

Simultaneous polyandry and heteropaternality in tiger (*Panthera tigris altaica*): Implications for conservation of genetic diversity in captive populations of felids

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Male tigers (*Panthera tigris altaica*) in captivity copulate alternatively with an estrous female, suggesting a potential for heteropaternality as an effective reproductive strategy to maximize genetic diversity of offspring. We analyzed microsatellites to test and compare the genetic output of multiple male mating (simultaneous polyandry) and single male mating (monogamy) with a female in a captive population. Simultaneous polyandry resulted in heteropaternality in 66.7% observed litters. No significant differences between parental populations and between offspring populations were detected in the number of alleles (A), expected heterozygosity (H_e), number of effective alleles (N_e) per locus and standard individual heterozygosity (SH) ($P > 0.05$ for all 4 indexes). Comparisons showed no significant reduction of A , H_o , H_e and SH from parental population to offspring population for the two mating modes ($P > 0.05$) except for SH in polyandrous families ($P = 0.029$). However, such reduction was equivalent to single mating families when the influence of relatedness was eliminated using effective SH (E_{SH}) ($P > 0.05$). These results highlight an alternative strategy for managing captive populations of tiger and other wild felids in which animals are combined at one location allowing for copulation by multiple males to encourage heteropaternality in favor of maintained genetic diversity among offspring.

tiger, *Panthera tigris altaica*, felid, polyandry, heteropaternality, individual heterozygosity

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Most felid species are listed by World Conservation Union (IUCN) as vulnerable or endangered (<http://www.iucnredlist.org>). Many captive populations have been established worldwide to conserve the most endangered species. The goal of captive breeding programs has been set as retention of 90% of genetic diversity for a period of 100 years [1]. Captive populations are necessarily small, therefore subject to several deleterious genetic changes, including inbreeding depression, loss of genetic variation, accumulation of new

deleterious mutations, genetic adaptation to captivity that are deleterious in the wild. These must all be counteracted by appropriate genetic management [2].

One commonly practiced genetic management protocol is pedigree-based targeting to control mating. For instance, population management software SPARKS and PM2000 are used to predict inbreeding coefficients and genetic diversity fluctuations among offspring based on pedigree data and possible mating schemes for captive south China tigers (*Panthera tigris amoyensis*). Some mating schemes planned by the model are implemented by bringing tigers together from different zoos. This is also the case for other felid spe-

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cies. However, every proposed mating presents a challenge. Animals must be transported from facility to facility for breeding. This is stressful to the animals and many times conception does not result, as the animals must accept new surroundings and new partners. Implementation of breeding plans is also potentially influenced by mate choice and genetic incompatibility [3]. For these reasons it is necessary to identify more feasible strategies to breed small populations without adversely impacting genetic resources.

All feline species are solitary except lion (*P. Leo*) and cheetah (*Acinonyx jubatus*). However, all can live in groups in captivity. The feral or free-living domestic cat (*Felis catus*) provides an example of the shift from a solitary life in the wild to group living in captivity. Feral cats can survive as individuals when food resources are too widely distributed to support a group. Social groups with internal structure, and in which group members recognize each other and engage in a variety of social behaviors, are formed when there are sufficient food resources to support a group [4]. Reproductive competition is an important factor influencing the formation and maintenance of sociality. However, adult males living in groups in captivity do not always fight when in the presence of an estrous female. Rather, in many cases, they alternate copulating with the female. The mating system is basically promiscuous, e.g. females mate with multiple males and males mate with multiple females [4]. Females avoid inbreeding by copulating with distant relatives rather than with close kin [5]. This mating system reduces the cost of competition and spreads reproductive chances to all individuals. It also results in heteropaternality in litters [6].

