

{2153}

An Analysis of Inbreeding within Leopards in Captivity

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A number of species of mammals and birds are entered into international studbook systems in an effort to conserve them while educating the public about animals and the need to preserve our environment. Some of these pedigreed species have a comparatively large number of original, wild-born individuals within their gene pool; others do not. All too frequently living individuals which have been born into captivity and which are numerically greater than the total number of imported ancestors, perhaps 2-4 generations away from the wild, are derived from a very small number of wild ancestors. Such is often the case with various species or subspecies of large felids, and is becoming commonplace among those subspecies of leopards, *Panthera pardus*, included with the studbook.

Patterns of Management

Traditions and techniques of individual animal selection, propagation, and long range breeding have changed markedly over the last several years. In many instances, however, today's zoological park staff is forced to manage species, utilize individuals and develop propagation programs based on older, more "traditional" breeding situations. The breeding of siblings or parent-offspring was at one time commonplace but has fallen into greater degrees of disuse because of recent changes in exotic animal propagation. With no further importations from the wild likely for many species, it is now very important that those individuals within our collections be bred on the basis of sound genetic practices rather than undirected pairings.

A review of the leopard studbooks reveals practices which have led to present day levels of inbreeding. Many breeding pairs were commonly composed of littermate or parent/offspring matings. Littermate pairs were particularly expedient, quickly providing needed exhibit space once the young were mature while minimizing potential problems of incompatibility. This type of acquisition was considerably less time consuming than searching for unrelated specimens, and solved acquisition demands at a time when leopards were still being imported from the wild. Searching for unrelated pairs was more expensive and greatly increased the possibility of incompatibility. Finally, owning institutions did not desire to break up more readily salable pairs and risk having to maintain single specimens for long periods of time. Today, the end result of some sibling matings are individuals 3 generations removed from the wild, each generation itself a sibling pairing. Although statements of "conservation" frequently accompany such pair formation, the likelihood of "saving" any species with these practices is minimal.

Studbooks for 3 subspecies of leopards, the Amur Leopard, *Panthera pardus orientalis*; the Chinese Leopard, *P. p. japonensis*; and the Persian Leopard, *P. p. saxicolor*,

have been in existence for 5 years (SHOEMAKER 1979). This has provided the opportunity to review breeding practices spanning more than 20 years, and provides information that may improve chances for continuing captive propagation programs. As with other large species of felids, the acquisition and breeding of littermates is still too commonplace. Many times a single ♂, perhaps selected for physical or phenotypic attributes that appeal to the owner, has been used for breeding a large number of ♀♀ to the exclusion of other ♂♂ having different or more distant ancestry. Behaviorally some individuals are no doubt more adapted to captivity than others, a factor which favors some over others in pair formation. Pairings have also occurred which are based on parent/sibling combinations, sometimes out of necessity, likewise increasing the likelihood of inbreeding problems in subsequent generations.

Some early pairings were made with the anticipation of periodic additions from the wild. Only later did it become apparent that no such importations were likely to occur, and indeed did not occur. Understandably, some degree of inbreeding is unavoidable where only 2–3 pairs were initially imported. Today, greater awareness has developed of various breeding schemes on a theoretical and practical level for animals (WRIGHT 1921, MALECOT 1948) and which can be adapted to other species such as the leopard. In the case of the Amur Leopard, carefully managed programs of outbreeding are paramount, urgent, and ideally need to incorporate at a later date, those wild-born solitary ♂♂ still present in some collections.

Existing Backgrounds

The Chinese Leopard is the most common of all pedigree subspecies maintained in captivity. Over 50 individuals are living today, nearly all of which were born in captivity. Numerous individuals are bilaterally 2. generation and some are 3. generation.

Nearly all the Chinese Leopards are derived from 3 importations: Leipzig, London and Berlin (GDR), each importation consisting of a single pair of young animals. Although the exact origin of 2 pair [London and Berlin (GDR)] are not precisely known, it is entirely possible that one, 2 or all 3 pairs are themselves littermates, and that first stages of inbreeding began with their mating. Some of the pairs of living individuals are 2. and 3. generation captive births, each resulting from littermate matings. Such increasingly high levels of inbreeding will be difficult for subsequent generations to withstand, with decreased viability, abnormal sex ratios, increased natality, and decreased reproductive potential are very realistic problems of future generations. Other animals are combinations of 2 or more pairs, with much lower levels of relationship.

