



**Conservation de l'éléphant d'Asie (*Elephas maximus*) par
l'étude des interactions entre humains et populations
sauvages et semi-captives d'éléphants : une approche intégrée
des dimensions démographiques, génétiques, économiques et
socioculturelles**

Gilles Maurer

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THÈSE POUR OBTENIR LE GRADE DE DOCTEUR DE L'UNIVERSITÉ DE MONTPELLIER

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**Conservation de l'éléphant d'Asie (*Elephas maximus*)
par l'étude des interactions entre humains, populations
sauvages et semi-captives d'éléphants: une approche
intégrée des dimensions démographiques, génétiques,
économiques et socioculturelles**

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Le 19 juin 2018

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Avant-propos

Ce travail de thèse est le fruit d'une longue histoire et de nombreuses rencontres qu'il me semble important de préciser au lecteur de ce manuscrit. Je me suis installé au Laos en 1995 où j'ai résidé pendant près de 15 ans. J'ai pu ainsi découvrir ce pays, apprendre la langue Lao, rencontrer les Laotiens (Lao) et bien entendu leurs éléphants. En 1998, l'agence australienne Ausaid m'a permis de financer l'achat d'un éléphant pour désenclaver un village situé dans une forêt de la province de Bokèo et qui ne disposait pas de route d'accès. C'était ma première véritable rencontre avec un éléphant et son cornac. Dès lors, j'ai pu observer, partager le quotidien de ces animaux et des personnes qui travaillent et vivent avec eux. En 2002, j'ai fondé l'association ElefantAsia et organisé une caravane de quatre éléphants qui a traversé le Laos pendant quatre mois, parcourant 1200 km pour récolter les traditions liées à cet animal vénéré mais que la plupart des Lao n'ont jamais vu. Le passage des éléphants de village en village a attiré une foule innombrable et acquis un retentissement national. De nombreux programmes ont suivi : formations aux soins vétérinaires, unité mobile de soins, sensibilisation, appui à la formation d'associations professionnelles ou encore l'organisation d'un festival de l'éléphant qui a accueilli jusqu'à 70 éléphants et 100 000 visiteurs, principalement Lao. Vatsana Chanthavong, vétérinaire du Département de l'Élevage a été de tous les combats. Le ZooParc de Beauval a financé la construction d'un hôpital.

Je me suis réinstallé en France en 2013 et j'ai repris des études en écologie à Montpellier. J'ai rencontré Olivier Gimenez et nous avons imaginé ce sujet de thèse, celui d'une histoire partagée entre les Lao, les éléphants de villages et leurs congénères sauvages. Une histoire dont le fil est soumis à de fortes tensions : bouleversements sociaux, économiques, environnementaux. Une approche interdisciplinaire basée sur les principes de l'écologie nous a semblé adaptée à la description et l'analyse des interactions et des dynamiques complexes du système socio-écologique humain - éléphant de village - éléphant sauvage. Baptiste Mulot, le ZooParc de Beauval et l'association Beauval Nature se sont impliqués dans ce projet dans le cadre d'une thèse CIFRE. Marie-Pierre Dubois m'a fait découvrir le travail de laboratoire, Finn Kjellberg m'a initié à la génétique de populations et Nicolas Lescureux m'a conduit dans mes travaux anthropologiques. Tous ont nourri mes réflexions. Merci, et bonne lecture.

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1 INTRODUCTION

1.1 L'éléphant dans le monde des humains

Depuis des millénaires, l'éléphant occupe une place importante dans la construction des nations d'Asie du Sud et du Sud-Est, leur identité, leur culture et leur économie (Lair 1997; Csuti 2006). Bien que vénéré dans les cultures et les religions, l'éléphant a été utilisé à la fois comme char d'assaut, moyen de transport, monture d'apparat, engin de débardage ou basketteur. Cette condition qui peut sembler paradoxale aux occidentaux illustre la relation complexe qui lie humains et éléphants en Asie.

1.1.1 Les limites de la dichotomie sauvage / domestique pour penser les éléphants

La diversité des espèces concernées par la domestication, les différentes formes qu'elle a pu prendre, les facteurs et les impacts des processus de domestications sur les espèces domestiquées et sur les sociétés sont autant de champs d'investigations pour de nombreuses disciplines telles que l'archéobiologie, l'anthropologie, la génétique ou l'éthologie parmi d'autres. Certains de ces débats semblent pertinents pour questionner le statut actuel complexe des éléphants d'Asie.

La combinaison des recherches en archéozoologie et en génétique permet de retracer l'histoire des domestications animales, qui aurait débuté avec la domestication du chien il y a environ 15 000 ans. Des processus différenciés selon les espèces semblent avoir été à l'œuvre, n'impliquant pas toujours d'intentionnalité humaine, voire relevant du commensalisme et de la construction de niche, comme pour le chien (Larson and Fuller 2014, Figure 3).

doit se réaffirmer au travers d'actions (dont le dressage) permettant de recréer le lien particulier entre humains et animaux dans un contexte domestique (Lescureux 2018).

Zeder (2015) propose la définition suivante de la domestication :

Domestication is a sustained multigenerational, mutualistic relationship in which one organism assumes a significant degree of influence over the reproduction and care of another organism in order to secure a more predictable supply of a resource of interest, and through which the partner organism gains advantage over individuals that remain outside this relationship, thereby benefitting and often increasing the fitness of both the domesticator and the target domesticate.

Cette définition privilégie une nature mutualiste de la relation sans présager du niveau d'altération biologique (génétique, phénotypique, comportementale) ou culturel (importance socio-culturelle des espèces exploitées) induit par la domestication (Zeder 2015).

Avec la domestication, la relation entre humain et non-humain change pourtant de paradigme (Cauvin 2000; Vigne 2015). Si pour Ingold (2000a) on passe d'une relation de confiance fondée sur un mélange d'autonomie et de dépendance à une relation de domination basée sur la force et la manipulation, il apparaît que des formes d'élevage pastoral basé sur l'autonomie animale et une alternance de périodes de liberté et de contrôle se pratiquent de par le monde et ont notamment été décrites en Asie du Nord (Stépanoff et al. 2017).

De plus, la domestication des animaux et des plantes induit le développement d'une distinction entre domestique et non-domestique, conduisant ainsi à l'apparition de la notion de sauvage, par opposition au domestique. Dans l'antiquité romaine la *silva* (terme à l'origine du mot sauvage) qualifie ainsi la forêt et les êtres qui y habitent en dehors de toute civilisation. D'abord valorisée comme le théâtre des exercices guerriers en période de paix, elle devient peu à peu un espace inculte et dangereux à défricher et à civiliser (Descola 2004). Cette opposition entre sauvage et domestique a perduré en occident jusqu'à nos jours. Cependant, dans une partie de la société occidentale, une forme d'inversion des valeurs s'est produite qui a vu le sauvage valorisé après des siècles de rejet. En effet, le

sauvage, surtout dans sa dimension spectaculaire, est réhabilité dans les arts et la littérature de la période romantique, au 19^{ème} siècle, en réaction au désenchantement lié à l'industrialisation et à la concentration des populations dans les villes (Descola 2004). Emerge également la philosophie du *Wilderness* avec des environmentalistes tels que Thoreau ou Muir (Nash 1967; Cronon 1996). Ce nouveau changement de paradigme n'est pas sans conséquences concrètes, puisque c'est également à cette époque que sont instaurés les premiers parcs nationaux et réserves naturelles comme Yellowstone en 1872, et neuf parcs nationaux en Suède en 1909. Cette valorisation du sauvage trouve également un écho positif avec le développement de l'écologie, une meilleure compréhension du fonctionnement des écosystèmes et des préoccupations grandissantes pour l'avenir de la planète et la sauvegarde de la biodiversité. Cependant, le concept de wilderness s'apparente à une idéalisation sans grand rapport avec l'histoire et l'écologie des milieux perçus comme sauvages (Cronon 1996).

Bien qu'une partie des sociétés naturalistes² occidentales (au sens de Descola 2005) aient été traversées par ce changement du sauvage négatif vers le sauvage positif, cela ne transforme pas (voire renforce) l'approche dualiste d'un monde séparé entre nature et culture et entre sauvage et domestique. La sauvegarde d'un sauvage perçu comme authentique et pur (Knight 2000; Lescureux & Linnell 2014) devient le cheval de bataille d'une partie de l'environnementalisme et de la conservation.

D'autres ontologies existent pourtant, notamment l'animisme que l'on retrouve en Asie du Sud et Sud-Est (Descola 2005) et certains auteurs remettent en cause cette séparation nature/culture en notant la perméabilité entre ces deux mondes à travers la prolifération des hybrides société-nature (Latour 1991), l'inadéquation entre des discours et les pratiques en conservation (Linnell et al. 2015) ou la conjonction de facteurs sociaux et écologiques particuliers comme fondement des relations entre humains et animaux (Ingold 2000c).

² P. Descola distingue quatre grandes ontologies gouvernant le rapport au monde des sociétés : l'animisme, le naturalisme, le totémisme et l'analogisme. Les sociétés occidentales modernes sont considérées comme des sociétés d'ontologie naturaliste. Cela implique l'existence d'une continuité dans les physicalités entre les humains et les non-humains, qui obéissent aux mêmes lois biologiques, mais une discontinuité dans l'intériorité (âme, conscience, intentionnalité, etc.) qui conduit à des modes d'organisations fondamentalement différents entre les humains et les autres êtres, seuls les humains sortant de l'état de nature via la culture et l'organisation en société. L'animisme est lui marqué par une discontinuité des physicalités et une continuité des intériorités.

Au cœur de ces différents débats, l'éléphant d'Asie constitue un cas hybride mêlant une forte relation symbolique, spirituelle, écologique et économique entre humains et éléphants depuis de multiples générations, parallèlement à une absence de contrôle de la reproduction et une forte autonomie des animaux. L'attention internationale portée à cette espèce emblématique, symbole du sauvage pour les uns, amie des humains pour les autres, s'affiche dans des programmes de conservation (de l'éléphant sauvage) ou des programmes d'amélioration du bien-être animal (de l'éléphant domestique), relevant tous deux d'une ontologie naturaliste bien éloignée de la vision et des perceptions des communautés locales.

1.1.2 Origine et symbolique de la relation humain-éléphant en Asie

1.1.2.1 Naissance d'une culture de l'éléphant

Il est difficile de reconstruire la relation éléphant-humain au début de l'Holocène (10 000-5000 ans avant nos jours), les fossiles d'*Elephas* étant rares ou inexistant pour cette période (Sukumar 2003b). Les premières traces archéologiques d'éléphants en captivité proviennent de sceaux sculptés retrouvés dans la vallée de l'Indus, et datant de la culture Harappan, il y a environ 4500 ans (Csuti 2006; Sukumar 2003b). Il est généralement considéré, souvent de façon implicite, que l'art et la science de l'élevage des éléphants se sont diffusés sur tout le continent à partir d'un centre situé dans le nord-ouest de l'Inde. Sans aucun doute, cette région a été le centre d'une large diffusion culturelle rayonnant à travers tout le sous-continent avec la montée de cultures aristocratiques liées à l'élevage de l'éléphant, mais ce centre n'était pas nécessairement la source de la première domestication (Lair 1997). Une abondante littérature sur l'animal se développe en parallèle. Par exemple le *Gajaśāstra* (traité sur les éléphants, en sanskrit) écrit par le sage *Pālakāpya* (VIe - Ve siècle av. J.-C), est considéré comme le texte fondateur de la science du savoir sur les éléphants (Lainé 2010). On retrouve également une importante littérature au Myanmar ou en Thaïlande, qui illustre l'investissement de ces sociétés dans l'acquisition de savoirs sur la biologie, le comportement de l'éléphant ou encore des techniques de dressage et de soins (Figure 4 in Gale 1974; Ringis 1996).