Heteropaternality in polytocous species is a consequence of multiple mating by females whose ova, released in a single estrus cycle, are fertilized by sperm from different males [7–10]. Sperm of different males compete for fertilization while they are stored and mixed within the female oviduct after multiple matings. During this process, ova select sperm that are relatively distant in kinship and dissimilar in haplotype from themselves [3,11]. Multiple-sired litters thus have increased genetic diversity relative to single-sired litters [12–16]. Multiple mating might provide females the opportunity to mate sires that provide genetically compatible genes for their offspring [17,18] and thus increase fitness of resulting offspring and reduce the costs of reproductive failure resulting from genetic incompatibility [19]. Multiple mating also creates paternity uncertainty, which deters infanticide and sexual harassment when females are not guarded by their mates [20].

This suggests an improved strategy for genetic management of captive felid populations: group living to encourage multiple matings, thereby helping to naturally avoid inbreeding, thus retaining individual heterozygosity and reducing risks of reproductive failure caused by genetic incompatibility.

Wild tigers are typically solitary except during the short mating season and when young are dependent on their

mother [21]. Males establish territories from which other males are excluded, but in which one to several females reside [22]. Wild tigers are polygynous. A territorial male monopolizes and mates those females whose territories are encompassed by his own [22,23]. Tiger territories can, however, overlap when food is not a limiting factor or when an area is over-populated by tigers [24,25]. Such behavior is most often seen in zoos where multiple tigers are held in one enclosure and where sufficient food is supplied. This makes tiger an ideal model to study the feasibility and outcomes of group living and multiple matings.

We hypothesized that if captive male tigers did not monopolize access to estrus females through territoriality and conflict, thereby allowing for copulation by other males in the population, and if female tigers would accept multiple male mating, this would lead to heteropaternality and elevated genetic diversity among offspring. This could aid management of captive tiger populations for conservation of genetic diversity, and would potentially be applicable to other wild cat species in captivity.

1 Materials and methods

1.1 Tigers and multiple mating

This study was performed in the Heilongjiang Siberian Tiger Park in Harbin, China. Tigers of the same age and roughly equal body mass were held in one enclosure and supplied with sufficient food. The number of males and females per enclosure varied from five to eleven and five to twelve, respectively. The sex ratio of each enclosure varied from 1:0.8 (M:F) to 1:1.5 (M:F). Such groups have been maintained for at least five years with no individuals moved out and moved in.

The estrous cycle of female tigers lasts 4 to 6 days. The park had two mating modes. One is monogamy mode that male and female tigers were paired up artificially based on pedigree data, the other is polyandry mode allowing tigers within one enclosure mate without any interference. When one of the females became estrous, it would immediately be courted by all males in the same enclosure except her full brothers. The estrous female was surrounded by males nearly all the time. When a male gripped a female's neck and accompanied her for a period of usually 5–10 min, the female would sit and accept mounting. After copulation, the female would lie on her back for a few minutes, and other males would come up to court her again by repeating the same procedure. Females copulated a few times on the first and last days of estrus but up to 56–62 times on the third and fourth days, and more than a hundred times over one estrous cycle.

When multiple males were courting a female simultaneously, they frequently sprayed urine to announce their claim to the site and the female. However, such claims were not recognized by other tigers, and indeed the marked sites were

repeatedly marked by different males.

1.2 Microsatellite characterization

Venous blood samples were collected from 130 tigers during medical examination. Blood was anticoagulated with EDTA at final concentration of 0.5 mmol/L and kept at 4°C for a few hours before DNA was isolated. Genomic DNA was isolated using the routine phenol:chloroform method. Ten microsatellites namely F53, C08, B04, G11, Fca441, F124, C12, C09, F85 and D06 were selected from cat STR 12-plex (Meowplex) [26] and characterized using samples from 109 individuals. Primer sequences and dye labels of microsatellites are shown in Table 1.

