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Cover: Indian Grey Wolf *Canis lupus pallipes* and Smooth-coated Otter *Lutrogale perspicillata* sharing the territory in Chambal basin. Digital art on Procreate by Aakanksha Komanduri.

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COMMUNICATION

Assessment of genetic variation for conservation implications in the Critically Endangered Bawean Deer *Axis kuhlii* Temminck, 1836 (Mammalia: Artiodactyla: Cervidae)

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Abstract: The Bawean Deer *Axis kuhlii*, endemic to the small Indonesian island of Bawean, is listed as 'Critically Endangered' with fewer than 250 mature individuals remaining in the wild. The first genetic assessment of captive *A. kuhlii* populations using 13 microsatellite markers were conducted. Samples included individuals from Bawean, multiple Indonesian zoos, and a European zoo. The goals were to assess genetic diversity and to test for potential hybridisation with *Rusa unicolor* and *Rusa timorensis*, due to frequent mixed-species housing in Javan facilities. STRUCTURE analysis revealed no evidence of hybridisation and identified three genetic clusters within *A. kuhlii*, likely reflecting drift and kinship effects. Genetic diversity was low across all *A. kuhlii* samples, but slightly higher in the Bawean population. Some alleles present in Java zoo populations were absent from Bawean. These findings suggest that while inbreeding may be a concern, managed translocation between captive and wild populations could enhance genetic diversity without introducing hybridisation risk. Targeted integration of ex-situ individuals and the inclusion of wild-caught stags into the Bawean breeding program are recommended to support genetic rescue efforts and long-term population viability.

Keywords: Captive breeding, conservation genetics, genetic diversity, genetic structure, inbreeding, microsatellites, translocation.

Bahasa Indoesia: Rusa Bawean *Axis kuhlii*, yang endemik di Pulau Bawean, Indonesia, dikategorikan sebagai "Kritis" (Critically Endangered), dengan jumlah individu dewasa yang tersisa di alam diperkirakan kurang dari 250 ekor. Penelitian ini merupakan penilaian genetik pertama terhadap populasi *A. kuhlii* dalam penangkaran dengan menggunakan 13 penanda mikrosatelit. Sampel mencakup individu yang berasal dari Bawean, beberapa kebun binatang di Indonesia, serta satu kebun binatang di Eropa. Penelitian ini bertujuan untuk menilai keragaman genetik dan menguji kemungkinan terjadinya hibridisasi dengan *Rusa unicolor* dan *Rusa timorensis*, mengingat ketiga spesies tersebut sering dipelihara bersama dalam fasilitas penangkaran di Jawa. Analisis STRUCTURE tidak menunjukkan adanya bukti hibridisasi dan mengidentifikasi tiga kelompok genetik dalam *A. kuhlii*, yang kemungkinan mencerminkan pengaruh hanyutan genetik dan hubungan kekerabatan. Keragaman genetik tergolong rendah pada seluruh sampel *A. kuhlii*, namun sedikit lebih tinggi pada populasi Bawean. Beberapa alel yang ditemukan pada populasi kebun binatang di Jawa tidak ditemukan pada populasi Bawean. Hasil ini menunjukkan bahwa meskipun perkawinan sedarah dapat menjadi perhatian, translokasi yang dikelola dengan baik antara populasi penangkaran dan populasi liar berpotensi meningkatkan keragaman genetik tanpa menimbulkan risiko hibridisasi. Integrasi terarah individu dari populasi ex-situ serta pemasukan rusa jantan yang berasal dari populasi liar ke dalam program pengembangbiakan di Bawean direkomendasikan untuk mendukung upaya penyelamatan genetik (genetic rescue) dan keberlanjutan populasi dalam jangka panjang.

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INTRODUCTION

The Bawean Deer is endemic to the small and isolated Indonesian island of Bawean (190 km^2; Image 1) and is listed as 'Critically Endangered' on the IUCN Red List (Semiadi et al. 2015). It is protected under Indonesian law and listed in Appendix I of CITES. Recent camera trap surveys show fewer than 250 mature animals (Ariyanto et al. 2025a). The species is already absent from the eastern part of the island. The threats are traditional hunting with dogs and nets, snares, predation by free roaming dog and poaching (Semiadi et al. 2016; Rahman et al. 2023; Ariyanto et al. 2025b).