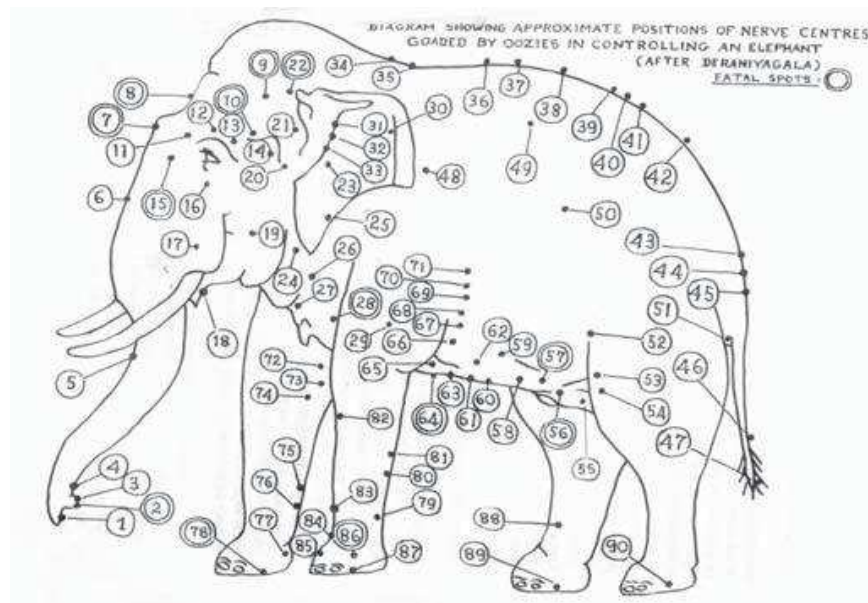


Figure 2 : Schéma des points nerveux permettant de contrôler les éléphants (Gale 1974)

1.1.2.2 Sacralisation et influence indienne en Asie du Sud-Est

Depuis l'époque Védique (3500 – 2500 avant nos jours) l'éléphant est une figure importante du panthéon hindouiste. Ganesh le dieu à tête d'éléphant (Figure 3a), chef des troupes divines, dieu de la sagesse, de l'intelligence et de l'éducation, est sans doute le dieu le plus vénéré en Inde. Son aura s'est étendue à l'ensemble de l'Asie du Sud-Est (Sukumar 2003b).



Figure 3 : Représentation de dieux d'origine hindoue au Laos

a - Enfants laotiens observant une image de Ganesh in La Caravane des éléphants, Actes Sud (2003), photo Thierry Renavand. b - Drapeau du Laos (1952-1975) représentant Erawan, l'éléphant tricéphale.

De la même façon *Airavata*, l'éléphant blanc tricéphale monture du dieu Indra, est connu en Thaïlande et au Laos sous le nom de *Erawan*. Il était représenté sur le drapeau du Laos et de la famille royale avant la révolution de 1975 (Figure 3b).

L'expansion du Bouddhisme Theravada depuis l'Inde jusqu'à l'Asie du Sud-Est à partir de 450 av JC. a amené avec lui la sacralisation de l'éléphant (Lamotte 1976). Tout au long de ces 500 existences, le Bouddha a été réincarné plusieurs fois en éléphant. Au cours de sa dernière existence, l'éléphant accompagna fidèlement Bouddha dans les moments essentiels de sa vie. Ce fut un éléphant blanc qui apparut en rêve à la reine Maya, pour lui annoncer la conception du futur Bouddha en son sein. De même, à la sortie d'un long jeûne dans l'Himalaya, l'éléphant était présent, accompagné du singe pour apporter de l'eau et du miel au Bouddha (Sukumar 2003b).

L'Eléphant Blanc est d'ailleurs considéré comme un être ayant atteint un très haut niveau d'illumination et est vénéré dans les pays d'Asie du Sud-Est. La possession d'un Eléphant Blanc est l'apanage des rois et des princes (Ringis 1996). Symbole royal de souveraineté, l'Eléphant Blanc reste un emblème de pouvoir au Laos et au Myanmar (Figure 4c).



Figure 4 : Quelques représentations symboliques de l'éléphant au Laos

Façades de pagodes laotiennes : a) T. Renavand ; b) A. Carron - 2002 ; c) L'éléphant Blanc du Laos ouvrant une parade à Luang Prabang, G. Maurer, 2015.

1.1.2.3 Vénération populaire au Laos

L'introduction du Bouddhisme, au Laos en particulier, n'a pas pour autant fait disparaître le culte des *Phi*, les Génies, et des Ancêtres (Condominas 1968). Les Lao, comme les autres peuples de langue tai, croient aux âmes (*kwan*), ou esprits vitaux, qui doivent être intégrées au corps pour assurer le bien-être de l'individu (Ngaosyvathn 1990). Leur absence peut provoquer des maladies, des malheurs ou laisser les esprits sauvages (*phi pa*) prendre le dessus. Un rituel appelé le *baci* ou *sukwan* est largement pratiqué pour y remédier. Comme les humains, l'éléphant est habité par 32 *kwan*. Chaque année au Nouvel An (*pi may*) ou à l'occasion d'un événement (départ en forêt, maladie, accident), le propriétaire d'un éléphant organise une cérémonie de *sukwan* pour son éléphant (Figure 5a-b). D'autres croyances, comme passer sous la trompe d'un éléphant pour s'assurer richesse, force et longévité (Figure 5 c-d), illustrent l'importance de l'éléphant dans les croyances populaires.

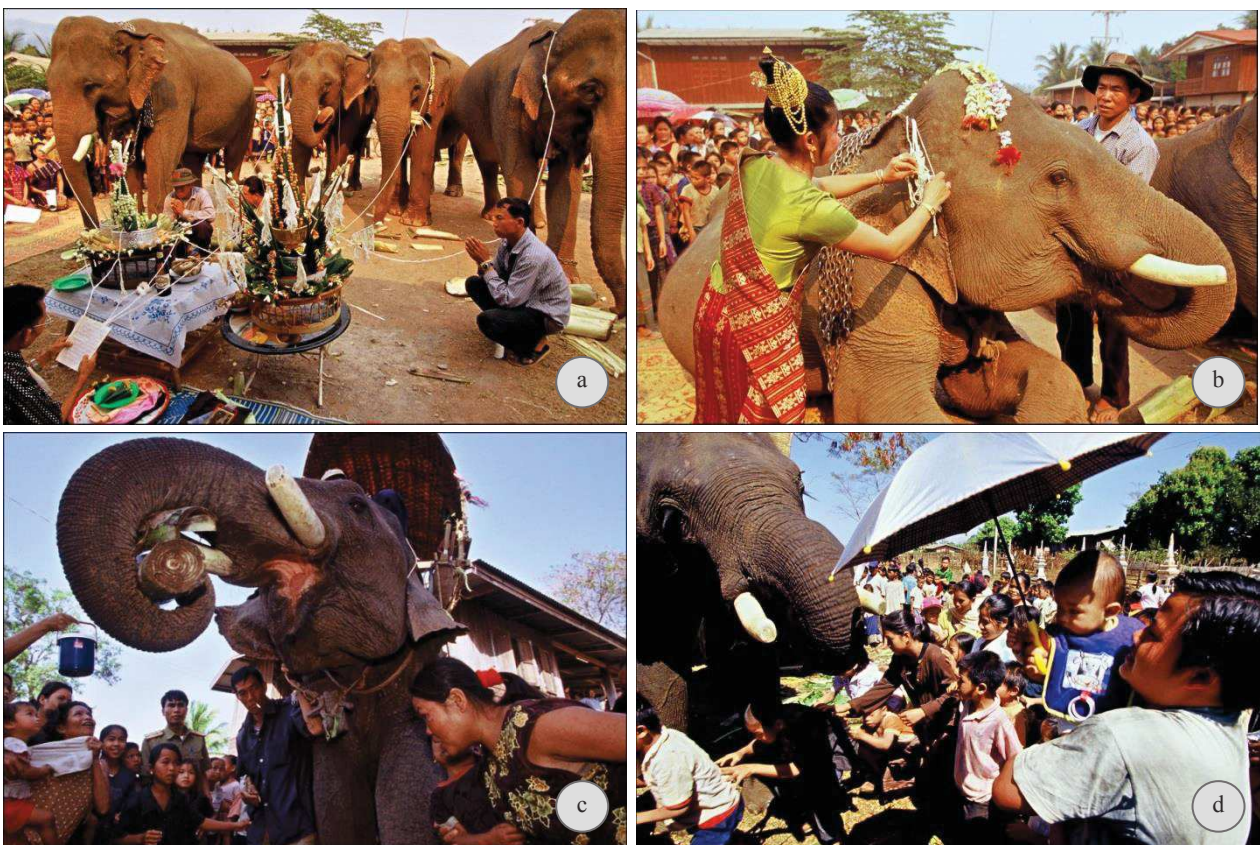


Figure 5 : Cérémonies et croyances populaires au Laos

a – b) cérémonies de baci ; c – d) Des villageois passent sous la trompe d'un éléphant
T. Renavand, (Duffillot et al. 2003).

L'expansion du Bouddhisme en Asie du Sud-Est a amené la sacralisation de l'éléphant mais également son utilisation comme machine de guerre.

1.1.3 L'éléphant de guerre, un animal vénéré au service de la construction des nations

Le *Ramayana* et le *Mahabharata*, deux récits épiques datant du IV^{ème} siècle av. J.C., décrivent l'utilisation d'éléphants au combat (Sukumar 2003b). L'éléphant de guerre a été la principale forme d'utilisation de l'éléphant en Inde et dans la région pendant près de trois millénaires (Trautmann 2015). De très nombreux récits de batailles rapportent l'utilisation d'éléphants de guerre, en Inde, mais également en Asie du Sud-Est, jusqu'à l'empire Perse et les guerres de conquêtes d'Alexandre Le Grand. Ainsi Chandragupta Maurya, qui usurpa le trône de Nanda en 321 av. J.-C. et fonda l'empire Maurya, aurait disposé d'une armée de 9 000 éléphants (Sukumar 2003b). Ils étaient utilisés pour briser les lignes adverses, effrayer l'ennemi mais également pour la logistique guerrière (Kistler 2007). La forme idéale de l'éléphant de guerre (un mâle adulte, porteur de défenses, agressif, sujet à des périodes de musth³ violentes) renseigne sur les caractéristiques recherchées lors de leur capture et, par extension, sur le profil de population des éléphants captifs (Trautmann 2015). Dans la seconde moitié du premier millénaire, un grand nombre d'éléphants captifs étaient détenus par les empereurs, principalement pour être utilisés dans leurs armées. C'est devenu une tradition pour les nobles et les membres de la famille royale de posséder des éléphants.

