

Genetics and the last stand of the Sumatran rhinoceros *Dicerorhinus sumatrensis*

BENOÎT GOOSSENS, MILENA SALGADO-LYNN, JEFFRINE J. ROVIE-RYAN
ABDUL H. AHMAD, JUNAIDI PAYNE, ZAINAL Z. ZAINUDDIN
SENTHILVEL K. S. S. NATHAN and LAURENTIUS N. AMBU

Abstract The Sumatran rhinoceros *Dicerorhinus sumatrensis* is on the brink of extinction. Although habitat loss and poaching were the reasons of the decline, today's reproductive isolation is the main threat to the survival of the species. Genetic studies have played an important role in identifying conservation priorities, including for rhinoceroses. However, for a species such as the Sumatran rhinoceros, where time is of the essence in preventing extinction, to what extent should genetic and geographical distances be taken into account in deciding the most urgently needed conservation interventions? We propose that the populations of Sumatra and Borneo be considered as a single management unit.

Keywords *Dicerorhinus sumatrensis*, extinction, genetics, genome resource banking, Sumatran rhinoceros, threatened

The rhinos...are unaware of their precarious existence. Their fate depends wholly on us, on our commitment to protect them forever. E. Dinerstein (2003)

Introduction

With as few as 216 wild individuals worldwide (Ahmad Zafir et al., 2011), the Sumatran rhinoceros *Dicerorhinus sumatrensis* is on the brink of extinction. Following a recent report by WWF on the fate of the Javan

rhinoceros *Rhinoceros sondaicus* in Vietnam (Brook et al., 2011), are we to witness the loss of another rhinoceros species? Genetic studies have played an important role in identifying conservation priorities (Moritz, 1994, 2002; De Salle & Amato, 2004; Caballero et al., 2009; Frankham, 2009; Laikre, 2010), including for species of rhinoceros (Ashley et al., 1990; Dinerstein & McCracken, 1990; Amato et al., 1995; Morales et al., 1997; Harley et al., 2005; Fernando et al., 2006; Scott, 2008; Kim, 2009; Willerslev et al., 2009). However, for a species such as the Sumatran rhinoceros, where time is of the essence in preventing extinction, to what extent should genetic and geographical distances be taken into account in deciding the most urgently needed human interventions?

Since its appearance in the Eocene, the family Rhinocerotidae has comprised > 40 genera (Guerin, 1989; Cerdeño, 1998). Nowadays it includes only four genera, with a total of five species (but see Groves et al., 2010). Comparisons of mitochondrial (mt) DNA sequences (including whole mt genomes) of contemporary Asian, African and fossil rhinoceros DNA suggest that the Sumatran rhinoceros is the most primitive extant species of the family and the closest related living species to the ancient woolly rhinoceros *Coelodonta antiquitatis* (Morales & Melnick, 1994; Cerdeño, 1998; Tougard et al., 2001; Orlando et al., 2003; Willerslev et al., 2009). Formerly existing across South-east Asia, including Thailand and Myanmar, the Sumatran rhinoceros is now Critically Endangered, with a decreasing population trend (IUCN, 2011), and confined to a few disjunct populations in Indonesia (Sumatra) and Malaysia (Borneo). The situation has been described as a problem of political endemism (Moritz, 2002). In the mid 1980s the governments of Indonesia and Malaysia, and international conservation organizations, supported management plans that included greater protection of wild populations and habitats, a controversial captive-breeding programme, and research (Khan, 1989; Rabinowitz, 1995; Foose & van Strien, 1997; Dinerstein, 2003). Today, there are 10 individuals in captivity: one female in Cincinnati Zoo and one male in Los Angeles Zoo (USA), two males (including a calf) and three females in the Sumatran Rhino Sanctuary at Way Kambas (Sumatra, Indonesia) and one male and two females at the Borneo Rhino Sanctuary (Sabah, Malaysia).

