day 100 mortality = Decade × Family			.619
Decade	1	217.738	<.001	
Family	12	2.939	.003	
Decade × Family	12	4.460	<.001	

TABLE 5 First year-mortality in zoo-kept carnivore families (Day 365 mortality) over decades

	df	*F*	*p*	*p* normality residuals
Model (*n* = 66)	Day 365 mortality = Decade × Family + VPreviousDecade			.491
Decade	1	216.093	<.001	
Family	12	3.951	<.001	
Decade × Family	12	3.656	.001	
Value previous decade	1	5.880	.020	
Model (*n* = 79)	Day 365 mortality = Decade × Family			.594
Decade	1	257.717	<.001	
Family	12	2.937	.003	
Decade × Family	12	4.131	<.001	

TABLE 6 Adult longevity (proportion of individuals having reached 1 year of age that attained at least 50% of the species' maximum lifespan) in zoo-kept carnivore families over decades

	df	*F*	*p*	*p* normality residuals
Model (*n* = 42)	Adult longevity = Decade × Family + VPreviousDecade			.236
Decade	1	37.015	<.001	
Family	12	18.500	<.001	
Decade × Family	12	1.922	.114	
Value previous decade	1	4.264	.056	
Model (*n* = 55)	Adult longevity = Decade × Family			.982
Decade	1	105.662	<.001	
Family	12	18.532	<.001	
Decade × Family	12	1.452	.199	