Only four to five deer ever left the island and were brought to Surabaya Zoo, Indonesia, in the 1940s. These animals were the founders of all ex-situ populations. Since then, there has been no population management plan. Like most cervids, *A. kuhlii* reproduces well in captivity. Today there are several ex situ populations on Java (e.g., Surabaya Zoo; Maharani Zoo; Taman Safari Bogor/Prigen) and three populations (Zoo Poznan - Poland; Tierpark Berlin - Germany; Edinburgh Zoo - UK) in Europe. In zoos and safari parks on Java, different species of cervids are occasionally kept together, which harbours the risk of hybridisation. An unmanaged captive breeding program has been running on Bawean island since 2010.

Microsatellite loci were used to conduct an initial assessment of genetic diversity in captive *A. kuhlii* populations and to evaluate their suitability for release on Bawean. Specifically, the study aimed to test for evidence of hybridization between *A. kuhlii* and *R. unicolor* and/or *R. timorensis*, particularly in the captive bred *A. kuhlii* from Java. We also aimed to get a first idea of the genetic diversity of the captive *A. kuhlii* populations.

MATERIALS AND METHODS

Ear tissue samples of *A. kuhlii* (n = 15) were collected from the captive population on Bawean. Samples were included from Borgor and Prigen Taman Safari (n = 3), Grati Zoo (n = 4), and Surabaya Zoo (n = 9). Blood samples from two animals from Berlin Zoo, Germany, were included. We also obtained samples of *R. unicolor* (n = 8) from East Kalimantan and *Rusa timorensis* (n = 6) from Sulawesi and Lombok, from museum voucher collections that had been collected between 2004 and 2008 and stored in LIPI (Indonesian Institute of Sciences), which know changes to BRIN (National Research and Innovation Agency).

DNA was extracted using the DNeasy Blood and Tissue Kit (Qiagen), following the manufacturer's instructions and samples were genotyped with 13 microsatellite loci in total. The methods outlined in Frantz et al. (2024) were followed to genotype 11 microsatellites (CSSM14, ETH225, T501, BM1818, CSSM16, OarFCB304, OarFCB5, T156; IDVGA55; TGLA57; TGLA226). Two further microsatellite loci, Ca13 (Gaur et al. 2003) and T26 (Jones et al. 2002) were amplified in PCRs that each contained 1 × GoTaq Master Mix (Promega; Walldorf; Germany) and 0.2 µM of each primer. PCR conditions were as follows: after a 5 min denaturation at 95 °C, the PCR consisted of 35 cycles of denaturation at 95 °C for 30 s, annealing at 56 °C (T26) or 58 °C (Ca13) for 45 s and an extension at 72 °C for 45 s. The PCR was ended with a final extension for 10 min at 68 °C. PCRs were performed using a Mastercycler Nexus cycler (Eppendorf), and products were separated on an ABI 3730XL DNA sequencer (Applied Biosystems).

The *A. kuhlii* samples from Bawean, Java and Tierpark Berlin, Germany, were each a priori defined as a population for deviations from Hardy–Weinberg equilibrium (HWE) using the Markov-Chain method (MCM) in GENEPOP3.4 (Raymond & Rousset 1995), with 1,000 dememorization steps, 500 batches and 1,000 iterations. GENEPOP was also used to test for linkage disequilibria among loci using an exact test based on the MCM. The false discovery rate technique was used to eliminate false assignment of significance by chance (Verhoeven et al. 2005).

Structure 2.3.4 (Pritchard et al. 2000) was used to test *A. kuhlii* for hybridisation with *R. unicolor* and *R. timorensis* as well as to test the intraspecific genetic structure between captive populations. Ten independent runs for K = 1 to K = 5 were carried out with 10^6 Markov-Chain-Monte-Carlo (MCMC) iterations after a burn-in period of 10^5 iterations, using the model with correlated allele frequencies and assuming admixture. A separate alpha was used to represent the degree of admixture between each population and a uniform prior was applied to the parameter. Individual assignments were based on the run with the highest log-likelihood for the given value of K.

Although the genetic analysis indicated the presence of three distinct genetic populations among the *A. kuhlii* samples (see Results), two priori defined populations were considered from Bawean and Java (all ex-situ populations) for the analysis of genetic diversity. The animals from Tierpark Berlin were included in the latter group, which we refer to simply as the 'Java' population for clarity. This approach was adopted because of the small number of samples obtained per enclosure or zoo and given that the clustering observed within *A. kuhlii* was probably due, at least in part, to the presence of related

Image 1. Bawean island in the Java Sea.

individuals in enclosures (see Discussion). The samples from *R. unicolor* and *R. timorensis* were also treated as distinct clusters. We estimated average number of alleles/locus (N_A), observed (H_O) and unbiased expected (H_E) heterozygosity of the four pre-defined populations using GENETIX4.05.2 (Belkhir et al. 2004). Allelic richness (A_r) was calculated using Fstat 2.9.3.2 (Goudet 1995).