BENOÎT GOOSSENS* (Corresponding author) and MILENA SALGADO-LYNN* Organisms and Environment Division, Cardiff School of Biosciences, Cardiff University, Cardiff, UK. E-mail goossensbr@cardiff.ac.uk

JEFFRINE J. ROVIE-RYAN Ex-Situ Conservation Division, Department of Wildlife and National Parks, Kuala Lumpur, Malaysia

ABDUL H. AHMAD Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Kota Kinabalu, Sabah, Malaysia

JUNAIDI PAYNE and ZAINAL Z. ZAINUDDIN Borneo Rhino Alliance, Kota Kinabalu, Sabah, Malaysia

SENTHILVEL K.S.S. NATHAN and LAURENTIUS N. AMBU Sabah Wildlife Department, Wisma Muis, Kota Kinabalu, Sabah, Malaysia

* Also at: Danau Girang Field Centre, c/o Sabah Wildlife Department, Wisma Muis, Kota Kinabalu, Sabah, Malaysia, and Sabah Wildlife Department, Wisma Muis, Kota Kinabalu, Sabah, Malaysia. BENOÎT GOOSSENS and MILENA SALGADO-LYNN contributed equally to the work.

Received 9 September 2012. Revision requested 28 November 2012.

Accepted 8 January 2013. First published online 9 May 2013.

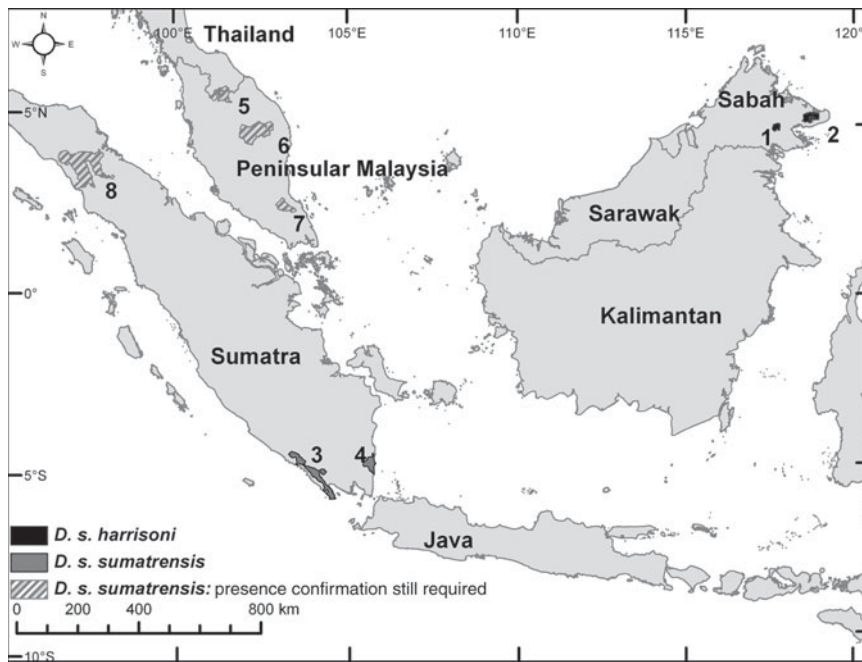


FIG. 1 The distribution of the Sumatran rhinoceros *Dicerorhinus sumatrensis* subspecies in Sumatra, Peninsular Malaysia and Sabah. The priority areas are Danum Valley Conservation Area (1), Tabin Wildlife Reserve (2), Bukit Barisan Selatan National Park (3) and Way Kambas National Park (4). Areas identified by the IUCN Asian Rhino Specialist Group as requiring scientifically defensible population estimates to confirm conservation status are Royal Belum State Park (5), Taman Negara National Park (6), Endau Rompin National Park (7) and Gunung Leuser National Park (8) (Ahmad Zafir et al., 2011).

Genetics and management

The geographical delimitation of the subspecies of rhinoceros on Sumatra was previously unclear and the question arose as to whether the populations in Peninsular Malaysia, Sumatra and Borneo (Fig. 1) should be treated as different management units, to preserve genetic diversity (Foose & van Strien, 1997). The issue persisted even after the 2009 meeting of the Sumatran Rhino Global Management and Propagation Board (responsible for management of the captive population of Sumatran rhinoceros; GMPB Technical Committee, 2009). However, in 1995 Amato et al. had already confirmed Groves' division of taxa, grouping individuals from Sumatra and Peninsular Malaysia as a single taxon (Groves, 1965, 1967, 1993). Almost in parallel, Morales et al. (1997) analysed the phylogeographic structure of *D. s. harrissoni* and *D. s. sumatrensis*. Both studies highlighted the differentiation of the Bornean population as a separate evolutionary unit. However, for Amato et al. (1995) the genetic differentiation was not enough evidence to support more than one conservation unit for the Sumatran rhinoceros, whereas Morales et al. (1997) advocated for the treatment of *D. s. harrissoni* (Borneo) and *D. s. sumatrensis* (Peninsular Malaysia and Sumatra) as distinct management units. Morales et al. (1997) argued that an average genetic divergence of 1% between the rhinoceros populations of Sumatra and Borneo justified treating them as separate conservation units. However, a range of 0–4% has been observed between other mammalian conspecifics (Avice & Lansman, 1983), and 0–2% has been observed among members of the same local population (Nei, 1972). A recent study requested by the GMPB shows a close