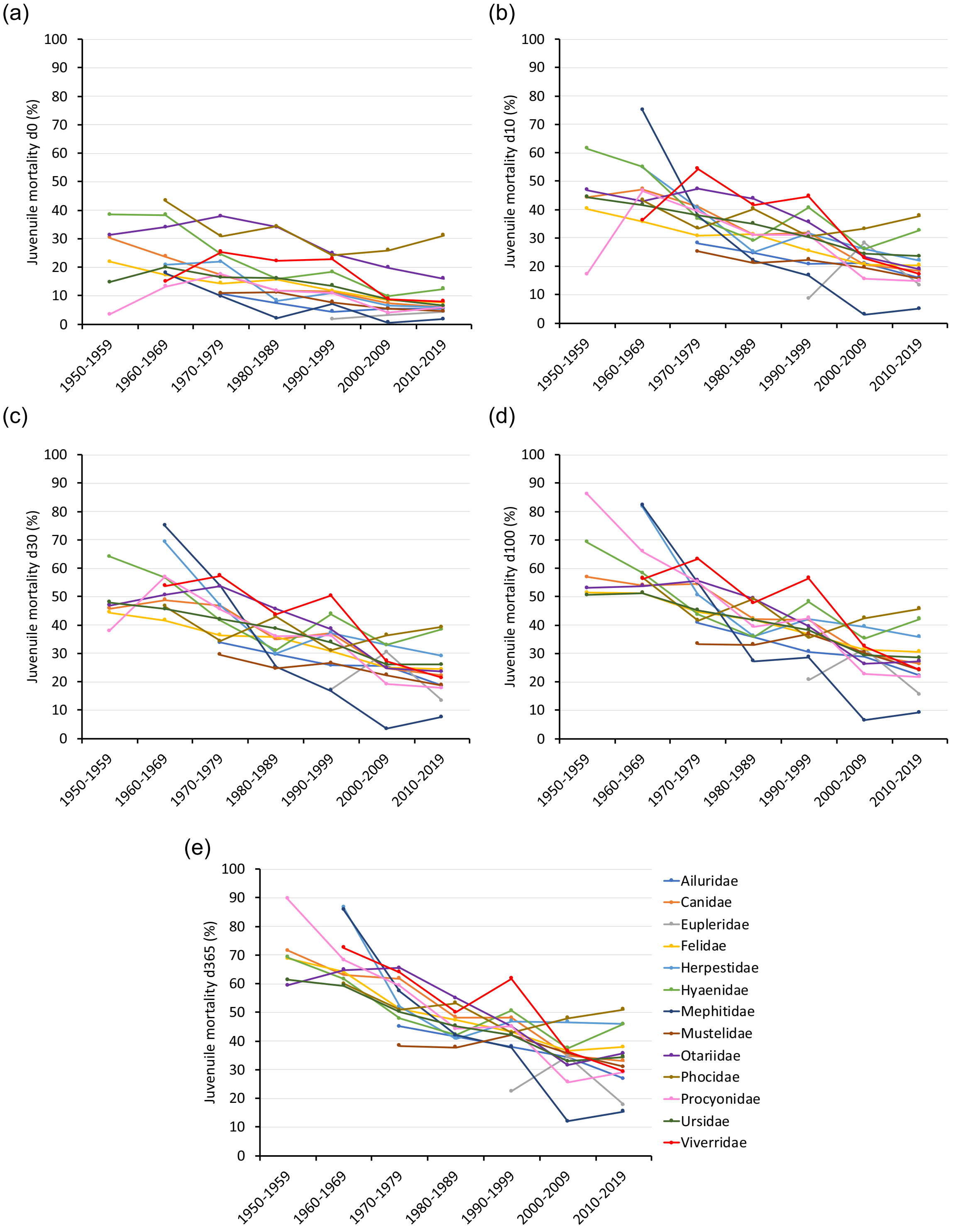

FIGURE 1 Historical development of (a) first-day mortality, (b) 10 day-mortality, (c) first month-mortality, (d) 100 day-mortality, and (e) first year-mortality in zoo-kept carnivore families. Evaluation based on cohorts born within the respective decades. For statistics, see Tables 1–5.

families but has decreased over the decades, with differences in the pattern of decrease between families. The data patterns indicate that it was particularly the 10 day-mortality that was distinctively reduced, with mortality at higher ages basically just following the same pattern at the expected staggered higher levels (Figure 1).

At the same time, the proportion of one-year-old animals that reached 50% of the species' maximum longevity again differed

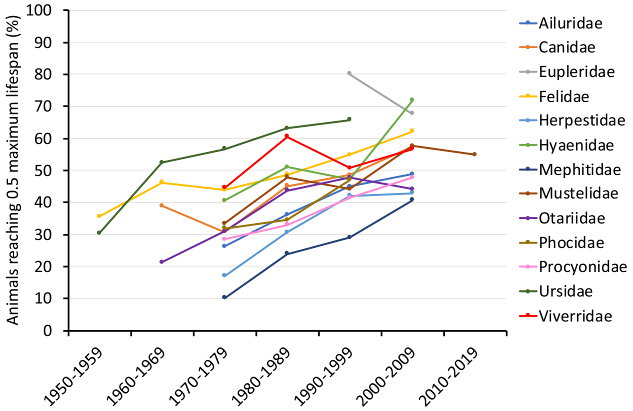

FIGURE 2 Historical development of adult longevity in zoo-kept carnivore families, measured as 1-year-old animals reaching 50% of the species' maximum lifespan. Evaluation based on cohorts born within the respective decades. For animals of most families born in the last decade, 50% of maximum lifespan could not be reached until the point of data evaluation.

between families, and increased significantly, uniformly for all families with at least three decades of data (Figure 2).

See the online Supporting Information for display of data at species level.

4 | DISCUSSION

The findings indicate that for the families represented in the study, in terms of neonatal-juvenile mortality and adult mortality, zoos' overall husbandry success has generally increased over the past decades. Therefore, when using zoo neonate mortality (Clubb & Mason, 2003) or zoo longevity as a covariate, one should ideally state the time frame reflected by the data and acknowledge that this is a "snapshot" of a specific period. Neither "zoo neonate mortality" nor "zoo longevity" should be considered "timeless" species-specific characteristics.

A decrease in mortality, and the corresponding increase in longevity, do not automatically represent an improvement in individual animal welfare. For example, if welfare is poor, one could argue that a longer life simply means a longer period of poor welfare. Yet, the opposite pattern—an increase in uncontrolled, life stage-specific mortality—would parsimoniously be interpreted as a compromise to welfare and to the global aim of zoo animal husbandry. It was previously suggested that zoo's general care, in particular, the absence of predators (or intra-guild competitors) and the absence of climate-induced food scarcity improves the longevity of zoo animals as compared with their free-ranging conspecifics in the majority of mammal species for which such a comparison was feasible (Tidière et al., 2016). In addition to that generally protective effect, the present data indicate that two easily measured indicators of husbandry success have been improving globally across zoos over the last decades. This should not induce complacency but be considered an indication that zoos are on the right track, and act as an incentive to maintain efforts for further improvement.