Avec l'avènement des armes à feu, l'éléphant a perdu son rôle stratégique militaire et a été reconverti à partir de la fin du 19^{ème} siècle dans le débardage du bois. Les qualités de force et d'agressivité des éléphants recherchées dans cette industrie privilégient toujours les mâles adultes. La capture, comme principale source d'approvisionnement en éléphant, s'impose alors face au défi d'entretenir et de faire reproduire une population de femelles susceptible de constituer une telle armée de mâles adultes.

1.1.4 Du monde sauvage au monde des humains

1.1.4.1 La capture

Le nombre total d'éléphants capturés depuis le 16^{ème} siècle est estimé entre deux et quatre millions. Au cours du 20^{ème} siècle, on estime que plus de 100 000 éléphants d'Asie ont été capturés pour le travail et les expositions zoologiques (Sukumar 2003b).

³ Le musth est un état périodique chez les éléphants mâles caractérisé par des sécrétions temporales et un comportement agressif.

Sanderson (1879) indique que l'éléphant se reproduit très rarement en captivité. Il explique cela par le mode de gestion des mâles et femelles qui, en Inde, sont séparés mais également pour des raisons physiques dues à une nourriture insuffisante et un dur labeur. D'un point de vue économique, il ne faisait aucun sens d'élever des éléphants en Inde, car avant qu'ils aient atteint l'âge utile au travail – 15 ans – ils auraient coûté beaucoup plus cher que ce que coûte la capture d'un mâle adulte prêt à travailler (Sanderson 1879).

Cependant, Sanderson indique également que dans certaines régions de Birmanie (actuel Myanmar) et du Siam (actuelle Thaïlande), les éléphants étaient élevés en semi-liberté. Les femelles étaient relâchées et pouvaient être saillies par des mâles sauvages. Mais en Birmanie, les forêts étaient abondantes et cela ne coûtait rien d'élever un éléphanteau jusqu'à ce qu'il soit vendu (Sanderson 1879).

Il existe quatre principales méthodes de capture décrites en détails (Mar 2007; Gale 1974; Williams 1950; Sanderson 1879) et reprises brièvement ici. La méthode de l'enclos ou palissade (*Keddakh* en Inde, *kraal* en Thaïlande ou *Kyone* au Myanmar) permet de capturer de nombreux éléphants (Figure 6). Des hommes, parfois montés sur des éléphants, rabattent la harde vers un enclos constitué de solides parois faites de troncs d'arbres. Une fois que la harde a pénétré dans l'enclos, une lourde porte s'abat pour en condamner la sortie, tandis que des hommes armés de piques et de lances repoussent les charges des éléphants contre les parois. Les éléphants sont alors extraits de l'enclos un par un pour être dressés. En raison de la nature de l'opération, l'âge moyen de capture est plus élevé que celui des deux autres méthodes décrites ci-après. La plupart des éléphants capturés sont des femelles, y compris des matriarches, des femelles gravides, des juvéniles. Les mâles avec des défenses sont évités car trop agressifs, dangereux et susceptibles de blesser ou de tuer d'autres éléphants dans l'enclos. Ils sont aussi plus difficiles à dresser. Les femelles gestantes et allaitantes et les femelles trop âgées sont en général relâchées. Cette méthode est considérée comme la plus destructrice des trois méthodes de capture en raison du taux de mortalité élevé estimé à 30% (Myint Aung 1997). Elle était également l'apanage des rois et des puissants ou des gouvernements car elle implique de pouvoir mobiliser une importante main d'œuvre ainsi que des circuits commerciaux permettant d'absorber plusieurs dizaines d'éléphants capturés ainsi.

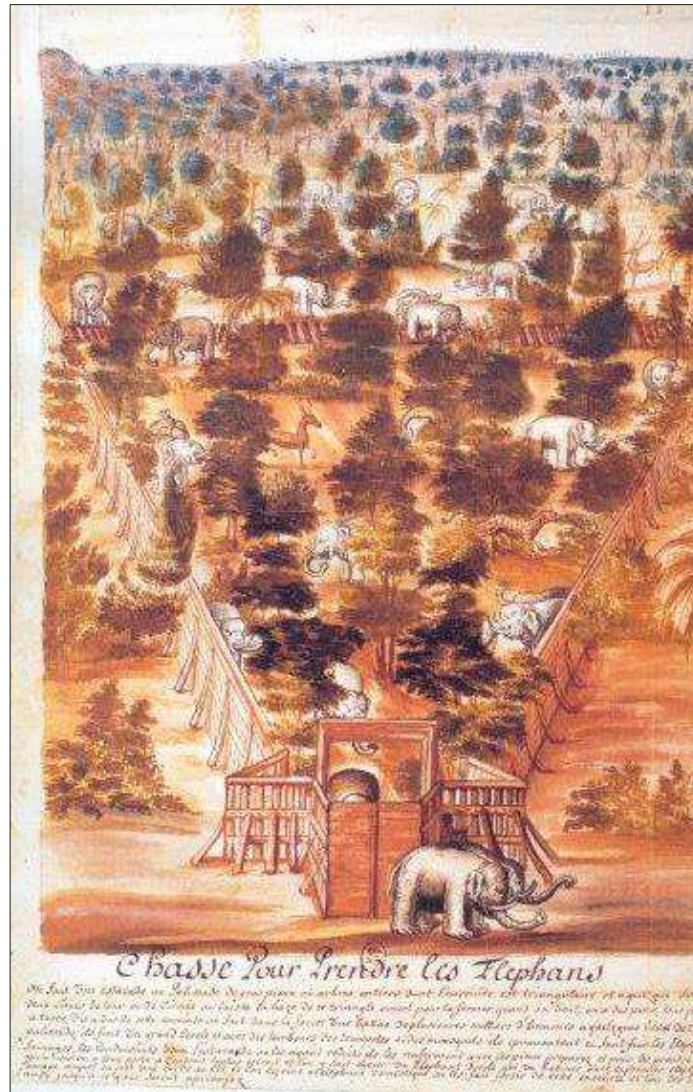


Figure 6 : Estacade ou palissade au Siam (Kraal) in Guy Tachard (1686)

La méthode du Lasso (Milarshikar) est la méthode traditionnelle de capture en Assam au Nord de l'Inde (Lainé 2010), dans la partie nord du Myanmar (Mar 2007), au Vietnam, au Cambodge (Ellul 1983) et au Sud du Laos. La description ci-dessous correspond à un témoignage récolté auprès d'un ancien captureur au Sud du Laos en 2002 dont des extraits sont présentés dans le film documentaire « Caravan Xang » (Maurer & Dufillot 2003). La méthode consiste à pourchasser les éléphants sauvages à l'aide d'éléphants dressés. L'équipe est composée d'éléphants poursuiveurs particulièrement endurants ou rapides qui se relaient pour courser l'éléphant sauvage sélectionné, souvent un jeune, et l'isoler du reste de la harde. Quand l'éléphant sauvage fatigue, un cornac monté sur un éléphant puissant crochète la patte arrière avec une lourde corde faite de cuir de buffle tressé et jette le rouleau de corde au sol (Figure 7 : Capture d'éléphants sauvages). L'éléphanteau poursuit sa

course trainant le rouleau jusqu'à épuisement. Pendant ce temps, des éléphants puissants, en général des *phay* (éléphant portant des défenses) repoussent la contre-attaque de la harde. Encadré par des éléphants montés, l'éléphanteau est ensuite ramené près du village où il sera dressé. Cette méthode, plus sélective et nécessitant moins de moyens était préférée des villageois.



Figure 7 : Capture d'éléphants sauvages par la méthode du lasso
Le Costume Ancien et Moderne by Jules Ferrario, pub. c.1820s-30s.

La dernière méthode traditionnelle est celle du fossé. De grandes fosses sont creusées sur les sentiers de passage des éléphants. Le haut de la fosse est recouvert de branchages et de feuilles pour la camoufler aux éléphants. Le fonds est également tapissé de branches feuillues pour amortir la chute. Les plus grands éléphants sont parfois capables de ressortir par eux-mêmes. Pour extraire l'éléphant prisonnier, une corde est attachée autour de son cou puis l'éléphant est hissé hors du trou avec l'aide d'éléphants captifs. Un tronc en guise d'échelle permet de faciliter l'opération. Selon Sanderson (1879), cette méthode provoque de nombreux décès, en particulier le poids des éléphants adultes est fatal lors de la chute. Cette technique a été utilisée dans le sud du Myanmar, au Cambodge et au Sri Lanka (Gale 1974) ainsi qu'au nord du Laos.

Ces méthodes traditionnelles décrites pour la plupart dès le 17^{ème} siècle n'ont que peu évolué et étaient encore pratiquées à la fin du 20^{ème} siècle. Elles ont été remplacées par la capture par immobilisation chimique à l'aide de fusils hypodermiques ou de fléchettes et de sédatifs puissants comme l'étorphine. La plupart des pays ont interdit la capture d'éléphants sauvages à partir des années 1970 (Csuti 2006; Pimmanrojnagool & Wanghonga 2002; Sukumar 2003a). Cependant, les éléphants sont toujours capturés dans les zones où les conflits humains-éléphants nécessitent des mesures d'atténuation. Fréquemment au Myanmar, des troupeaux de 10, 20 ou plus sont retirés des zones de conflit et dressés pour travailler (Leimgruber et al. 2008). L'éloignement n'est pas propre au Myanmar. En Indonésie, les éléphants conflictuels sont fréquemment capturés et déplacés vers des camps (Mikota et al. 2008).

1.1.4.2 *Le dressage*

Une fois capturés, les éléphants sauvages sont amenés près du village pour y être dressés. Cependant le dressage ne concerne pas uniquement les éléphants capturés mais également ceux nés d'une femelle captive. Dans ce cas, l'éléphanteau est dressé vers l'âge de trois ou quatre ans. Le dressage traditionnel des éléphants a été décrit au Myanmar (Gale 1974; Williams 1950; Mar 2002), en Inde du Nord-Est (Lainé 2014) ou encore au Népal (Locke 2012). Je reprendrais ici brièvement la description d'un dressage que j'ai observé à Hongsa au Nord du Laos en 2006.

Le dressage (*khrao keuan*), littéralement « rentrer dans la cage », se déroule aux mois de décembre-janvier après les moissons lorsque la température est encore clémente. La date et le site du dressage sont choisis par le maître-dresseur. Tout le village participe à la construction de la zone de dressage et aux préparatifs, ce qui est l'occasion d'une grande fête offerte par le propriétaire de l'éléphanteau. La zone de dressage (Figure 8 a,b) est composée d'un poteau central, d'un travail, une sorte de cage de contention, et d'une hutte où le maître-dresseur, le propriétaire et les visiteurs s'abriteront et dormiront pendant toute la durée de l'opération. Une cage symbolique est construite à l'intérieur de la hutte où le propriétaire restera « encagé » pendant la nuit, à l'instar de son éléphant.