Persian Leopards are of much more diverse ancestry. Not only do they come from at least 2 countries (Afghanistan and Iran) but very few importations consisted of young pairs which could potentially have been littermates. Further, the mixing of the imported genepool is better and a greater number of inter-zoo loans have assisted in minimizing potential inbreeding.

Amur Leopards are by far the rarest race of leopards in captivity, with most individuals derived from only 2 pairs of ancestors. With such a minimal background, some inbreeding is unavoidable and great care needs to be taken in order to lessen any damage to future generations. A number of solitary ♂♂ exist in zoos of USSR all of which are imported from the wild. Ideally these individuals need to be incorporated into the captive gene pool, an event that should happen soon.

Inbreeding Analysis

In the 3 tables which follow, studbook data for all registered individuals of the Amur, Persian and Chinese subspecies are listed, along with coefficients of inbreeding and relationship. It is hoped that institutions presently holding these subspecies may utilize this information to more readily determine whether inbreeding in their collections is presently or potentially progressing beyond acceptable levels. A coefficient of inbreeding (f) of CROW and KIMURA (1970) is used here, and represents the likelihood that homologous genes at any particular locus are identical. Mathematically, such values range from 0 (a totally non-inbred individual) to 1.0, a totally inbred or isogenic individual in which all homologous genes are identical.

As a basis for comparison, it should be kept in mind that offspring of a sibling or parent-offspring mating have an inbreeding coefficient of .25. Therefore, specimens with an inbreeding coefficient of less than .25 are offspring of individuals less closely related. More important, individuals with f values over .25 are the result of at least 2 generations of inbreeding, since without inbreeding, there is no closer relationship than siblings and parent-offspring.

The coefficient of relationship (r) or WRIGHT (1921) is also useful, and defined as the percentage of genetic material any 2 individuals have received from a common ancestor(s). Parents and their offspring have exactly 50% of the same genetic material, a known biological fact. Regarding all other relatives, r is a probability figure. Full siblings are assigned an r value of .50 because on the average, full siblings will share 50% of the same genes. Coefficients of relationship for other relatives are as follows: half siblings, uncles and nieces or aunts and nephews, double first cousins, grandparents and grandchildren all have an r value of .25. First cousins, great-grandparents and great-grandchildren all have an r value of .125. It is apparent then that genetically speaking, matings between half-siblings, a grandfather and his granddaughter for instance, are equivalent.

With successive generations of inbreeding, both r and f become more complex. The offspring of a father-daughter mating is doubly related to both parents. In some case the father ($f = .50$) is also the maternal grandfather ($f = .25$), the double relationship yielding an r of .75. The mother ($r = .50$) is also the paternal half-sister ($r = .25$) in some cases, again yielding an r of .75. Any full siblings of parent-offspring matings would also have an r of .75, being full siblings to each other ($r = .50$) as well as simultaneously being half-aunts/uncles ($r = .125$) and halfnieces/nephews ($r = .125$). Matings between any of these complex relationships produce offspring with an f of .375, and an r to parents and siblings of .875.

Discussion and Recommendations

Recently, much has been written on the ill effects of inbreeding and its contributions to reduced fertility, vigor and the increase in congenital defects (BOUMAN 1977, FLESHNESS 1977, FOOSE 1977). Although degrees of inbreeding may be more significant in one species than another, the following examples may help to clarify the phenomenon. In humans, *Homo sapiens*, the frequency of congenital disease is about 1% at birth. But if the parents are first cousins (offspring $f = .063$), this figure raises to 2% (FELSENSTEIN unpub. data). The figure is double the non-inbred frequency but is not significant to the survival of the population. On the other hand, it has been demonstrated with vertebrate laboratory species, mice, rats, chickens, pigs, cattle, etc., that 10 generations

Table 1. Studbook data for all registered individuals of the Chinese Leopard, *Panthera pardus japonensis* (Gray, 1862), noting coefficients of inbreeding. Coefficients of relationship are also given for individuals considered actual or potential breeding pairs. Figures in parenthesis are given where it is possible that wild-born ancestors were themselves littermates.