An important limitation of studies like ours is the lack of certainty of whether mortality was undesired, or was due to management culling. Theoretically, the developments outlined in our study could be the result of a global reduction in management culling. We do not consider this a likely scenario for two reasons. First, the personal observation on reporting practices mentioned in the methods section makes it unlikely that individuals that had been culled were reported in the earlier decades of the previous century. Second, the trend of an increase in the global zoo-kept Carnivora population (cf. Online Supporting Information) suggests that incentives for management-related culling should have increased in recent times with less available holding space in which to place offspring.

Evident questions arising from these broad analyses are the differences between carnivore families (and species). Whereas improvements in longevity for animals that have reached an age of at least 1 year were similar between Carnivora families, the improvement in early life mortality differed significantly between the families. This indicates that further improvement depends on family-, and most likely species-specific husbandry measures. An important question for the zoo community is what level of first-year mortality should generally be aimed for. In the natural habitat, first-year mortalities of 45% have been reported for polar bears (*Ursus maritimus*) (Wiig, 1998; current zoo decade: 52%), or more than 75% in cheetahs (*Acinonxy jubatus*) (Laurenson et al., 1992; current zoo decade: 33%). Detailed comparisons will be required to set goals for individual species. Specific comparisons with biological characteristics, living conditions, and timing of births in the natural habitat could help to improve the rearing of young animals. For example, the climate at the location of birth has been shown to affect the survival of zoo-kept okapi (Müller et al., 2010) or red panda (*Ailurus fulgens*) neonates (Princée & Glatston, 2016).

Whereas a reduction of *uncontrolled* mortality (due to accidents, diseases, intraspecific aggression, or other stressors that cannot be compensated for) is a clear aim of husbandry and welfare improvement, this need not necessarily apply to *controlled* mortality, that is, culling. Managed breeding of surplus to maintain populations at certain sizes, with the inevitable necessity of culling healthy individuals (a "breed and cull" system), has been repeatedly proposed to secure population sustainability and promote individual animal welfare (Bertelsen, 2018; Clauss & Schiffmann, 2021; EAZA, 2015; Hosey et al., 2013). Such a system allows animals the opportunity to experience the full range of their behavioral spectrum, with mating and raising offspring as a fundamental part of the ethogram of every species. This view hinges on the perception that a painless, unexpected, and well-timed death itself is not considered a welfare impediment. This practice typically involves culling at dispersal age, which is younger than the 50% mark used in the present study. Therefore, it will be important in future studies to differentiate between controlled mortality due to surplus culling, and unwanted mortality due to accident or disease. Finally, it will be a challenge to test whether zoos make similar progress in terms of increasing the nonmedical quality of life for the animals in their care. This includes a global reduction of stereotypies, increased use of species-specific adequate social groups, and an increase in mentally and physically appropriately challenging feeding methods. For example, a large number of methods have been suggested to improve feeding of specific species in terms of a number of meals, spatial distribution, and cognitive challenge (e.g., Clubb & Mason, 2007; De Cuyper et al., 2019; Law & Kitchener, 2019; Law et al., 1997; Shepherdson et al., 1993; Williams et al., 1996). For bears, Carlstead et al. (1991) performed a survey to provide an inventory of the feeding methods used and an estimate of how many zoos used them. Such surveys could be done for different groups—like the different carnivore families—on a decade basis, documenting whether such husbandry measures are increasingly applied in practice.

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CONFLICT OF INTERESTS

All authors are either employed by, or have major involvement with, zoological gardens.

DATA AVAILABILITY STATEMENT

Data availability Original data on a family level is available as an electronic supplement, and is graphically displayed for individual species in the supplementary information. Requests for original data on a species level should be addressed to Species360 at www.Species360.org.

ORCID

Marco Roller http://orcid.org/0000-0001-5678-0892
Dennis W. H. Müller http://orcid.org/0000-0001-9996-064X
Mads F. Bertelsen http://orcid.org/0000-0001-9201-7499
Jean-Michel Hatt http://orcid.org/0000-0002-7043-7430
Marcus Clauss http://orcid.org/0000-0003-3841-6207

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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