relationship between the three populations (Borneo, Peninsular Malaysia, and Sumatra; J. Rovie-Ryan et al., unpubl. data).

The three genetic studies (Amato et al., 1995; Morales et al., 1997; J. Rovie-Ryan et al., unpubl. data) were based solely on mtDNA but reliance on mtDNA in phylogenetics has been contentious since 2005 when it became clear that individual genes and species phylogenetic trees are not always congruent (Ballard & Rand, 2005; Hurst & Jiggins, 2005; Rubinoff & Holland, 2005; Wiens et al., 2010). In the case of the family Rhinocerotidae there are difficulties in satisfactorily resolving the rhinoceros phylogeny even using the whole mitochondrial genome (Morales & Melnick, 1994; Tougaard et al., 2001; Orlando et al., 2003; Fernando et al., 2006; Willerslev et al., 2009), and resolution may not be achieved without additional analyses of substantial amounts of nuclear DNA (Willerslev et al., 2009). However, the subspecies' genetic differences, as shown by mtDNA in the three separate studies, seem to be minimal. In our roles as biologists, wildlife managers, veterinarians and geneticists closely involved in ongoing efforts to prevent the extinction of the Sumatran rhinoceros in Sabah (northern Borneo, Malaysia) we strongly believe that the observed differences do not justify keeping the Sumatran and Bornean populations as separate management units. This is now even more so, in view of (1) the low and declining number of individuals in each Bornean and Sumatran wild population, (2) that at least two of the 10 individuals in captivity are too old to breed, and (3) that three of those are closely-related males.

A study of the Javan rhinoceros showed that it had low genetic diversity and that there was a critical need for

population expansion for the species to survive (Fernando et al., 2006). Despite clear results demonstrating that the Ujung Kulon (Indonesia) and Cat Tien (Vietnam) populations represented separate evolutionary significant units it was argued that demographic considerations should override genetic issues in the short term. The Indonesian and Vietnamese governments were urged to exchange Javan rhinoceroses before it was too late. No action was taken and, in Cat Tien National Park, the last individual in Vietnam was found dead in April 2010 (Brook et al., 2011).

In addition to the low genetic differentiation between the geographical populations of the Sumatran rhinoceros, the family Rhinocerotidae is chromosomally conservative. All species have a karyotype of $2n = 82$ despite sharing a common ancestor more than 15 million years ago (Houck et al., 1994). This chromosomal conservation reduces concerns about cytogenetic incompatibility between the populations of Sumatra and Borneo. The shared karyotype coupled with the degree of sequence divergence make outbreeding depression a less likely outcome if individuals, or their gametes, are translocated as part of a conservation management plan.

The genetic diversity of the Sumatran rhinoceros is probably also low (Amato et al., 1995; Morales et al., 1997; J. Rovie-Ryan et al., unpubl. data), and evidence is starting to accumulate that the Bornean population may have reduced reproductive fitness (S. Nathan, pers. comm.) possibly indicating inbreeding depression (Crnokrak & Roff, 1999). Where no unrelated individuals of the same taxon are available, individuals from another subspecies can, in extremis, be used to alleviate inbreeding depression (Frankham et al., 2002; Tallmon et al., 2004; Allendorf & Luikart, 2007). Members of the American Association of Zoological Parks and Aquariums have concluded that mixing of subspecies is appropriate when the extinction of the smallest population would jeopardise the higher taxon (Ryder, 1986), as is the case of the Sumatran rhinoceros and the population of Sabah. From a genetic perspective, the worst situation is where a threatened species exists as a single, inbred population, with no subspecies or related species with which to hybridize. In a few cases, some taxa might only be recovered through the use of intentional hybridization, yet this is least likely to result in outbreeding depression when there is limited genetic divergence between populations (Allendorf & Luikart, 2007).