RESULTS

Four loci (Ca13; T501; CSSM16; T156) were monomorphic in *A. kuhlii* (but not in *R. unicolor* or *R. timorensis*). After correction for multiple tests, three loci (CSSM14; ETH225; IDVGA55) deviated from the HWE ($P < 0.017$) in the *A. kuhlii* sampled in the enclosure on Bawean, and loci CSSM14 and ETH225 were in linkage disequilibrium ($P < 0.014$). After multiple-test correction, no locus deviated from HWE and no loci were in linkage disequilibrium in the deer sampled from captive populations outside of Bawean. All 13 loci were therefore retained for further analysis.

Structure identified the presence of at least three genetic clusters K = 3 in the dataset (Image 2). Eight of the ten log-likelihood values obtained for K = 3 converged well and all values at K = 3 were higher than the log-likelihood values obtained at K = 2. At K = 3, the algorithm split *A. kuhlii* into two populations (with the second population being formed by individuals from Bawean), but pooled all *R. unicolor* or *R. timorensis* into a single separate population. At K = 4, some log-likelihood values were higher than the values observed for K = 3, but the log-likelihood values of the different K = 4 runs did not converge well. The assignment values of the K = 4 run with the highest log-likelihood split *A. kuhlii* into three clusters — with the new, fourth cluster mainly consisting of animals from Surabaya zoo — while still grouping all *R. unicolor* and *R. timorensis* into a single cluster. No evidence of admixture was found between *A. kuhlii* and *R. unicolor*/*R. timorensis* at any K between K = 2 to K = 4.

All *A. kuhlii* genetic diversity statistics were low, but higher in the deer from Bawean than in those from the Java population (Table 1). However, the estimate of allelic richness was based on two diploid individuals only and the other estimates were not significant different (Wilcoxon signed rank; number of alleles: V=6.0; p=0.317; H_o: V = 30.0; p = 0.407; H_e: V = 25.0; p = 0.362). With two exceptions, all alleles observed in the Java population were also present on Bawean. One allele at locus BM1818 was found in all five ex-situ populations that make up the Javan population but was not observed on Bawean. Another allele at the same locus was detected