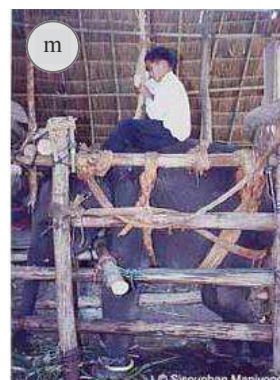
Une cérémonie est organisée la veille du dressage pour éloigner les esprits sauvages qui habitent encore le jeune éléphant, symbolisés par des figurines en argile, et apaiser les

esprits du village (Figure 8 f,g,h). Le premier jour du dressage, l'éléphanteau est séparé de sa mère maintenue attachée loin de la scène tandis que les villageois le tirent à l'aide d'une corde à l'intérieur du travail avec l'aide de deux ou trois éléphants adultes. L'éléphanteau est alors attaché à l'intérieur du travail avec des cordes tressées, ses pattes sont entravées par des menottes faites de rotin (Figure 8c). Il est gardé à l'intérieur du travail pendant plusieurs jours, frappé régulièrement avec un bâton jusqu'à ce qu'il accepte la nourriture de la main du dresseur. Cette phase de déboufrage peut durer de deux jours à une semaine. Si l'éléphant résiste trop, il peut en mourir. Il est ensuite ressorti chaque jour, attaché au poteau central et suspendu par une corde (Figure 8n), puis il apprend les commandes de base : avancer (*phay*), s'arrêter (*tjot, hao*), tourner à droite (*lio koua*) ou à gauche (*lio say*). Des enfants chevauchent l'éléphanteau lorsqu'il est à l'intérieur du travail pour l'habituer à être monté (Figure 8m).

Le dressage dure généralement trois à quatre semaines. Le maître-dresseur conduit plusieurs cérémonies pour lutter contre les esprits sauvages qui possèdent encore l'éléphant. Le site et les équipements sont purifiés plusieurs fois, un poulet est relâché sur le dos de l'animal et emportera dans sa fuite les mauvais esprits avec lui (Figure 8o,p).

A la fin du dressage, une cérémonie est organisée pour accueillir l'animal dans le monde des hommes et choisir son nom. L'éléphant le choisit lui-même en attrapant un bâton de canne à sucre parmi plusieurs où sont gravés différents noms (Figure 8q,r). A l'instar de celui pratiqué au Népal (Locke 2012), le dressage constitue au Laos un rite de passage entre le monde des esprits sauvages et le monde des hommes. Le propriétaire partage symboliquement cette séparation-transition violente pour son éléphant. Contrairement aux pratiques décrites par K. U Mar (2007) au Myanmar ou N. Lainé (2017) dans le Nord-Est de l'Inde, les chants ne font pas partie du cérémonial du dressage au Laos.

Récemment, sous l'impulsion d'organisations de bien-être animal en particulier, de nouvelles méthodes de dressage basées sur le renforcement positif sont testées en Asie (Fagen et al. 2016). Que ce soit les méthodes traditionnelles ou le renforcement positif, chacun reconnaît qu'il faudra des années avant que l'éléphanteau puisse effectuer les tâches complexes qui lui seront demandées.



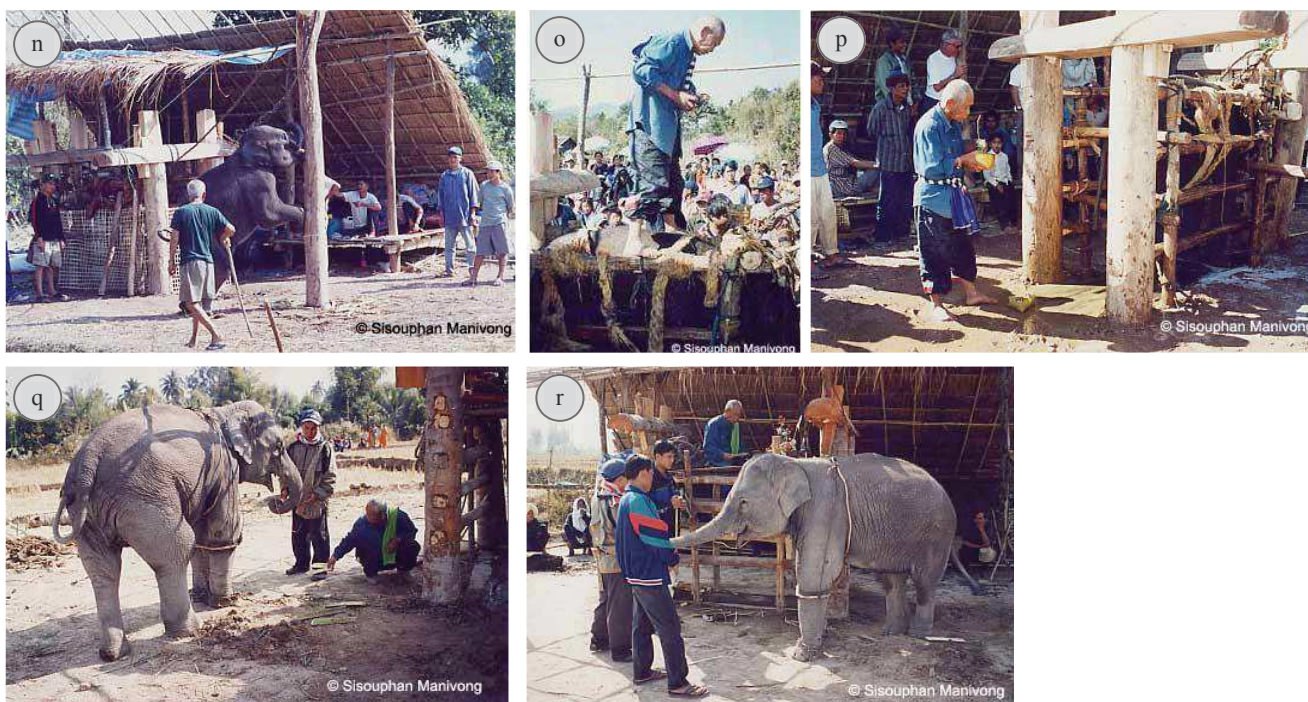


Figure 8 : Cérémonie de dressage d'un éléphant à Hongsa, Laos

(a,b) construction de la zone de dressage ; (c) menottes en rotin ; (d) corde tressée ; (e) nourriture donnée à l'éléphant ; (f) figurines d'argile représentant les esprits sauvages ; (g,h) cérémonie avant le dressage ; (i,j) l'éléphant est tiré dans le travail ; (k,l) dans le travail ; (m) un enfant monte l'éléphant pour l'accoutumer ; (n) sorti du travail et suspendu au poteau central ; (o,p) le maître-dresseur tient un poulet qui emportera les mauvais esprits ; (q,r) l'éléphant choisi son nom en attrapant un morceau de canne à sucre grâvé. Photos S. Manivong 2006

1.1.4.3 Modes d'élevage et travail

La période de dressage initial est suivie d'une longue formation qui permettra à l'éléphant d'acquérir les compétences requises pour le travail qui lui sera demandé et le cas échéant la force nécessaire pour tirer des grumes de bois en forêt.

Les systèmes d'élevage traditionnels en Asie peuvent se définir comme « extensifs » ou « intensifs » en fonction de l'accessibilité des zones d'alimentation et de la liberté de déplacement sans surveillance et sans restriction des éléphants (Kurt & Mar 2003). Dans les systèmes extensifs, les éléphants vivent généralement dans des camps forestiers. Ils sont utilisés pour le transport et comme animaux de bât. Les femelles sont généralement gardées en groupes familiaux, mais les mâles juvéniles et adultes sont isolés en particulier pendant la période de musth. Les éléphants se nourrissent en forêt la nuit sans surveillance et sans restriction, ou avec les pattes avant entravées, et rencontrent à l'occasion leurs congénères captifs et sauvages (Mar 2007). Ces modes d'élevages perdurent aujourd'hui au Myanmar,

au Laos, au nord-est de l'Inde et plus rarement en Thaïlande. Les systèmes d'élevage intensif sont ceux dans lesquels les animaux sont gardés dans les temples ou par des propriétaires privés. En général l'éléphant est maintenu isolé de ses congénères, nourri exclusivement avec du fourrage préparé, enchaîné par la patte postérieure ou parfois par une patte postérieure et antérieure opposées (Mar 2007; Kurt & Mar 2003). Ce système intensif est également pratiqué dans de nombreux camps de tourisme.

Dans les cas d'élevage extensif comme au Myanmar ou au Laos, l'éléphant à partir d'une dizaine d'années est utilisé pour le transport de charges légères (sacs de riz, bois de chauffe, équipements pour une saison de débardage en forêt) et peut tirer de petits troncs. Il ne deviendra véritablement opérationnel que vers l'âge de 15 ans (Mar 2007; Lair 1997; Gale 1974). Les travaux de débardage nécessitent deux cornacs, dont l'un est généralement le propriétaire au Laos. Le cornac chargé de la conduite de l'animal est juché sur son cou (*khuan xang*, cornac de l'éléphant), son assistant (*khuan tin*, cornac à pied) reste au sol. Ce dernier s'occupe des chaînes et de faciliter le travail de l'éléphant. Le travail de l'éléphant est saisonnier. La période de la mousson est généralement chômée, les conditions de travail étant trop difficiles et les cornacs occupés à la culture du riz. Les opérations de débardage se déroulent le matin, lorsque la température n'est pas trop chaude. Les grumes sont tractées en forêt vers un point de rassemblement (*sanam may*) accessible en camion où ils seront chargés sur la benne avec l'aide de l'éléphant. L'éléphant est ensuite reconduit en forêt pour qu'il puisse se nourrir par lui-même, soit en liberté, soit attaché avec une chaîne d'une vingtaine de mètres (*sô*).

Le débardage du bois avec des éléphants a été abandonné dans la plupart des pays à l'exception du Laos et du Myanmar. Dans ce dernier pays, l'exploitation du bois à large échelle est toujours pratiquée sous l'égide de la Myanma Timber Enterprise (MTE), entreprise d'état sous la tutelle du Ministère des Ressources Naturelles et de l'Environnement, qui possède plus de 3 000 éléphants. Près de 2 000 éléphants appartiennent également à des propriétaires privés (Leimgruber et al. 2011).



Figure 9 : Eléphants au travail, Laos
Photos G. Maurer, sauf c) S. Demange.

L'interdiction du débardage du bois en Inde et en Thaïlande a perturbé les conditions socio-économiques des cornacs et des propriétaires d'éléphants (Lainé 2013; Suter et al. 2013; Vanitha et al. 2009) condamnant certains à la mendicité dans les rues de Bangkok (Pimmanrojnagool & Wanghongsa 2002). La plupart des éléphants ont été reconvertis dans l'industrie du tourisme, attirant l'attention du public, des médias et du monde académique sur les questions de bien-être animal, autant dans leurs conditions passées de travailleurs du bois, que dans leurs nouvelles fonctions de représentation et de divertissement, ou encore sur les pratiques de dressage (Suter et al. 2013; Duffy & Moore 2010; Kontogeorgopoulos 2010; Godfrey & Kongmuang 2009).