Genetic rescue

To alleviate or prevent deleterious genetic consequences in isolated fragments, gene flow can be re-established by genetic rescue: moving individuals (translocation) or gametes (usually sperm, or pollen for plants) (Frankham et al., 2002; Hogg et al., 2006; Allendorf & Luikart, 2007;

Hedrick & Fredrickson, 2009). The classic example of genetic rescue (or genetic restoration, see Hedrick, 2005) by intentional hybridization comes from the Florida panther *Puma concolor coryi*. A population of < 50 inbred individuals was augmented with individuals from another subspecies (*P. c. stanleyana*) and in only 4 years the Florida panther no longer had a high risk of extinction (Hedrick, 1995; Maehr et al., 2002), with numbers increasing by 14% per year between 1996 and 2003 (Johnson et al., 2010). Translocation of individuals among populations may be costly, especially for large animals, and carries the risks of injury, disease transmission and behavioural disruption when individuals are released (Frankham et al., 2002; Tallmon et al., 2004; Bouzat et al., 2008). The 1989 Asian Rhino Action Plan (Khan, 1989) placed great emphasis on ex situ programmes for Asian Rhinoceros. Success was achieved in India and Nepal but not for the Sumatran rhinoceros. Foose & van Strien (1997) demonstrated a 60% mortality of the captured animals during the 1980s.

Genome resource banking

A viable alternative for the genetic restoration of the Sumatran rhinoceros is genome resource banking (systematic banking of genome resources using cryopreservation) (Johnston & Lacy, 1995; Holt & Pickard, 1999). This procedure can facilitate managed gene flow into isolated populations without the risks of translocating individuals (Allendorf & Luikart, 2007). Genome resource banking coupled with artificial insemination or in vitro fertilization can reduce translocation costs and also equalize sex ratios of breeders by inseminating females with semen from males other than the local dominant, or sole, male (Fickel et al., 2007). The first successful artificial insemination in a white rhinoceros was performed in 2007 using fresh semen (Hildebrandt et al., 2007). In 2009 the frozen and then thawed semen of a white rhinoceros was used successfully in an artificial insemination, thus proving resource banking useful (Hermes et al., 2009). Implementation of such procedures may now be key for preventing the extinction of the Sumatran rhinoceros.

Conclusion

It has been 18 months since the Sumatran Rhino Global Management and Propagation Board decided that further genetic studies are not necessary to reach a decision to treat the captive populations (Way Kambas in Sumatra, Borneo Rhino Sanctuary in Borneo, and Cincinnati Zoo in the USA) as a single population following the predictions of a population viability analysis (GMPB 2011, unpubl. data) and the genetic arguments advanced here, and to combine efforts to improve gamete transfer (through genome resource

banking) between captive Sumatran rhinoceroses. Perhaps the recent capture of Puntung, a young wild female, in Sabah (Borneo Post Online, 2011) will boost government endorsement of the need to exchange gametes between countries. Actions to initiate genome resource banking and artificial insemination or in vitro fertilization are underway in Borneo (S. Nathan, pers. comm.; Sabah Wildlife Department, 2011). Any further prevarication in the use of all possible techniques to boost reproduction in the Sumatran rhinoceros, including the mixing of gametes between populations considered to be separate subspecies, will mean the eventual extinction of populations of Sumatran rhinoceros in Borneo and Sumatra, duplicating the tragedy of the extinction of the Javan rhinoceros population in Vietnam. By agreeing to exchange the animals' gametes, the Indonesian and Malaysian governments will have made an historical step towards the survival of one of the most charismatic, ancient and enigmatic large mammals.