Stud. No.	Sex	Sire	Dam	Birthplace	Coefficient of Inbreeding (f)	Coefficient of Relationship (r)
Artem, USSR						
0118	♂	0058	0064	Leipzig	.183(.219)	
Calgary, Canada						
0221	♂	0141	0166	Toronto	.25(.305)	
Circus Central, Berlin, GDR						
0184	♂	0077	0089	Berlin (Cap. GDR)	0(0)	
Copenhagen, Denmark						
0056	♂	0014	0015	London	0(.25)	
Cottbus, GDR						
0167	♂	0076	0064	Leipzig	.375(.469)	
0178	♀	0076	0064	Leipzig	.375(.469)	.875(.938)
0244	♀	0167	0178	Cottbus	.469(.532)	
Dortmund, FRG						
0180	♂	0074	0069	Stuttgart	.188(.234)	
0181	♀	0074	0069	Stuttgart	.188(.234)	.688(.719)
Dresden, GDR						
0086	♂	0027	0048	Leipzig	.125(.188)	
0093	♀	0027	0048	Leipzig	.125(.188)	.625(.688)
Tierpark Berlin, GDR						
0029	♀	0019	0020	Berlin (Cap. GDR)	0(.25)	0
0077	♂	0001	0009	Leipzig	.25(.375)	0
0089	♀	0019	0029	Berlin (Cap. GDR)	.25(.375)	
0212	♀	0077	0089	Berlin (Cap. GDR)	0(0)	
Halle, GDR						
0142	♀	0074	0069	Stuttgart	.188(.234)	
Hamburg (HAGENBECK), FRG						
0067	♂	0001	0028	Leipzig	0(0)	
0068	♀	0001	0028	Leipzig	0(0)	.50
0207	♀	0067	0068	Hamburg	.25	
Joelton, TN, USA						
0101	♀	0050	0041	Edmonton	0	
Leipzig, GDR						
0048	♀	0001	0028	Leipzig	0	.375(.438) to 0076
0064	♀	0001	0009	Leipzig	.25(.375)	.75(.875)
0076	♂	0001	0001	Leipzig	.25(.375)	
0168	♂	0076	0064	Leipzig	.375(.469)	

Table 1 (continued)

Stud. No.	Sex	Sire	Dam	Birthplace	Coefficient of Inbreeding (f)	Coefficient of Relationship (r)
Lešna, Czechoslovakia						
0085	♂	0027	0048	Leipzig	.125(.188)	
0138	♀	0076	0048	Leipzig	.187(.219)	.416(.547)
1087	♂	0085	0138	Lešna	.203(.277)	
0226	♀	0085	0138	Lešna	.203(.277)	
Liberec, Czechoslovakia						
0078	♂	0001	0009	Leipzig	.25(.375)	0
0099	♀	0019	0029	Berlin (Cap. GDR)	.25(.375)	
London, England						
0096	♂	0014	0015	London	0(.25)	
0097	♀	0014	0015	London	0(.25)	.50(.75)
Lowetsch, Bulgaria						
0196	♂	0077	0089	Berlin (Cap. GDR)	0(0)	.50
0197	♀	0077	0089	Berlin (Cap. GDR)	0(0)	
MÜLLER (Krechting), FRG						
0148	♂	0027	0064	Leipzig	0(0)	
0210	♀	0076	0064	Leipzig	.375(.469)	.438(.468)
0209	♂	0076	0064	Leipzig	.375(.469)	.875(.938)
München, FRG						
0140	♂	0074	0069	Stuttgart	.188(.234)	
1309	♀	0076	0048	Leipzig	.188(.219)	.333(.485)
Munroe Moortsele/Gent, Belgium						
0237	♂	0077	0089	Berlin (Cap. GDR)	0(0)	
Neunkirchen, FRG						
0163	♂	0074	0069	Stuttgart	.188(.234)	
0215	♀	0074	0069	Stuttgart	.188(.234)	.688(.719)
Nürnberg, FRG						
0058	♂	0001	0028	Leipzig	0(0)	.375(.438)
0092	♀	0027	0028	Leipzig	.25(.375)	
0190	♂	0058	0092	Nürnberg	.188(.25)	
0191	♀	0058	0092	Nürnberg	.188(.25)	
0219	♀	0058	0092	Nürnberg	.188(.25)	
0239	♀	0058	0092	Nürnberg	.188(.25)	
0240	♀	0058	0092	Nürnberg	.188(.25)	
Paris, France						
0137	♂	0076	0048	Leipzig	.188(.219)	
0145	♀	0027	0028	Leipzig	.250(.375)	.188(.129)
0208	♀	0137	0145	Paris	.094(.125)	
0209	♂	0137	0145	Paris	.094(.125)	
0230	♀	0137	0145	Paris	.094(.125)	