1.1.5 Un statut discuté : captif, dressé, domestiqué, domestique...

La situation atypique de l'éléphant, utilisé par les humains depuis des millénaires, qui a participé à la construction sociale, culturelle, économique et politique des nations, mais dont la reproduction n'a jamais été contrôlée, questionne quant à son statut dans le cadre des processus de domestication décrits ci-avant. Les modes d'élevages, et donc le niveau de

contrôle et de domination exercé, sont également très variables entre les éléphants gardés dans des zoos ou des temples et ceux élevés en forêt et relâchés par intermittence. Les débats sur le(s) statut(s) des éléphants transparaissent dans la difficulté à adopter une terminologie consensuelle les désignant. De nombreux termes sont utilisés tels que : éléphant apprivoisé/dressé (tame elephant), éléphant de travail (working elephant), éléphant de débardage (timber elephant), éléphant domestique (domestic elephant), éléphant domestiqué (domesticated elephant) et, le terme dernièrement en vogue, éléphant captif (captive elephant) (Lair 1997).

Si le terme domestique implique généralement une modification biologique et comportementale par rapport à l'ancêtre sauvage, il ne convient guère à des animaux dont la grande majorité ont été capturés sauvages. Le terme « dressé » correspond à un conditionnement individuel de l'animal indépendamment d'un contrôle sur plusieurs générations. Le dressage concerne tout autant des animaux sauvages que des animaux domestiques (chiens ou dauphins détecteurs d'explosifs par exemple) mais cette terminologie n'est que rarement utilisée, renvoyant probablement à l'image d'éléphants pouvant effectuer des tours complexes dans les cirques ou les centres touristiques. Les termes d'éléphants de travail ou éléphants de débardage sont restreints à certaines utilisations (Lair 1997). Finalement, la terminologie d'éléphants captifs s'est imposée dans la littérature scientifique, en particulier dans les disciplines de la biologie, de l'écologie et de la conservation. Ce terme n'est pas sans ambiguïté dans le cas de l'éléphant d'Asie. Les éléphants maintenus dans les zoos et les temples sont certainement captifs. Peut-on véritablement parler de captivité pour les éléphants du Laos ou du Myanmar qui sont relâchés en forêt pendant plusieurs mois ? Dit-on d'un chien tenu en laisse par intermittence qu'il est captif ? La terminologie de captif renvoie donc à l'origine sauvage des éléphants, nombre d'entre eux ayant été capturés par le passé. Mais cela fait l'omission des éléphants nés captifs qui ont toujours existé et dont la proportion augmente de nos jours. Le terme de captif est rarement attribué au renne des éleveurs nomades qui partage pourtant des similitudes avec l'éléphant, telles que la perméabilité entre populations sauvages et d'élevage, l'alternance de périodes de pâture libre et de contrôle des éleveurs, ou encore le rôle symbolique, culturel, social et économique de l'animal dans les communautés d'éleveurs (Stépanoff et al. 2017; Forbes et al. 2009; Ingold 2000b). Dans le cas de l'éléphant, le terme de captif, en plus d'être ambigu, est surtout connoté négativement avec

l'idée de privation, voire de maltraitance, mobilisant alors des questionnements d'ordre éthique (Hedges et al. 2018). Certains chercheurs ont d'ailleurs pris le parti d'employer le terme de semi-captivité en traitant le cas des éléphants au Myanmar (Crawley et al. 2017; Hayward et al. 2014; Mumby et al. 2013a; Robinson et al. 2012). Cette polémique sémantique ne touche d'ailleurs pas les habitants des pays concernés par l'élevage des éléphants qui préfèrent la terminologie d'éléphants familiaux – de famille (Lair 1997; Locke 2014) à l'exception des auteurs publiant dans les revues scientifiques internationales qui utilisent alors le terme captif.

En langue lao, les éléphants captifs (*xang ban*) sont littéralement appelés « éléphants de village » où *ban* signifie village ou maison, rappelant la notion de domestique dérivée de *domus* – la maison en latin. Les interprétations *émiques* reflètent les catégories cognitives et linguistiques des autochtones, alors que les interprétations *étiques* sont celles qui ont été développées par le chercheur à des fins d'analyse (Harris 1976). J'adopterai dès lors la terminologie d'éléphants de village pour le cas des éléphants du Laos et du Myanmar et réserverai le terme consacré en biologie d'éléphants captifs pour les autres pays.

Quel que soit le statut actuel de l'éléphant, l'intensification de la domination de l'humain sur les éléphants captifs et le relâchement du lien avec le sauvage que l'on observe en Asie ne s'apparentent-ils pas à un processus de domestication de l'espèce ? Quelles conséquences ce processus peut-il induire sur la diversité génétique, la démographie, l'exploitation économique de l'éléphant et les savoirs locaux ?

1.2 Situation actuelle de l'éléphant d'Asie et enjeux de conservation

1.2.1 Aire de distribution et habitat

L'aire de répartition historique de l'éléphant d'Asie (Figure 10) s'étendait autrefois de l'Asie occidentale le long de la côte iranienne au sous-continent indien, jusqu'en Asie du Sud-Est, y compris Sumatra, Java et Bornéo, et en Chine, au moins jusqu'au fleuve Yangtze-Kiang (Sukumar 2003b). L'aire de répartition actuelle comprend 13 pays d'Asie du Sud et du Sud-Est (Figure 10). Quatre sous-espèces d'*Elephas maximus* sont reconnues principalement sur la base de la taille corporelle et de différences mineures de coloration (Shoshani & Eisenberg 1982): *E. m. indicus* sur le continent; *E. m. maximus* au Sri Lanka ; *E. m. sumatranus* sur l'île

indonésienne de Sumatra. L'origine introduite ou native de l'éléphant de Bornéo *E. m. borneensis* fait actuellement l'objet de discussions (Sharma et al. 2018; Fernando, T N C Vidya, et al. 2003).

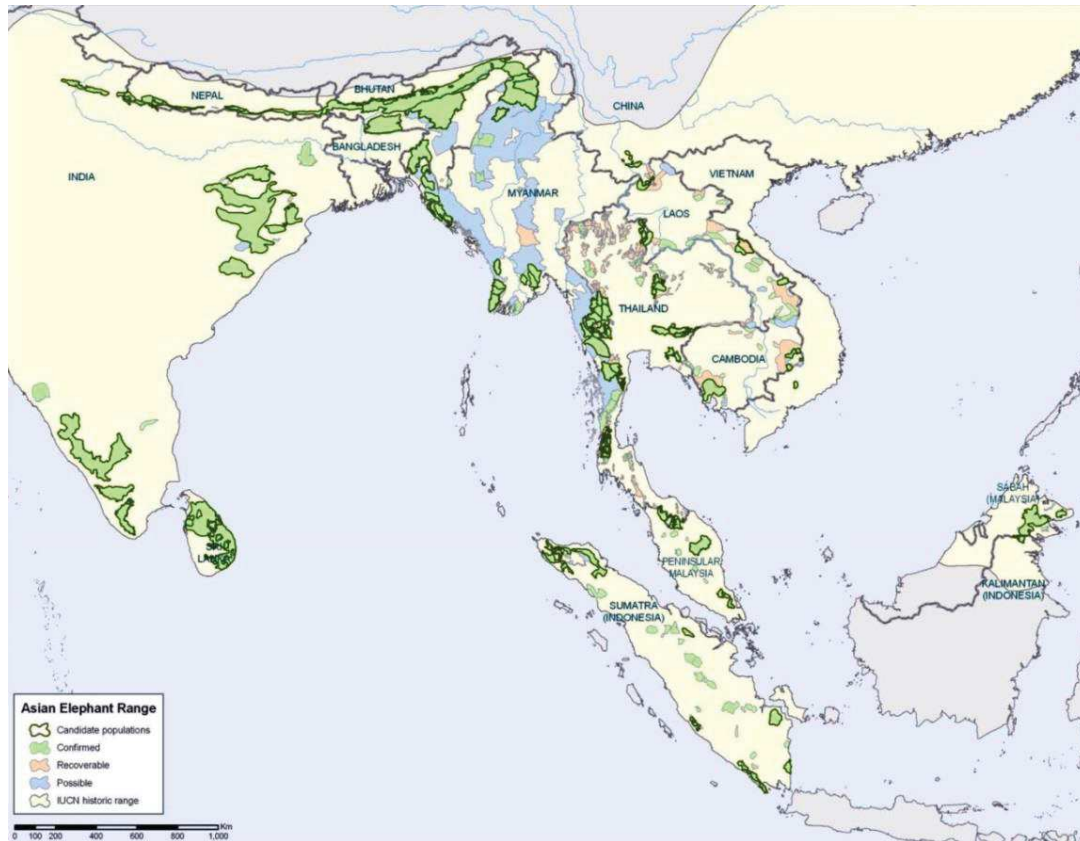


Figure 10 : Aire de répartition historique et actuelle des éléphants sauvages en Asie
Les catégories indiquent les zones de présence confirmée, possible et récupérable, les populations sélectionnées pour leur importance en termes de conservation ("populations candidates") et l'aire de répartition historique de l'éléphant d'Asie. Extrait de Hedges et al. (2008).

Les éléphants d'Asie habitent les prairies, les forêts tropicales décidues et caduques, sèches ou humides, ainsi que des forêts secondaires et cultivées ou les friches (Sukumar 2003b). Ce sont des herbivores généralistes à la fois pisseurs (grazer) et brouteurs (browser). Ils consomment un grand nombre de plantes allant des graminées aux feuilles, branches, racines, plantules et fruits (Sukumar 2003b). Lorsqu'ils peuvent trouver des graminées, les éléphants s'en nourrissent de préférence⁴. Là où il n'y a pas d'herbe, les éléphants se nourrissent de feuilles, racines ou autres (Sukumar 2003b). Ainsi les densités d'éléphants dans les forêts sèches sont plus fortes que dans les forêts humides. 30 à 40 % de la population totale vit dans des zones principalement constituées de forêts sèches (Fernando

⁴ Les bambous (*Bambuseae*) appartiennent à la famille des *Poaceae* (Graminées).

& Leimgruber 2011). En raison de leur stratégie d'alimentation mixte, de la combinaison et du passage opportuniste entre des stratégies de pâturage et de broutage, les éléphants d'Asie sont particulièrement adaptés aux forêts à canopée ouverte, aux forêts perturbées et aux forêts de succession comme les friches et jachères (Fernando & Leimgruber 2011).