References

- AHMAD ZAFIR, A.W., PAYNE, J., MOHAMED, A., LAU, C.F., SHARMA, D.S.K., ALFRED, R. et al. (2011) Now or never: what will it take to save the Sumatran rhinoceros *Dicerorhinus sumatrensis* from extinction? *Oryx*, 45, 225–233.
- ALLENDDORF, F.W. & LUIKART, G. (2007) *Conservation and the Genetics of Populations*. Blackwell Publishing, Oxford, UK.
- AMATO, G., WHARTON, D., ZAINUDDIN, Z.Z. & POWELL, J.R. (1995) Assessment of conservation units for the Sumatran rhinoceros (*Dicerorhinus sumatrensis*). *Zoo Biology*, 14, 395–402.
- ASHLEY, M.V., MELNICK, D.J. & WESTERN, D. (1990) Conservation genetics of the black rhinoceros (*Diceros bicornis*), I: evidence from the mitochondrial DNA of three populations. *Conservation Biology*, 4, 71–77.
- AVISE, J.C. & LANSMAN, R.A. (1983) Polymorphism of mitochondrial DNA in populations of higher animals. In *Evolution of Genes and Proteins* (eds M. Nei & R.K. Koehn), pp. 147–164. Sinauer, Sunderland, USA.
- BALLARD, J.W.O. & RAND, D.M. (2005) The population biology of mitochondrial DNA and its phylogenetic implications. *Annual Review of Ecology, Evolution, and Systematics*, 36, 621–642.
- BORNEO POST ONLINE (2011) *Christmas miracle, healthy female rhino found in Tabin*. Borneo Post, 25 December. <http://www.theborneopost.com/2011/12/25/christmas-miracle-healthy-female-rhino-found-in-tabin> [accessed 15 March 2013].
- BOUZAT, J.L., JOHNSON, J.A., TOEPFER, J.E., SIMPSON, S.A., ESKER, T. L. & WESTEMEIER, R.L. (2008) Beyond the beneficial effects of translocations as an effective tool for the genetic restoration of isolated populations. *Conservation Genetics*, 10, 191–201.
- BROOK, S., VAN COEVERDEN DE GROOT, P., MAHOOD, S. & LONG, B. (2011) Extinction of the Javan Rhinoceros (*Rhinoceros sondaicus*) from Vietnam. WWF-Vietnam.
- CABALLERO, A., RODRÍGUEZ-RAMILO, S.T., ÁVILA, V. & FERNÁNDEZ, J. (2009) Management of genetic diversity of subdivided populations in conservation programmes. *Conservation Genetics*, 11, 409–419.
- CERDEÑO, E. (1998) Diversity and evolutionary trends of the family Rhinocerotidae (Perissodactyla). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 141, 13–34.
- CRNOKRAK, P. & ROFF, D.A. (1999) Inbreeding depression in the wild. *Heredity*, 83, 260–270.
- DESALLE, R. & AMATO, G. (2004) The expansion of conservation genetics. *Nature Reviews Genetics*, 5, 702–712.
- DINERSTEIN, E. (2003) *The Return of the Unicorns: The Natural History and Conservation of the Greater One-Horned Rhinoceros*. Columbia University Press, New York, USA.
- DINERSTEIN, E. & MCCracken, G.F. (1990) Endangered greater one-horned rhinoceros carry high levels of genetic variation. *Conservation Biology*, 4, 417–422.
- FERNANDO, P., POLET, G., FOEAD, N., NG, L.S., PASTORINI, J. & MELNICK, D.J. (2006) Genetic diversity, phylogeny and conservation of the Javan rhinoceros (*Rhinoceros sondaicus*). *Conservation Genetics*, 7, 439–448.