Table 1 (continued)

Stud. No.	Sex	Sire	Dam	Birthplace	Coefficient of Inbreeding (f)	Coefficient of Relationship (r)
Peking, China						
0025	♀	—	—	Wild	0(0)	
Presov, Czechoslovakia						
0188	♂	0085	0138	Lešna	.203(.227)	
Rome, Italy						
0124	♂	0073	0062	Zürich	0	
0200	♀	0073	0062	Zürich	0	.50
Rome (SPINELLI), Italy						
0223	♂	0073	0062	Zürich	0	
0224	♀	0073	0062	Zürich	0	.50
Rostock, GDR						
0182	♂	0076	0064	Leipzig	.188(.219)	
0179	♀	0076	0048	Leipzig	.375(.469)	.624(.688)
Rostov, USSR						
0245	♀	—	—	Wild	0	
San Diego, USA						
0036	♀	—	—	Wild	0	
0071	♀	0040	0036	San Diego	0	0
São Paulo, Brazil						
1020	♂	0019	0029	Berlin (Cap. GDR)	.25(.375)	
0121	♀	0019	0029	Berlin (Cap. GDR)	.25(.375)	.75(.875)
Stuttgart, FRG						
0074	♂	0027	0048	Leipzig	.125(.188)	
0069	♀	0001	0028	Leipzig	0	.375(.438)
Toronto, Canada						
0141	♂	0074	0069	Stuttgart	.188(.234)	
0166	♀	0027	0048	Leipzig	.125(.188)	.438(.468)
0233	♀	0141	0166	Toronto	.250(.305)	
Wassenaar, Netherlands						
0176	♂	0078	0099	Liberec	0	
0177	♀	0078	0099	Liberec	0	.50
0235	♀	0176	0177	Wassenaar	.250	
Winnipeg, Canada						
0164	♂	0027	0048	Leipzig	.125(.188)	
0035	♀	—	—	Wild	0	0
0047	♀	0001	0028	Leipzig	0	.375(.438) to 0164
Zürich, Switzerland						
0073	♂	0027	0048	Leipzig	.125(.188)	
0062	♀	0014	0015	London	0(.250)	0
0063	♀	Neutered				
0224	♂	0073	0062	Zürich	0	
0256	♀	0073	0062	Zürich	0	

Table 2. Studbook data for all registered individuals of the Persian Leopard, *Panthera pardus saxicolor*, noting coefficients of inbreeding. Coefficients of relationship are given for individuals considered actual or potential breeding pairs.

Stud. No.	Sex	Sire	Dam	Birthplace	Coefficient of Inbreeding	Coefficient of Relationship
Bristol, England						
0089	♂	0052	0037	Münster	.125	0
0080	♀	0043	0039	Rotterdam	.250	
Cincinnati, USA						
0011	♀	—	—	Wild	0	
0033	♀	0004	0011	Cinn.	0	
0034	♂	0004	0011	Cinn.	0	
0035	♀	0004	0011	Cinn.	0	.50
0063	♀	0034	0035	Cinn.	.250	
0078	♂	0034	0035	Cinn.	.250	
0079	♀	0034	0035	Cinn.	.250	.75
0069	♂	0010	0026	Leipzig	0	0 with any above
Dvůr Králové, Czechoslovakia						
0052	♂	0010	0026	Leipzig	0	
0056	♀	0044	0040	Berlin (West)	.250	0
Köln, FRG						
0030	♂	—	—	Wild	0	
Leipzig, GDR						
0010	♂	0006	0003	Münster	.250	
0041	♂	0010	0026	Leipzig	0	
0042	♀	0010	0026	Leipzig	0	
0062	♂	0034	0035	Cinn.	.250	
Chicago (LPZ), USA						
0058	♂	0030	0029	Köln	0	
0067	♀	—	—	Wild	0	0
München, FRG						
0076	♂	0030	0029	Köln	0	
0072	♀	0044	0040	Berlin (West)	.250	.50
Münster, FRG						
0006	♂	0001	0003	Münster	0	0
0037	♀	0021	0026	Leipzig	0	
0051	♂	0010	0026	Leipzig	0	
0088	♂	0052	0037	Münster	.125	
0093	♂	0006	0037	Münster	0	
0095	♀	0006	0037	Münster	0	.50
0110	♂	0006	0037	Münster	0	
0111	♀	0006	0037	Münster	0	.50