1.2.2 Abondance

En 2011, la population totale d'éléphants sauvages d'Asie était estimée à dire d'experts entre 40 000 et 47 000 individus et la population captive à près de 12 000 (Fernando & Pastorini 2011). La répartition par pays des populations sauvages et captives est indiquée dans le Tableau 1. Peu de données issues d'études robustes sur la répartition et l'abondance sont disponibles à ce jour et les chiffres avancés restent des estimations d'experts (Calabrese et al. 2017; Fernando & Pastorini 2011; Hedges et al. 2008a). L'Inde et le Sri Lanka abritent près des trois quarts de la population sauvage et leur nombre semble en augmentation contrairement aux autres pays (Anon 2017a). Les pays d'Asie du Sud-Est comme le Myanmar, le Laos et le Cambodge en particulier, disposent de grandes étendues d'habitats naturels avec de faibles densités de populations humaines mais également avec peu d'éléphants (Tableau 1). En ce qui concerne la population captive, trois pays le Myanmar, l'Inde et la Thaïlande, rassemblent à eux seuls 86% de la population captive. Le Myanmar, pays qui compte la plus importante population captive avec 4775 individus, est également le seul pays dont la population captive est notablement plus élevée que la sauvage (Figure 11).

Pays	Superf. Km ²	Humains (milliers)	Elephants sauvages			captifs	Source
			Min.	Max.	Moy.	Num.	
Bangladesh	147 570	142 319	300	350	325	94	Islam et al. (2011)
Bhoutan	38 394	695	60	150	105	10	Jigme & Williams (2011)
Bornéo	747 996	19 871	1 200	3 670	2 435	14	Alfred et al. (2011)
Cambodge	181 035	13 395	250	600	425	101	Maltby & Bouchier (2011)
Chine	9 572 900	1 339 724	178	193	186	50	Zhang (2011)
Inde	3 166 391	1 210 193	26 000	28 000	27 000	3 500	Baskaran et al. (2011)
Indonésie (Sumatra)	456 167	47 728	2 400	2 800	2 600	484	Azmi & Gunaryadi (2011)
Laos	236 800	6 128	600	800	700	500	Khounboline (2011)
Malaisie (Pénins.)	132 723	22 656	1 223	1 677	1 450	62	Saaban et al. (2011)
Myanmar	676 577	52 171	1 181	2 056	1 619	4 755	Leimgruber et al. (2011)
Népal	147 181	26 620	109	142	126	208	Pradhan et al. (2011)
Sri Lanka	65 610	20 653	5 879	5 879	5 879	189	Fernando et al. (2011)
Thaïlande	513 120	65 479	2 500	3 000	2 750	2 700	Hedges et al. (2008)
Vietnam	331 212	85 846	83	110	97	54	Cao Thi Ly (2011)
Total	16 413 676	3 053 484	39 463	47 427	43 445	12 721	

Tableau 1 : Effectifs des populations humaines et des éléphants en Asie

Tableau extrait de (Fernando & Pastorini 2011)

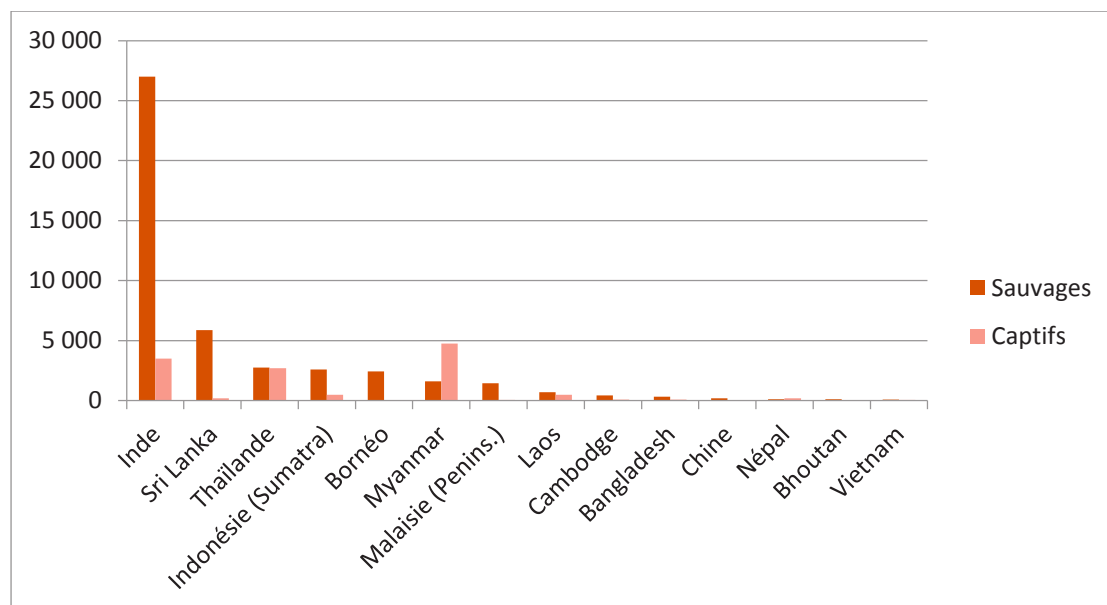


Figure 11 : Populations d'éléphants sauvages et captifs par pays

Réalisé à partir de Fernando et Pastorini (2011)

Sur l'ensemble de l'aire de répartition, le nombre d'éléphants captifs semble diminuer, leur rôle d'animaux de bât étant de plus en plus supplanté par les machines. Cependant, leur utilisation dans le tourisme est en augmentation et pourrait soutenir la demande (Fernando & Pastorini 2011). Traditionnellement les éléphants captifs partagent le même habitat que

les sauvages, leur aire de répartition est sensiblement la même que celle des sauvages, à l'exception du développement récent de camps touristiques, notamment dans des zones balnéaires en Thaïlande (Lair 1997).

Sur l'ensemble de l'aire de répartition, on compte en moyenne 70 000 humains pour un éléphant. Leur avenir dépendra donc largement de l'attitude des humains envers les éléphants et leur conservation (Fernando & Pastorini 2011).

1.2.3 Menaces et enjeux de conservation

Toutes les populations d'éléphants d'Asie sont inscrites à l'Annexe I de la CITES⁵ et le statut mondial de l'espèce sur la Liste rouge de l'UICN est en danger (Choudhury et al. 2008). Les éléphants de Sumatra (*E. m. sumatranus*) figurent sur la liste des espèces en danger critique d'extinction (Gopala et al. 2011).

Les principaux problèmes et menaces identifiés par les représentants des agences gouvernementales et des Organisations Non-Gouvernementales (ONG) à la conférence de Jakarta (Asian Elephant Range State Meeting 2017) étaient par ordre de priorité : la réduction de l'habitat et l'accaparement de surfaces forestières (par la construction d'infrastructures, les mines, l'agriculture industrielle ou villageoise), la fragmentation de l'habitat, les conflits humain-éléphant, la perte de corridors, le manque de communication entre les parties, l'augmentation de la population humaine et le braconnage (Anon 2017a).

1.2.3.1 Perte d'habitat, fragmentation et isolement des éléphants sauvages

La perte d'habitat due à sa conversion en zones d'occupation humaine permanentes et en cultures représente une menace majeure pour les éléphants sauvages (Calabrese et al. 2017; Fernando & Pastorini 2011; Hedges et al. 2008b; Leimgruber et al. 2003; Sukumar 2003b). L'expansion agricole, l'exploitation forestière et le développement économique, soutenus par une forte croissance de la population humaine en Asie, sont les principales causes de la perte et de la fragmentation de l'habitat de l'éléphant (Dublin et al. 2006). Ces pertes d'habitat sont largement dues à la conversion d'importantes surfaces forestières en agriculture commerciale à grande échelle comme la culture de l'huile de palme ou les

⁵ Convention sur le commerce international des espèces de faune et de flore sauvages menacées d'extinction

plantations de thé (Calabrese et al. 2017; Fernando & Pastorini 2011). La conversion de petites surfaces forestières pour une agriculture villageoise entraîne aussi une perte significative de l'habitat mais elle a surtout un impact sur la fragmentation de l'habitat. Dans la plupart des cas, cette expansion agricole à petite échelle conduit à une hétérogénéité de l'habitat avec un mélange complexe d'habitats naturels et anthropisés (Fernando & Pastorini 2011). Des zones d'habitat relativement petites et fragmentées en Inde et au Sri Lanka abritent la grande majorité des populations d'éléphants sauvages, alors même qu'elles présentent les plus fortes densités de population humaine et les plus importants taux de déforestation - Figure 12, (Calabrese et al. 2017; Leimgruber et al. 2003).

Cette déforestation a bloqué les routes migratoires traditionnelles et poussé les éléphants vers des îlots de végétation dont la surface ne cesse de rétrécir (Leimgruber et al. 2003). Les petites populations sont plus vulnérables aux menaces d'extinction car elles sont exposées à la variabilité environnementale, aux risques d'appauvrissement génétique et aux catastrophes (Dublin et al. 2006). Cette situation d'isolement dans des zones fragmentées, où les éléphants se rabattent régulièrement sur les cultures à la recherche de ressources alimentaires, occasionne des rencontres et des conflits fréquents avec les humains (Nyhus et al. 2000; Sitompul et al. 2010; Fernando et al. 2005).

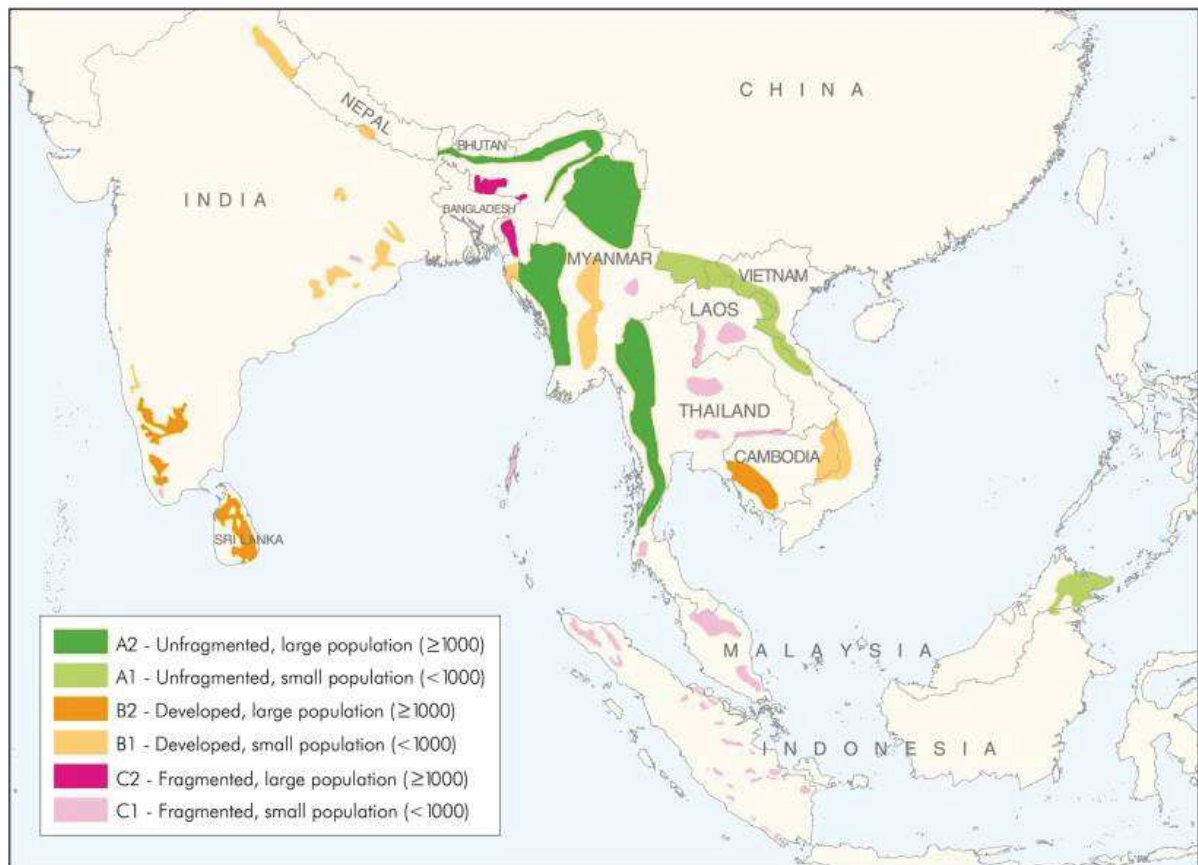


Figure 12 : Aires de gestion selon le niveau de fragmentation/anthropisation et la taille des populations d'éléphants

Le groupe A représente de grandes étendues d'habitat naturel non fragmenté ; le groupe B comprend des zones avec des réseaux de transport denses et de fortes densités de population humaine ; et le groupe C est caractérisé par des zones très fragmentées avec peu de développement routier et d'implantations humaines. La catégorie de population 1 indique que la zone abrite une population d'éléphants estimée inférieure à 1000 individus, la catégorie 2 représente les zones avec des populations supérieures à 1000 éléphants. Extrait de (Leimgruber et al. 2003).