- FICKEL, J., WAGENER, A. & LUDWIG, A. (2007) Semen cryopreservation and the conservation of endangered species. *European Journal of Wildlife Research*, 53, 81–89.
- FOOSE, T.J. & VAN STRIEN, N.J. (1997) *Asian Rhinos—Status Survey and Conservation Action Plan*. IUCN, Gland, Switzerland, and Cambridge, UK.
- FRANKHAM, R. (2009) Where are we in conservation genetics and where do we need to go? *Conservation Genetics*, 11, 661–663.
- FRANKHAM, R., BALLOU, J.D. & BRISCOE, D.A. (2002) *Introduction to Conservation Genetics*. Cambridge University Press, Cambridge, UK.
- GMPB TECHNICAL COMMITTEE (2009) *Sumatran Rhino Global Management and Propagation Board Meeting 4 & 5 March 2009*. Bogor, Indonesia. http://www.rhinosourcecenter.com/pdf_files/130/1300587412.pdf [accessed 22 April 2013].
- GROVES, C.P. (1965) Description of a new subspecies of rhinoceros, from Borneo, *Didermocerus sumatrensis harrissoni*. *Saugetiere Mitteil*, 13, 128–131.
- GROVES, C.P. (1967) On the rhinoceroses of South-east Asia. *Saugetiere Mitteil*, 15, 221–237.
- GROVES, C.P. (1993) Testing rhinoceros subspecies by multivariate analysis. In *Rhinoceros Biology and Conservation* (ed. O.A. Ryder), pp. 92–100. San Diego Zoological Society, San Diego, USA.
- GROVES, C.P., FERNANDO, P. & ROBOVSKÝ, J. (2010) The sixth rhino: a taxonomic re-assessment of the Critically Endangered northern white rhinoceros. *PLOS ONE*, 5, e9703.
- GUERIN, C. (1989) La famille des Rhinocerotidae (Mammalia, Perissodactyla): systématique, histoire, évolution, paléocologie. *Cranium*, 2, 3–14.
- HARLEY, E.H., BAUMGARTEN, I., CUNNINGHAM, J. & O'RYAN, C. (2005) Genetic variation and population structure in remnant populations of black rhinoceros, *Diceros bicornis*, in Africa. *Molecular Ecology*, 14, 2981–2990.
- HEDRICK, P.W. (1995) Gene flow and genetic restoration: the Florida panther as a case study. *Conservation Biology*, 9, 996–1007.
- HEDRICK, P.W. (2005) 'Genetic restoration': a more comprehensive perspective than 'genetic rescue'. *Trends in Ecology & Evolution*, 20, 109.
- HEDRICK, P.W. & FREDRICKSON, R. (2009) Genetic rescue guidelines with examples from Mexican wolves and Florida panthers. *Conservation Genetics*, 11, 615–626.
- HERMES, R., GÖRITZ, F., SARAGUSTY, J., SÓS, E., MOLNAR, V., REID, C.E. et al. (2009) First successful artificial insemination with frozen-thawed semen in rhinoceros. *Theriogenology*, 71, 393–399.
- HILDEBRANDT, T.B., HERMES, R., WALZER, C., SÓS, E., MOLNAR, V., MEZÖSI, L. et al. (2007) Artificial insemination in the anoestrous and the postpartum white rhinoceros using GnRH analogue to induce ovulation. *Theriogenology*, 67, 1473–1484.
- HOGG, J.T., FORBES, S.H., STEELE, B.M. & LUIKART, G. (2006) Genetic rescue of an insular population of large mammals. *Proceedings of the Royal Society of London B*, 273, 1491–1499.