PCR reaction for each locus was set up in a 10 µL system containing 1×Easy Taq buffer containing 1.5 mmol/L MgCl₂ (TransGen Biotech, China), 250 mmol/L each of four dNTPs (TaKaRa, Dalian, China), and 0.16 mg/mL bovine serum albumin (BSA; Sigma), 4 pmol/L each of forward and reverse primers 0.5 U of easy TaqE DNA polymerase (TransGen Biotech, China) and 20 ng genomic DNA. PCR amplification was performed in a Model 9700 Thermocycler (Perkin-Elmer) using the following program: 1 cycle of 5 min at 94°C, 30 cycles of 94°C for 30 s, 59°C for 30 s, 72°C for 45 s, and 1 cycle of 72°C for 10 min. PCR products were sized on an ABI PRISM 3100 Genetic Analyzer (Applied Biosystems, Inc.) and genotyped with GeneScan 3.7 and GenOType 3.7 (Applied Biosystems, Inc.). Alleles of each locus were defined using the method described by [27]. For all loci, homozygotes whose signals were not perfect were reamplified once or twice to confirm the genotypes.

Parameters including number of alleles per locus (A),

number of effective alleles per locus (N_e), observed heterozygosity (H_o), expected heterozygosity (H_e) and polymorphism information content (PIC) were calculated using software POPGENE Version 1.32 [28]. Exclusion power (EP) of each locus and cumulative exclusion power (CEP) throughout the 10 loci were estimated according to [29]. GENEPOP Version 3.3 [30] was used to examine the null alleles occurring on each locus by Dempster's EM method.

1.3 Testing of paternity and heterozygosity of offspring

We selected seven monogamous matings (artificially paired) and 15 polyandrous matings for comparison of offspring genetic diversity. Three months after kittens were born, venous blood samples were collected from all kittens, dams, and suspected sires. The monogamous matings included 12 parents and 22 kittens. The polyandrous matings included 29 parents and 39 kittens. These 102 samples were included in the 130 samples for characterization.

All individuals were genotyped using the procedure described above. Genotypes were compared within kitten-dam-suspected sire groups to judge paternity. Relative chance of paternity (RCP) of each included sire was calculated based on a paternity index (PI) that was calculated based on the allelic frequency of the 130 tigers using the simplified method described by [31].

1.4 Effectiveness of genetic diversity preservation in two mating modes

Offspring standardized individual heterozygosity (SH) was calculated as the proportion of heterozygous loci divided by

Table 1 Primer sequences and dye labels of microsatellites used in this study

Locus	Primer sequence (5'→3')	Dye label
F53	Forward: CCTATGTTGGGAGTAGAGATCACCT Reverse: GTGTCTTGAGTGGCTGTGGCATTTC	5'-6FAM
C08	Forward: GATCCATCAATAGGTAATGGATAAAGAAGATG Reverse: TGGCTGAGTAATATCCACTGTCTCTC	5'-6FAM
B04	Forward: TGAAGGCTAAGGCACGATAGATAGTC Reverse: GTGTCTTCCACCCAGGTGCTCTGCTTC	5'-6FAM
G11	Forward: ATCCATCTGTCCATCCATCTATT Reverse: GGTCAGCATCTCCACTTGAGG	5'-6FAM
Fca441	Forward: GTGTCTTGATCGGTAGGTAGGTAGATATAG Reverse: ATATGGCATAAGCCTTGAAGCAAA	5'-VIC
D09	Forward: CCGAGCTCTGTTCTGGGTATGAA Reverse: GTGTCTTCTAGTTGGTCGGTCTGTCTATCTG	5'-VIC
F124	Forward: TGTGCTGGGTATGAAGCCTACTG Reverse: GTGTCTTCCATGCCCATAAAGGCTCTGA	5'-VIC
C12	Forward: GAGGAGCTTACTTAAGAGCATGCGTTC Reverse: GTGTCTTAAACCTATATTCGGATTGTGCCTGCT	5'-VIC
C09	Forward: AAATTTCAATGTCTTGACAACGCATAAG Reverse: GTGTCTTCCAGGAACACCATGTTGGGCTA	5'-NED
F85	Forward: TAAATCTGGTCTCACGTTTTC Reverse: GCCTGAAAATGTATCCATCACTTCAGAT	5'-NED
D06	Forward: CCAAGGAGCTCTGTGATGCAAA Reverse: GTTCCACAGGTAAACATCAACCAA	5'-NED