Table 2 (continued)

Stud. No.	Sex	Sire	Dam	Birthplace	Coefficient of Inbreeding	Coefficient of Relationship
Rotterdam, Netherlands						
0043	♂	0030	0029	Köln	0	
0039	♀	0030	0029	Köln	0	.50
0102		0043	0039	Rotterdam	.25	
0103		0043	0039	Rotterdam	.25	
0104		0043	0039	Rotterdam	.25	
Stuttgart, FRG						
0047	♂	0030	0029	Köln	0	
0048	♀	0030	0029	Köln	0	.50
0049	♀	0030	0029	Köln	0	.50 with 0047
0087	♂	0039	0043	Rotterdam	.25	.50 with 0047/ 0048
Berlin (West)						
0044	♂	0030	0029	Köln	0	
0040	♀	0030	0029	Köln	0	.50
0170	♂	0044	0040	Berlin (West)	.25	
0108	♀	0044	0040	Berlin (West)	.25	.75

of siblings inbreeding results in the extinction of 95% of all lines observed (FALCONER 1964). Similar results have been observed with invertebrate species as well: fleas, mites and flies.

No one knows exactly how much inbreeding leopard races can tolerate but certainly some collections (particularly among *P. p. japonensis*) may be approaching the limit. We might arbitrarily decide at this point to label pairings of animals with an *r* value of .50 or above as unacceptable. It is fortunate however that because inbreeding has been intense in some collections, many of the resulting offspring are totally unrelated to animals in other collections. Matings between such inbred but unrelated stock would yield offspring with an inbreeding coefficient of 0.

It is not recommended that successful but closely related breeding pairs be separated; however, it should be considered essential that their offspring be carefully paired with unrelated or distantly related stock as available. Closely related breeding pairs producing no offspring or offspring with high incidences of stillbirths, post-natal mortality, or low resistance to infection, should be separated and paired with less related animals. Regarding young sibling pairs recently acquired, it would undoubtedly be more advantageous to re-pair them now while they are still young and adaptable than to wait until they prove to be behaviorally or genetically incompatible.

In any event, it would be extremely prudent for holding institutions to agree not to send opposite sex littermates (or any siblings) to the same receiving institution for pair formation. This policy alone would virtually eliminate future inbreeding of the intensity presently occurring. Coordination of future transactions through the studbook keeper could further facilitate pairings, making it possible to locate and match the least related animals available.

Table 3. Studbook data for all registered individuals of the Amur Leopard, *Panthera pardus orientalis*, noting coefficients of inbreeding. Coefficients of relationship are given for individuals considered actual or potential breeding pairs.

Stud. No.	Sex	Sire	Dam	Birthplace	Coefficient of Inbreeding	Coefficient of Relationship
Asahiyawa, Japan						
0074	♂			Wild	0	
Bekesbourne, England						
0053	♂	0018	0040	Frankfurt/M.	.250	
0054	♀	0018	0040	Frankfurt/M.	.250	.750
Columbia, USA						
0026	♂	0002	0003	Frankfurt/M.	0	
0048	♀	0002	0003	Frankfurt/M.	0	.50
Frankfurt, FRG						
0002	♂			Wild	0	
0003	♀			Wild	0	0
0018	♂	0002	0003	Frankfurt/M.	0	
0040	♀	0002	0003	Frankfurt/M.	0	.50
0075	♂	0002	0003	Frankfurt/M.	0	
0081	♀	0018	0040	Frankfurt/M.	.25	
Joelton (TFG), TN, USA						
0010	♂	0002	0003	Frankfurt/M.	0	
Kaunas, USSR						
0600	♂			Wild	0	
Kazan, USSR						
0070	♂			Wild	0	
Leipzig, GDR						
0014	♂			Wild	0	
0015	♀			Wild	0	0
0042	♀	0014	0015	Leipzig	0	
0049	♀	0014	0015	Leipzig	0	
Moscow, USSR						
0035	♂			Wild	0	
Novosibirsk, USSR						
0023	♂			Wild	0	
0024	♂			Wild	0	
Ostrava, Czechoslovakia						
0055	♂	0002	0003	Frankfurt/M.	0	
0056	♀	0002	0003	Frankfurt/M.	0	.50
Peking, China						
0033	♂			Wild	0	
0034	♀			Wild	0	0(.50)
Prague, Czechoslovakia						
0071	♂	0018	0040	Frankfurt/M.	.250	
0072	♀	0018	0040	Frankfurt/M.	.250	(.750)