- HOLT, W.V. & PICKARD, A.R. (1999) Role of reproductive technologies and genetic resource banks in animal conservation. *Reviews of Reproduction*, 4, 143–150.
- HOUCK, M., RYDER, O., VAHALA, J., KOCK, R. & OOSTERHUIS, J. (1994) Diploid chromosome number and chromosomal variation in the white rhinoceros (*Ceratotherium simum*). *Journal of Heredity*, 85, 30–34.
- HURST, G.D.D. & JIGGINS, F.M. (2005) Problems with mitochondrial DNA as a marker in population, phylogeographic and phylogenetic studies: the effects of inherited symbionts. *Proceedings of the Royal Society of London B*, 272, 1525–1534.
- IUCN (2011) *IUCN Red List of Threatened Species v. 2011.2*. <http://www.iucnredlist.org> [accessed 2 January 2012].
- JOHNSON, W.E., ONORATO, D.P., ROELKE, M.E., LAND, E.D., CUNNINGHAM, M., BELDEN, R.C. et al. (2010) Genetic restoration of the Florida panther. *Science*, 329, 1641–1645.
- JOHNSTON, L. & LACY, R. (1995) Genome resource banking for species conservation: selection of sperm donors. *Cryobiology*, 32, 68–77.
- KHAN, M. (1989) *Asian Rhinos: An Action Plan for their Conservation*. IUCN, Gland, Switzerland.
- KIM, M.H. (2009) *The utility of DNA microsatellite markers in conservation of a Namibian population of the black rhinoceros (Diceros bicornis)*. MSc thesis. Queen's University, Ontario, Canada.
- LAIKRE, L. (2010) Genetic diversity is overlooked in international conservation policy implementation. *Conservation Genetics*, 11, 349–354.
- MAEHR, D.S., LACY, R.C., LAND, E.D., BASS, O.K. & HOCTOR, T.S. (2002) Evolution of population viability assessments for the Florida panther: A multiperspective approach. In *Population Viability Analysis* (eds S.R. Beissinger & D.R. McCullough), pp. 284–311. University of Chicago Press, Chicago, USA.
- MORALES, J.C., ANDAU, P.M., SUPRIATNA, J., ZAINUDDIN, Z.Z. & MELNICK, D.J. (1997) Mitochondrial DNA variability and conservation genetics of the Sumatran rhinoceros. *Conservation Biology*, 11, 539–543.
- MORALES, J.C. & MELNICK, D.J. (1994) Molecular systematics of the living rhinoceros. *Molecular Phylogenetics and Evolution*, 2, 129–134.
- MORITZ, C. (1994) Defining 'Evolutionarily Significant Units' for conservation. *Trends in Ecology & Evolution*, 9, 373–375.
- MORITZ, C. (2002) Strategies to protect biological diversity and the evolutionary processes that sustain it. *Systematic Biology*, 51, 238–254.
- NEI, M. (1972) Genetic distance between populations. *American Naturalist*, 106, 283–292.
- ORLANDO, L., LEONARD, J.A., THENOT, A., LAUDET, V., GUERIN, C. & HÄNNI, C. (2003) Ancient DNA analysis reveals woolly rhino evolutionary relationships. *Molecular Phylogenetics and Evolution*, 28, 485–499.
- RABINOWITZ, A. (1995) Helping a species go extinct: the Sumatran rhino in Borneo. *Conservation Biology*, 9, 482–488.
- RUBINOFF, D. & HOLLAND, B. (2005) Between two extremes: mitochondrial DNA is neither the panacea nor the nemesis of phylogenetic and taxonomic inference. *Systematic Biology*, 54, 952–961.
- RYDER, O. (1986) Species conservation and systematics: the dilemma of subspecies. *Trends in Ecology & Evolution*, 1, 9–10.
- SABAH WILDLIFE DEPARTMENT (2011) *Rhinoceros Action Plan*. Kota Kinabalu, Sabah, Malaysia.
- SCOTT, C.A. (2008) *Microsatellite variability in four contemporary rhinoceros species: implications for conservation*. MSc thesis. Queen's University, Ontario, Canada.
- TALLMON, D.A., LUIKART, G. & WAPLES, R.S. (2004) The alluring simplicity and complex reality of genetic rescue. *Trends in Ecology & Evolution*, 19, 489–496.
- TOUGARD, C., DELEFOSSE, T., HÄNNI, C. & MONTGELARD, C. (2001) Phylogenetic relationships of the five extant Rhinoceros species (Rhinocerotidae, Perissodactyla) based on mitochondrial cytochrome *b* and 12S rRNA genes. *Molecular Phylogenetics and Evolution*, 19, 34–44.
- WIENS, J.J., KUCZYNSKI, C.A. & STEPHENS, P.R. (2010) Discordant mitochondrial and nuclear gene phylogenies in emydid turtles: implications for speciation and conservation. *Biological Journal of the Linnean Society*, 99, 445–461.
- WILLERSLEV, E., GILBERT, M.T.P., BINLADEN, J., HO, S.Y.W., CAMPOS, P.F., RATAN, A. et al. (2009) Analysis of complete mitochondrial genomes from extinct and extant rhinoceroses reveals lack of phylogenetic resolution. *BMC Evolutionary Biology*, 9, 95.

Biographical sketches

The team has a common interest in bringing the Sumatran rhinoceros back from the brink of extinction. BENOÎT GOOSSENS and MILENA SALGADO-LYNN focus their research on biodiversity responses to habitat fragmentation and degradation. They integrate approaches such as landscape ecology, geographical information systems, animal behaviour, wildlife disease, parasitology and population genetics to understand animal adaptation to landscape disturbance. JEFFRINE ROVIE-RYAN is a population geneticist. ABDUL AHMAD is chairman of the Borneo Rhino Alliance and has a special interest in the ecology and conservation of large mammals. JUNAIDI PAYNE is a wildlife ecologist with more than 30 years of experience in tropical ecology and wildlife conservation. ZAINAL ZAINUDDIN is a wildlife veterinarian working for BORA and managing the Borneo Rhino Sanctuary in Tabin Wildlife Reserve. SENTHILVEL NATHAN is the Chief Wildlife Veterinarian of Sabah Wildlife Department and is currently studying the conservation genetics of the proboscis monkey. LAURENTIUS AMBU'S main interest is in sustainable management of wildlife populations.