mean expected heterozygosity of typed loci [32]. Significance of SH differences between multiple-male-mating litters and single-male-mating litters was tested using the two-tailed independent samples t -test at $\alpha=0.05$. A relatedness coefficient between parents was calculated for each case using software ML-RELATE [33]. In order to eliminate the effects of parents' relatedness on the standard heterozygosity of offspring during comparisons between polyandrous matings and single monogamous matings, we proposed the effective standard heterozygosity (E_{SH}) to assess the actual heritage of genetic diversity. E_{SH} means the offspring SH was expressed as the average of the parents' SH by excluding the proportion of relatedness. E_{SH} was calculated using the equation below:

$$E_{SH} = \frac{1}{2}(SH_{\text{sire}} + SH_{\text{dam}})(1-r),$$

where SH_{sire} stands for SH of sire, SH_{dam} stands for SH of dam, r stands for relatedness coefficient between parents. By using the 2-sample independent sample t -test in software STATISTICA 9 (StatSoft), means of SH were compared between two parental groups, two offspring groups, the parental population and the offspring population of the two mating modes. Means of E_{SH} were compared between offspring populations of the two mating modes using the same method. Significance criteria for all comparisons were set at 0.05.

2 Results

2.1 Characteristics of microsatellites

All 130 individuals were successfully genotyped throughout the 10 microsatellite loci. GENEPOP analysis indicated that null alleles were most likely to occur on C08 and G11new at a likelihood of 0.8593 and 0.4689, respectively. The likelihood values of null alleles on the remaining loci ranged from 0 to 0.0618. Therefore, C08 and G11new were ignored in further analyses. Characteristics of the remaining 8 loci are shown in Table 2. Number of alleles (A) per locus varied

from 4 to 10, averaging 7.13. Number of effective alleles (N_e) per locus varied from 1.834 to 7.131, averaging 4.422. Observed heterozygosity (H_o) varied from 0.539 to 0.969, averaging 0.803. The minimum expected heterozygosity (H_e) was 0.457 observed on B04, and the maximum H_e was 0.863 on C09. Mean H_e was 0.730. PIC varied from 0.368 to 0.844, averaging 0.685. Exclusion power of a random male from paternity (EP) ranged from 0.216 to 0.731, averaging 0.537. The accumulative exclusion power (CEP) across all 8 loci was 0.9953.

2.2 Paternity testing

A male was included as a biological father if its genotype matched that of the dam and kittens across all loci, otherwise, it was excluded. The number of excluding loci ranged from 2–6 loci in this study (genotype data not shown). RCP for each kitten-sire pair ranged from 0.9403775 to 0.9999883, averaging 0.99334778. In 15 polyandrous-mating litters, 5 litters (33.3%) were confirmed as being sired by a single male, and the other 10 litters (66.7%) were sired by 2 to 3 different males.

2.3 Changes of allele number and heterozygosity

For polyandrous matings, the parental population had 3 to 10 alleles on all 8 loci, averaging 6.25 alleles per locus. The offspring population had 2 to 9 alleles on all loci, averaging 5.75 alleles per locus. Mean allele loss per locus was 0.08. N_e of the parental population varied from 2.097 to 7.250 on the 8 loci, averaging 4.282. N_e of the offspring population varied from 1.938 to 7.493, averaging 4.180. Mean effective allele loss per locus was 0.02. H_e of the parental population ranged from 0.532 to 0.877, averaging 0.738, while in the offspring population H_e ranged from 0.490 to 0.878, averaging 0.720. Loss rate of H_e from the parental to the offspring population ranged from 0 to 0.08, averaging 0.02. The differences between parental and offspring populations in A , N_e and H_e across the 8 loci were not significant ($|t_A|=0.416$, $d.f.=14$, $P=0.684$; $|t_{N_e}|=0.108$, $d.f.=14$, $P=0.915$; $|t_{H_e}|=$

Table 2 Characteristics of 10 microsatellites in the Siberian tiger population ($n=130$)