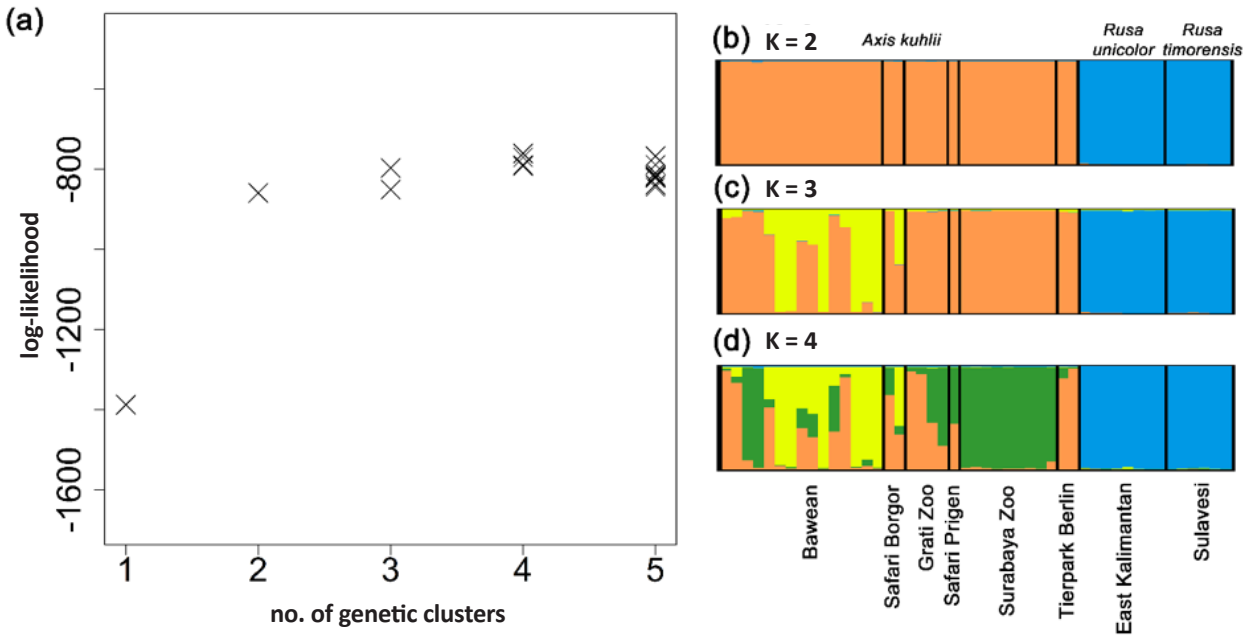

Image 2. Structure plot and log likelihood.

Table 1. Summary of the genetic diversity observed at 13 microsatellite loci in Indonesian cervids. Estimates of allelic richness (A_r) are based on two diploid individuals.

Species/population	n	A	A_r	uH_e	H_o
A. kuhlii wild Bawean	15	2.23	1.59	0.29	0.21
A. kuhlii ex situ Java	18	2.00	1.39	0.20	0.14
R. unicolor	8	4.23	2.55	0.68	0.65
R. timorensis	6	2.92	2.13	0.54	0.41

in a single individual from Grati captive breeding facility only. All diversity statistics were higher in *R. unicolor* and *R. timorensis* than in the two *A. kuhlii* populations (Table 1) and a Kruskal-Wallis test revealed a significant difference between the four groups (χ^2 = 23.49; d.f. = 3; $p < 0.001$).

DISCUSSION

Small island populations are particularly vulnerable to inbreeding depression because of low genetic diversity (Frankham 1998). Apart from increasing the number of individuals, translocation can facilitate genetic rescue, whereby increased heterozygosity and reduced inbreeding improve population fitness (Bell et al. 2019). The low genetic diversity observed in *A. kuhlii* therefore suggests that carefully managed genetic rescue could be beneficial. While genetic rescue has its benefits, it can also have long-term negative effects if the source population is larger than the population to be rescued, as it can introduce recessive deleterious mutations (Hedrick et al. 2019). In addition, a recent study has shown that translocation can lead to counterproductive outcomes when dealing with historically small populations that have had time to eliminate highly deleterious mutations (Kyriazis et al. 2021).

Captive breeding conditions pose a risk of hybridisation with other cervids for ex situ *A. kuhlii* populations on Java. No evidence of hybridisation was found between the Bawean Deer and *R. unicolor* or *R. timorensis*. Nevertheless, due to hybridisation within captive populations, *R. timorensis* and *R. unicolor* formed a single cluster in our STRUCTURE analysis. The three clusters confirmed by STRUCTURE for *A. kuhlii* are probably the result of related individuals and/or genetic drift. In general, genetic diversity (A_r) appears to be very low in *A. kuhlii*. The results suggest that some genetic diversity (i.e. alleles) is present in captive populations on Java that is absent from Bawean. As it was impossible to catch deer born in the wild on Bawean, and as faeces were not useful for sampling due to the tropical conditions, DNA could only be collected from captive-born deer on Bawean. Consequently, the ex situ population on Bawean may not fully represent the island's entire genetic diversity.

There are currently plans to improve and expand the captive breeding programme at Mombul/Bawean, led by the Prigen Conservation Initiative, Malang, Indonesia. As

the in situ population is already restricted to the western part of Bawean, and there is only one record of a female in the north-eastern part of the island (Ariyanto et al. 2025a)— most probably the offspring of a deer released from a captive population — it is recommend to release more deer from the captive breeding programmes (Bawean and Java) in the eastern part of the island. To increase the genetic diversity of the captive breeding program on Bawean, it is recommended to catch one or two stags from the wild population.

The reproduction rate in the wild *A. kuhlii* population is low, with only 17 fawns per 100 does (Ariyanto et al. 2025a). This could be a sign of inbreeding depression due to genetic isolation and a small population size of less than mature 250 individuals. Therefore, it can be concluded that translocation of selected individuals between ex situ populations, as well as between wild and ex situ populations, could be a reliable conservation measure to restore genetic diversity, despite the risk of outbreeding. In the long term, captive breeding programmes only make sense if they are managed to increase genetic diversity and exclude deleterious alleles, and if the offspring are successfully released into the wild.

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