1.2.3.2 Conflits humain-éléphant

Les Conflits Humain-Eléphant (CHE) sont l'un des problèmes les plus graves pour la conservation des éléphants (Gunaryadi et al. 2017; Neupane et al. 2017; Münster & Münster 2012; Barua 2010; Sitati & Walpole 2006; Campos-Arceiz et al. 2009; Fernando et al. 2005; Zhang & Wang 2003). Ils entraînent la mort d'humains et d'éléphants. En Inde, en moyenne, 250 personnes sont tuées chaque année par les éléphants. L'abattage des éléphants en représailles devient également un problème sérieux, qui a conduit à la l'éviction de certaines populations d'éléphants (Dublin et al. 2006). L'escalade des conflits peut également favoriser l'intolérance des populations vis-à-vis des éléphants et de leur conservation (Jigme & Williams 2011 ; Maltby & Bouchier 2011 ; Pradhan et al. 2011). Un grand nombre de techniques et méthodes de réduction des conflits ont été testées telles que la capture-

translocation, le repoussement des éléphants s'approchant des zones habitées et des cultures par des feux d'artifices ou avec l'aide d'éléphants captifs (Emergency Elephant Respond Units), la protection des cultures par des clôtures électriques, des fossés ou des répulsifs à base d'huile de piment, l'organisation d'une surveillance des cultures par les communautés, ou encore le paiement de compensations financières pour les dégâts occasionnés (Gunaryadi et al. 2017; Hedges & Gunaryadi 2010; Perera 2009; Sitati & Walpole 2006; Fernando et al. 2005). Mais les impacts de ces activités sur les éléphants et leurs réponses à ces mesures n'ont pas été évalués en détail (Fernando & Pastorini 2011).

1.2.3.3 Abattage, braconnage et captures

Le braconnage des éléphants d'Asie pour l'ivoire fait partie des principales menaces pour l'espèce (Sampson et al. 2018; Hedges et al. 2005), bien que seuls les mâles sont pourvus de défenses et que la proportion de mâles avec des défenses varie entre 10% et 90% selon les zones, affectant certaines populations plus que d'autres (Sukumar 2003a). Les autres types de braconnage concernent les captures vivantes pour les temples, l'exploitation forestière ou les camps de tourisme (Leimgruber et al. 2008). Les conflits humains-éléphants peuvent aussi conduire à des représailles contre les éléphants. Des rapports indiquent également que les éléphants sont braconnés pour la peau, la viande, les organes génitaux et les poils, mais les impacts démographiques de ce commerce sont considérés comme mineurs par rapport à ceux du commerce de l'ivoire et de la capture d'animaux vivants (Shepherd & Nijman 2008). Cependant dans un article récent intitulé « A new elephant crisis », les auteurs constatent une évolution du braconnage pour l'ivoire vers le braconnage pour la viande et la peau destinée à la médication traditionnelle au Myanmar et dans les pays voisins (Sampson et al. 2018).

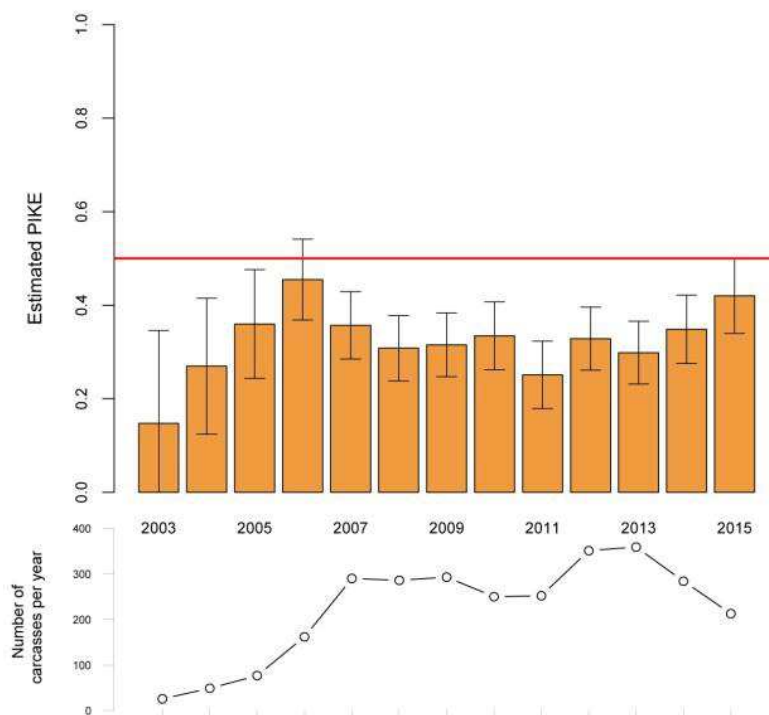


Figure 13 : Indice PIKE pour l'Asie (Proportion of Illegal Killing of Elephants)

Le graphique du haut montre la tendance PIKE en Asie (intervalles de confiance 90%), basé sur 2 892 carcasses d'éléphants (tués illégalement ou non) signalées à MIKE (Monitoring Illegal Killing of Elephants) pour la période 2003-2015. La ligne horizontale à 0,5 indique le niveau où la moitié des carcasses retrouvées sont dues à un abattage illégal. Le graphique du bas montre le nombre total de carcasses déclarées par année, quelle que soit la cause du décès. Source : Status of Elephant Populations, Levels of Illegal Killing and the Trade in Ivory: A Report to the CITES Standing Committee 2017 - SC69 Doc. 51.1 2017.

L'indice PIKE (Proportion of Illegal Killing of Elephants) qui donne la proportion de décès dus à un abattage illégal sur le nombre total de carcasses trouvées, est resté relativement stable de 2007 à 2013 et semble augmenter depuis. Les éléphants tués illégalement ne se limitent pas aux cas de braconnage mais incluent les éléphants tués dans des situations de conflit, qui représentent une proportion substantielle du total. Par exemple, 40% des éléphants tués illégalement entre 2007 et 2013 étaient des femelles, qui ne portent pas d'ivoire (Report to the CITES Standing Committee 2017). Des cas de braconnage pour l'ivoire et les poils de la queue d'éléphants de villages ont été rapportés au Laos (Maurer données non-publiées).

1.2.3.4 Menaces et enjeux concernant les éléphants captifs

La population totale d'éléphants captifs régresse sur l'ensemble de l'aire de répartition (Fernando & Pastorini 2011). D'une part, l'utilisation de l'éléphant comme animal de bât et de transport a été remplacée par les machines. Ainsi, même si le tourisme se développe, le rôle économique des populations captives s'est amoindri (Godfrey & Kongmuang 2009).

D'autre part, la reproduction en captivité ne permet pas d'assurer une population stable (Fernando & Pastorini 2011). Longtemps soutenue par la capture, la dynamique de la population captive ne dépend plus aujourd'hui que de la reproduction des femelles captives. Or l'éléphant ne s'est jamais bien reproduit en captivité (Mar 2007; Kurt & Mar 2003; Sukumar et al. 1997). Les taux de fécondités observés sont extrêmement variables en fonction du mode d'élevage pratiqué (Kurt & Mar 2003). Dans les systèmes d'élevage intensif, la reproduction est pratiquement inexistante pour plusieurs raisons, la plus importante étant le manque d'incitations économiques pour les propriétaires à élever des éléphants (Mar 2007). Mais beaucoup d'éléphants élevés de manière intensive ne sont ni physiologiquement ni psychologiquement capables de se reproduire. L'isolement des mâles et des femelles, les conditions de travail et l'inadéquation de l'alimentation limite la capacité de reproduction. De plus les éléphant souffrent d'un déficit de socialisation (Mar 2007) et ont tendance à pratiquer l'infanticide (Kurt & Mar 1996).

Dans les systèmes extensifs, les taux moyens de fécondité sont extrêmement variables selon les populations de la région et au fil du temps, avec un taux de fécondité de 0,023 (2,3% des femelles en âge de se reproduire) au Laos (Suter et al. 2014), 0,083 au Myanmar (Mar 2007), et variant de 0,095 à 0,155 pour une population d'éléphants en captivité en Inde au cours du 20^{ème} siècle (Sukumar et al. 1997). Les éléphants dans les camps forestiers, comme au Myanmar, ou ceux qui sont maintenus dans des conditions semi-naturelles dans les zones forestières en Inde, ont des taux de fécondité supérieurs, en grande partie parce que femelles s'accouplent avec des mâles sauvages (Thitaram, Somgird, Mahasawangkul, Angkavanich, Roongsri, Thongtip, Colenbrander, van Steenbeek & J. a. Lenstra 2010; Raman Sukumar 2006; Sanderson 1879).

Des progrès importants doivent être réalisés dans la gestion des populations captives au niveau régional et dans chacun des pays (Anon 2017a; Fernando & Pastorini 2011; Vanitha et al. 2011; Suter et al. 2013; Dublin et al. 2006; Hedges et al. 2005; Kurt & Mar 2003; Lair 2002). En particulier, le recensement et l'enregistrement systématique des éléphants captifs permettrait d'améliorer le suivi des dynamiques de populations, de renforcer l'application des législations et le suivi sanitaire, ainsi que de lutter contre le trafic transfrontalier (Lair 2002). Plus d'attention aux soins, au bien-être physique et psychologique, et aux besoins sociaux des éléphants captifs sont également nécessaires (Fernando & Pastorini 2011).

Les gestionnaires et les organisations de conservation se sont également emparés des questions relatives à la gestion des éléphants d'Asie en captivité. Cela n'est pas seulement dû au nombre d'éléphants en captivité, mais aussi à leur valeur potentielle pour la conservation et à la menace que les captures illégales pourraient représenter pour les populations d'éléphants sauvages (Dublin et al. 2006).