Locus	Allelic frequency										H_o	H_e	A	N_e	PIC	EP	
	A	B	C	D	E	F	G	H	I	J							
F53	0.023	0.100	0.173	0.289	0.112	0.300	0.004					0.862	0.777	7	4.422	0.739	0.584
B04	0.004	0.669	0.312	0.015								0.539	0.457	4	1.834	0.368	0.216
FCA441	0.119	0.039	0.358	0.212	0.192	0.081						0.792	0.771	6	4.312	0.734	0.579
F124	0.039	0.019	0.035	0.419	0.331	0.115	0.035	0.008				0.800	0.700	8	3.303	0.649	0.481
C12	0.073	0.127	0.119	0.231	0.054	0.046	0.073	0.008	0.189	0.081		0.915	0.862	10	7.073	0.843	0.730
C09	0.035	0.042	0.162	0.158	0.104	0.058	0.115	0.219	0.104	0.004		0.969	0.863	10	7.131	0.844	0.731
F85	0.092	0.104	0.108	0.200	0.358	0.123	0.008	0.008				0.823	0.789	8	4.670	0.759	0.612
D06	0.350	0.481	0.162	0.008								0.723	0.623	4	2.633	0.545	0.367
Mean												0.803	0.730	7.13	4.422	0.685	0.537

0.280, $d.f.=14$, $P=0.784$).

For monogamous matings, A on each locus in the parental population ranged from 3 to 8, and averaged 5.50 per locus. In the offspring population A varied from 3 to 8, averaging 5.38 per locus. Mean allele loss per locus was 0.02. N_e ranged from 1.767 to 6.261, averaging 3.957 in the parental population, and ranged from 1.501 to 6.676, averaging 3.758 in the offspring population. Mean effective allele loss per locus was 0.05. H_e of the parental population ranged from 0.453 to 0.877, averaging 0.737. In the offspring population H_e ranged from 0.341 to 0.870, averaging 0.695. Loss rate of H_e from the parental to the offspring population ranged from 0 to 0.25, averaging 0.06. There were no significant differences between parental and offspring populations in A , N_e and H_e across the 8 loci ($|t_A|=0.144$, $d.f.=14$, $P=0.887$; $|t_{N_e}|=0.253$, $d.f.=14$, $P=0.804$; $|t_{H_e}|=0.551$, $d.f.=14$, $P=0.590$).

Values of A , N_e and H_e did not differ across the 8 loci between the parental populations of polyandrous matings and monogamous matings, ($|t_A|=0.727$, $d.f.=14$, $P=0.479$; $|t_{N_e}|=0.389$, $d.f.=14$, $P=0.703$; $|t_{H_e}|=0.019$, $d.f.=14$, $P=0.985$). There were also no significant differences in values of A , N_e and H_e across the 8 loci in the offspring populations from the two mating modes ($|t_A|=0.353$, $d.f.=14$, $P=0.730$; $|t_{N_e}|=0.469$, $d.f.=14$, $P=0.647$; $|t_{H_e}|=0.341$, $d.f.=14$, $P=0.739$). Changes in values of A , N_e and H_e from parental to offspring populations were not significantly different between the two mating modes ($|t_A|=1.793$, $d.f.=14$, $P=0.095$; $|t_{N_e}|=1.238$, $d.f.=14$, $P=0.236$; $|t_{H_e}|=0.720$, $d.f.=14$, $P=0.483$).

2.4 Changes of individual heterozygosity

For polyandrous matings, the individual SH of the parental population ranged from 0.846 to 1.354, averaging 1.173. Individual SH values of the offspring population ranged from 0.5205 to 1.3881, averaging 1.081. For monogamous matings, individual SH values in the parental population ranged from 0.679 to 1.357, averaging 1.131. This figure for the offspring population ranged from 0.540 to 1.439, averaging 1.104. The independent samples t -test showed no significant difference in individual SH values of the parental populations between polyandrous matings and monogamous matings ($|t_{SH}|=0.735$, $d.f.=39$, $P=0.467$). There was no significant difference in individual SH values between offspring populations of the two mating modes ($|t_{SH}|=0.410$, $d.f.=59$, $P=0.683$). Comparisons of individual SH between the parental and offspring populations within the polyandrous matings confirmed a significant decline of mean SH ($|t_{SH}|=2.239$, $d.f.=66$, $P=0.029$). Similar comparison for monogamous matings also showed no significant difference between parental and offspring populations ($|t_{SH}|=0.319$, $d.f.=32$, $P=0.752$).