Table 3 (continued)

Stud. No.	Sex	Sire	Dam	Birthplace	Coefficient of Inbreeding	Coefficient of Relationship
Rostov, USSR						
0008	♂			Wild	0	
Stralsund, GDR						
0025	♂	0002	0003	Frankfurt/M.	0	
Tallin, USSR						
0063	♀			Wild	0	0
0055	♂			Wild (on loan from Moscow)	0	

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Zusammenfassung

Es ist viel geschrieben worden über die negativen Folgen der Inzucht, insbesondere über die Auswirkungen der Inzucht im Hinblick auf eine Verringerung der Fruchtbarkeit und Lebenskraft sowie eine Zunahme im Auftreten von Erbschäden. Obgleich die Folgen des Grades der Inzucht von Art zu Art verschieden sein mögen, sollten die nachfolgenden Beispiele dabei helfen, diesen Tatbestand zu verdeutlichen. Beim Menschen treten Erbschäden zum Zeitpunkt der Geburt mit einer Häufigkeit von 1% auf. Wenn jedoch die Eltern in erster Linie verwandt sind (Nachkomme $f = .063$), erhöht sich die Zahl auf 2% (FELSENSTEIN, unpubl. data). Diese Zahl ist also doppelt so hoch wie beim Fehlen von Inzucht, doch ist sie wahrscheinlich noch nicht von Bedeutung, was den Fortbestand der Bevölkerung betrifft. Andererseits haben Versuche mit im Labor gezüchteten Wirbeltieren gezeigt, daß Inzucht nach 10 Generationen zum Aussterben von 95% aller Gruppen führt (FALCONER 1964). Ähnliche Beobachtungen hat man bei wirbellosen Arten gemacht.

Niemand kann mit Sicherheit sagen, wieviel Inzucht Leoparden tolerieren können, doch haben einige Gruppen (insbesondere in der Reihe *P. p. japonensis*) die Grenze der Belastbarkeit erreicht, könnte sich an diesem Punkt dazu entscheiden, keine Paarung von Tieren mit einem Faktor von $r = .50$ und mehr vorzunehmen. Glücklicherweise ist es so, daß infolge intensiver Inzucht in einigen Gruppen einige der aus dieser Inzucht stammenden Tiere keinerlei Verwandtschaft zu Tieren in anderen Gruppen zeigen. Paarungen zwischen solchen, aus Inzucht hervorgegangenen, aber einander nicht verwandten Tieren würden Nachkommen mit einem Inzuchtkoeffizienten von 0,0 ergeben.

Es soll hier nicht dafür plädiert werden, erfolgreiche, aber untereinander eng verwandte Zuchtpaare zu trennen. Es ist jedoch außerordentlich wichtig, daß die aus einer solchen Paarung hervorgegangenen Tiere nur mit nichtverwandten bzw. entfernt verwandten Tieren gepaart werden. Eng verwandte Zuchtpaare, die keine Nachkommen hervorbringen bzw. Nachkommen mit einem Anteil an Totgeburten, Säuglingssterblichkeit oder großer Anfälligkeit für Infektionen sollten vermutlich

getrennt und mit Tieren geringeren Verwandtschaftsgrades gepaart werden. Was junge, erst kürzlich erworbene Geschwisterpaare betrifft, so wäre es zweifellos besser, sie mit anderen Tieren zu paaren, solange sie noch jung und anpassungsfähig sind, als so lange zu warten, bis sich eine genetische Inkompatibilität herausstellt.

Auf jeden Fall wäre es dringend geboten, wenn sich alle Zoos darauf einigten, keine Paarungen von Tieren aus demselben Wurf (überhaupt von Geschwisterpaaren) vorzunehmen. Ein solches Überkommen würde eine Inzucht im gegenwärtigen Ausmaß künftig verhindern.

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