ML-RELATE calculated a relative coefficient (r) for all pairs of breeders. In polyandrous-mating cases, 41.67% of breeder pairs had positive r values. The maximum r value

was 0.612, averaging 0.101. r values in monogamous cases ranged from 0 to 0.247, averaging 0.039, and only 28.57% of breeder pairs had positive r values. To eliminate the impact of parental relatedness, we used a new index, effective standard individual heterozygosity (E_{SH}) to predict offspring standard heterozygosity. E_{SH} for the offspring of polyandrous matings ranged from 0.427 to 1.270 with a mean 1.041, and E_{SH} for the offspring of monogamous matings ranged from 0.8307 to 1.272 with a mean 1.072. Independent t -test showed no difference of offspring E_{SH} between the two mating modes ($|t_{E_{SH}}|=0.335$, $d.f.=27$, $P=0.740$).

3 Discussion

The experience of zoos demonstrates that tigers living in limited space are able to shift from solitude to sociality if food is sufficient. Competition for mating also shifts to a ritualized mode wherein a male cannot monopolize an estrous female as in the wild, but copulates with the female alternately. Two outcomes potentially result from this alternate mating strategy. First, the opportunity for males to deliver their genes to the next generation is extended to all adult males. This facilitates the maintenance of genetic diversity. Second, the polyandrous mating strategy forces loss of the function of selecting a male's genetic quality and may lead to degradation of offspring. If tigers are able to overcome this loss, the group living strategy encouraging simultaneous polyandry can be an important option to preserve genetic diversity.

We noted that multiple matings with different males does not mean that females did not select mates. Indeed, copulation was more likely to occur between less related male-female pairs. Fragmentary observations by zookeepers showed that copulations between full siblings accounted for only about 5.8% to 16.5% of the total (Wang et al., personal communication). This type of mate selection was also observed in feral cats [5] and cheetah [34] when females avoided mating with close kin but not with more distant relatives. In contrast to the feral cat where only females selected against close relatives, both sexes of Harbin tigers appeared to avoid mating with close relatives. This suggests that tigers possess some natural ability to avoid inbreeding.

High individual heterozygosity reduces the likelihood that recessive deleterious alleles are expressed, or increases the number of potentially useful gene products [35]. An example is from an inbred wolf (*Canis lupus*) population in Scandinavia. At each level of inbreeding, only the most heterozygous wolves established themselves as breeders. This selection process decelerated the loss of heterozygosity despite a steady increase in the overall inbreeding level [36]. In our study, heteropaternality was detected among tigers, proving our hypothesis that the opportunity for males to deliver their genes to next generation is extended to all adult males and further influences offspring heterozygosity.

Molecular tests showed individual SH values for the parental populations did not differ between polyandrous and monogamous matings ($|t_{SH}|=0.735$, $d.f.=39$, $P=0.467$). Breeder pairs had higher relatedness in polyandrous matings than in monogamous matings. We can predict that polyandrous matings had a higher probability to lose genetic diversity, resulting in lower SH values among offspring. However, in comparisons between the two mating modes, changes were not significantly different in A , H_e , N_e from the parental to the offspring populations. Polyandrous matings even showed lower loss of N_e and H_e (Table 3) than did monogamous matings. This suggests that polyandrous mating is functional to minimize the loss of genetic diversity.

Comparisons of individual SH between parental and offspring populations polyandrous matings showed significant reduction of individual SH ($P=0.029$), while the reduction was not significant for monogamous matings ($P=0.752$). However, considering the higher parental relatedness in polyandrous matings, we introduced a novel index, E_{SH} , to eliminate the influence of parental relatedness on the individual SH values of offspring. The resulting E_{SH} of offspring of the two mating modes were not different ($P=0.740$). This suggests polyandry is functional to maintain individual heterozygosity of offspring. It has been reported that heterozygosity of offspring increased significantly in polygamous species [16]. Offspring SH values did not increase due to polyandry in this study. This might be due to the relatively small size of the parental population and our small sample of offspring. We expect that continued investigation of larger

numbers of kittens born from polyandrous matings would confirm that polyandry of captive tigers at Harbin maximizes the heterozygosity of offspring.

To summarize, this study showed that, at a minimum, a polyandrous mating strategy maintained heterozygosity through heteropaternality in a captive tiger population. This implies that multiple male and female tigers, and possibly other felids, can be kept in large semi-free environments without human management of their reproduction. Multiple matings will occur and will result in heteropaternality. The rate of heteropaternality litters in this study was 67%. Cheetah and domestic cat have also shown high frequencies of heteropaternality litters, 43% and 80% respectively [6,34]. The rate of heteropaternality and number of sires per litter are influenced by many factors, such as capability of males at mate-guarding [37], population structure [6], mate choice [38], and male-female relatedness [5]. It is not difficult for population managers to optimize these influencing factors to favor increased heteropaternality and individual heterozygosity of offspring.

South China tiger (*P. t. amoyensis*) is the most endangered subspecies of *P. tigris*, with 108 remaining individuals in captivity at various zoos in China. The population is managed using a single-mating system whereby one estrus female is paired with one male. Xu et al. [39] showed that all surviving south China tigers are related and display declining trends in individual heterozygosity simultaneous with severe inbreeding depression expressed as low reproductive rates and low kitten survival. Polyandry might be a

Table 3 Inheritance of genetic diversity by offspring populations in the scenario of polyandry and monogamy

Locus	Parental A	Offspring A	Change of A	Parental N_e	Offspring N_e	Change of N_e	Parental H_e	Offspring H_e	Change of H_e
Polyandrous cases ($n=15$)									
F53	6	6	0.00	4.163	4.003	-0.04	0.773	0.760	-0.02
B04	3	2	-0.33	2.097	1.938	-0.08	0.532	0.490	-0.08
Fca441	6	5	-0.17	4.143	4.133	0.00	0.772	0.768	-0.01
F124	5	5	0.00	3.009	2.773	-0.08	0.679	0.648	-0.05
C12	10	9	-0.10	7.250	7.493	0.03	0.877	0.878	0.00
C09	8	8	0.00	6.596	6.472	-0.02	0.863	0.857	-0.01
F85	8	8	0.00	4.426	4.237	-0.04	0.788	0.774	-0.02
D06	4	3	-0.25	2.572	2.390	-0.07	0.622	0.589	-0.05
Mean	6.25	5.75	-0.08	4.282	4.180	-0.02	0.738	0.720	-0.02
Monogamous cases ($n=7$)									
F53	5	5	0.00	3.646	3.482	-0.04	0.757	0.729	-0.04
B04	3	3	0.00	1.767	1.501	-0.15	0.453	0.341	-0.25
Fca441	6	6	0.00	3.165	2.696	-0.15	0.714	0.644	-0.10
F124	6	6	0.00	4.114	3.409	-0.17	0.790	0.723	-0.08
C12	7	6	-0.14	5.143	5.068	-0.01	0.841	0.821	-0.02
C09	8	8	0.00	6.261	6.676	0.07	0.877	0.870	-0.01
F85	6	6	0.00	5.053	4.654	-0.08	0.837	0.803	-0.04
D06	3	3	0.00	2.504	2.581	0.03	0.627	0.627	0.00
Mean	5.50	5.38	-0.02	3.957	3.758	-0.05	0.737	0.695	-0.06

useful measure to help overcome these problems if the reproductively capable but geographically isolated tigers were combined at one location in a single breeding population as the Siberian tigers were at Harbin.

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