1.2.4 Limites des politiques de conservation actuelles

Selon Fernando et Pastorini (2011), la principale approche de la conservation des éléphants et de l'atténuation des CHE est la « restriction des éléphants aux aires protégées ». Cependant, dans la plupart des pays, le nombre d'éléphants vivant en dehors des aires protégées dépasse largement le nombre d'éléphants à l'intérieur de ces mêmes aires. La présence spatiale extensive de CHE dans les pays de l'aire de répartition en témoigne, puisque les conflits se produisent en dehors des aires protégées. L'une des principales raisons pour lesquelles la limitation des éléphants aux aires protégées a échoué est que l'habitat optimal pour les éléphants n'est pas une forêt non perturbée mais un habitat présentant un régime de perturbation intermédiaire, ces habitats se trouvant surtout à l'extérieur des aires protégées (Fernando & Leimgruber 2011).

De la même façon, Evans et collègues (2018) ont montré que l'habitat optimal des éléphants de Bornéo était constitué de forêts perturbées et de forêts de régénération. Moins d'un quart des forêts protégées constituent un habitat favorable aux éléphants car les zones de protection se concentrent généralement sur des forêts primaires et anciennes. Les zones forestières exploitées pour l'extraction du bois, les mosaïques paysagères issues des agricultures de rotation constituent un habitat particulièrement favorable pour les éléphants mais ne sont pas intégrées dans les programmes de conservation. Le paradigme de ségrégation territoriale entre zones protégées et zones exploitées ne convient manifestement pas à l'écologie de l'éléphant d'Asie.

D'autre part, la séparation des éléphants captifs de leurs congénères sauvages limite leur rôle potentiel en faveur de la conservation de l'espèce en tant que population réservoir, réservoir de diversité génétique ou encore ambassadeur en faveur de la conservation d'une espèce avec une forte portée symbolique dans les cultures locales.

1.3 Cadre conceptuel

1.3.1 De la biologie de la conservation aux systèmes socio-écologiques

La recherche en écologie s'est longtemps focalisée sur l'étude d'écosystèmes supposés vierges de toute intervention humaine, tentant de comprendre et caractériser le fonctionnement de cette nature hors de toute présence humaine. A partir des années 60, la prise de conscience d'une forte régression de la biodiversité et de la modification des écosystèmes sur l'ensemble des continents est à l'origine de l'émergence de la biologie de la conservation, une nouvelle discipline scientifique qui tente de comprendre les causes de ce déclin, de l'enrayer et de maintenir, voire de restaurer cette biodiversité (Soulé 1985).

Reconnaissant que l'équilibre n'est pas un état habituel de la nature, que les perturbations sont communes et répandues et que les écosystèmes sont ouverts et interconnectés, la biologie de la conservation s'affranchit de plus en plus des principes de protection de la nature et de mise sous cloche longtemps prônés par des environnementalistes tels que Thoreau ou Muir (Nash 1967). Elle applique désormais les principes de l'écologie, dont la biogéographie, l'écologie du paysage, la dynamique et la génétique des populations (Barbault 1997). Elle s'intéresse en particulier aux capacités adaptatives et à la résilience de populations ou d'écosystèmes dits dégradés. Nombre de ces perturbations étant d'origine anthropique, elle adopte une démarche multidisciplinaire en associant des disciplines telles que l'anthropologie, les sciences économiques et la sociologie (Barbault 1997; Soulé 1985) dans le cadre par exemple de la résolution des conflits humain-nature ou la mise en place de nouveaux modes de gestion (corridors biologiques, réserves ou parcs naturels, valorisation de la biodiversité).

La biologie de la conservation est décrite comme une « discipline de crise, science de l'action, qui doit gérer l'incertitude, alimenter des réflexions pour des prises de décision rapides, dans un contexte d'anthropisation aux impacts complexes » (Soulé 1985). Ainsi les études visant à estimer la viabilité à long terme d'une population selon différents scénarios de gestion ou les études de diversité génétique et de dépression de consanguinité poursuivent le double objectif 1) d'identifier les problèmes et leurs solutions et 2) de faire le lien entre la science et la gestion.

Cependant, l'approche holistique et pluridisciplinaire annoncée par ses fondateurs contraste encore souvent avec de nombreux travaux se réclamant de la biologie de la conservation. Ceux-ci mobilisent peu de disciplines ou relèvent simplement d'une biologie des populations s'intéressant à la survie des espèces. La biologie de la conservation, issue d'une vision naturaliste du monde, a inspiré des stratégies et des programmes d'action dans des pays aux ontologies différentes, générant des malentendus, des contradictions et des oppositions voire des conflits avec les valeurs culturelles et les besoins des communautés locales (Infield et al. 2017). Mathevet et Poulin (2006) soulignent ainsi le déficit de prise en compte des dimensions socio-économiques dans l'identification des causes et des solutions proposées. Mais ils notent également le développement d'un courant d'écologie appliquée à la conservation associé aux sciences humaines depuis une vingtaine d'années qui permet de mieux comprendre les interactions environnement / sociétés dans de nombreux projets de recherche et/ou de conservation.

Ainsi des programmes interdisciplinaires intègrent les sciences écologiques et sociales pour étudier les systèmes couplés humain-nature (*coupled human and natural systems*) appelés encore Systèmes Socio-Écologiques (SSE). Les SSE sont des systèmes complexes et intégrés dans lesquels l'homme fait partie de la nature (Berkes & Folke 1998). Les SSE ne sont pas statiques, ils changent avec le temps et sont intrinsèquement dynamiques (Liu et al. 2007). Comme les humains et leur environnement interagissent et forment des boucles de rétroaction complexes, les changements dans les systèmes sociaux auront un impact sur l'environnement et réciproquement (Liu et al. 2007). La nature complexe et dynamique des systèmes socio-écologiques exige un processus décisionnel souple et transparent qui englobe la diversité des connaissances et des valeurs, et implique la participation de l'ensemble des acteurs aux prises de décisions, à la gouvernance et à la gestion des programmes de conservation (Reed 2008).

1.3.2 Résilience des systèmes socio-écologiques

La résilience est un concept utilisé dans de nombreux domaines et disciplines dont la physique, la psychologie, le développement humain ou encore l'écologie (Folke 2016). Les concepts, terminologies et définitions présentés ci-après se réfèrent au domaine de l'étude de la résilience des systèmes socio-écologiques.

La résilience écologique est un concept introduit à l'origine par Holling (1973). Les écosystèmes ne sont pas stables intrinsèquement mais possèdent plusieurs « bassins d'attraction » vers lesquels le système peut basculer à la suite d'une perturbation ou du changement d'une de ses multiples variables d'état. Ces basculements ou changements soudains vers un autre état ont été décrits dans de nombreuses études. Par exemple, un lac peut basculer d'un état d'eau claire avec une végétation benthique vers un état eutrophisé avec des algues bleues-vertes (Carpenter et al. 2001). La résilience écologique représente donc une propriété dynamique des écosystèmes correspondant à leur aptitude à revenir à un état d'équilibre après une perturbation, état qui n'est pas nécessairement l'état antérieur.

Les humains étant une force majeure affectant la trajectoire des écosystèmes (McMichael et al. 2003), le concept de résilience a été étendu à des SSE complexes et adaptatifs couplant humain et nature. Ainsi, de nombreux travaux sur la pensée dite résiliente ont été réalisés sous les auspices de la Resilience Alliance⁶, un groupement international rassemblant des écologistes, des économistes, des sociologues et des mathématiciens (Holling 2001; Walker et al. 2004; Folke et al. 2004).

La résilience d'un système socio-écologique est sa capacité à absorber ou à résister aux perturbations et autres facteurs de stress de sorte que le système reste dans le même régime, en maintenant essentiellement sa structure et ses fonctions (Holling 1973; Gunderson & Holling 2002; Walker et al. 2004). La résilience est la propriété d'un système dynamique, la capacité des personnes, des communautés, des sociétés, des cultures à s'adapter ou même à se transformer vers de nouvelles voies de développement face au changement dynamique.

Folke (2016) résume les principaux concepts de la résilience :

Resilience thinking is about how periods of gradual changes interact with abrupt changes, and the capacity of people, communities, societies, cultures to adapt or even transform into new development pathways in the face of dynamic change. It is about how to navigate the journey in relation to diverse pathways, and thresholds and tipping points between them. In resilience thinking, adaptation refers to human

⁶ www.resalliance.org

actions that sustain development on current pathways, while transformation is about shifting development into other emergent pathways and even creating new ones.

Lorsque la résilience est augmentée, un système est plus susceptible de tolérer des perturbations sans évoluer vers un état qualitativement différent, contrôlé par un ensemble de processus différents. En outre, une analyse de la résilience des SSE doit permettre aux humains d'anticiper et de gérer les changements, voire d'influencer le développement du système vers de nouvelles voies à l'avenir. Par contre, une réduction de la résilience augmente la vulnérabilité d'un système à des perturbations de moindres importances auxquelles il pouvait auparavant faire face. Même en l'absence de perturbation soudaine, un changement graduel des conditions, telles qu'un changement climatique, la fragmentation de l'habitat ou une modification des conditions socio-économiques, peut provoquer un dépassement de seuil qui déclenchera une réaction abrupte du système et le basculement de ce système vers un nouveau puit d'attraction. Le nouvel état du système peut être jugé moins souhaitable si les services écosystémiques qui profitent aux humains sont diminués, comme dans le cas des lacs d'eau douce qui s'eutrophisent et perdent leur biodiversité.

1.3.3 Le cycle adaptatif

Le modèle des cycles adaptatifs permet de décrire les dynamiques des SSE. Ce modèle est dérivé de l'étude comparative de la dynamique des écosystèmes. Traditionnellement, l'écologie s'est concentrée sur le concept de succession qui décrit la transition d'une phase où l'accent est mis sur l'exploitation (c.-à-d. la colonisation rapide des zones récemment perturbées) à une phase où la conservation (c.-à-d. l'accumulation lente et le stockage de l'énergie et de la matière) est mise en valeur. Gunderson et Holling (2002) indiquent cependant que deux fonctions supplémentaires - la libération et la réorganisation - sont nécessaires. Afin de comprendre les systèmes complexes, des cellules aux écosystèmes et aux sociétés, ces deux auteurs proposent comme unité fondamentale un « cycle adaptatif » alternant de longues périodes d'agrégation et de transformation des ressources avec des périodes plus courtes qui créent des opportunités d'innovation.

Les dynamiques des SSE peuvent être représentées par un cycle adaptatif présentant quatre phases distinctes (Figure 14). Deux d'entre elles - une phase de croissance et d'exploitation (r) fusionnant dans une phase de conservation (K) - forment la boucle-avant du cycle, lente

et cumulative, au cours de laquelle la dynamique du système est raisonnablement prévisible. Au fur et à mesure que la phase K se poursuit, les ressources sont de plus en plus contraintes et le système devient de moins en moins souple et réactif aux chocs externes. Cette phase K est inévitablement suivie d'une phase chaotique d'effondrement et de relâchement (Ω) qui cède rapidement la place à une phase de réorganisation (α), qui peut être rapide ou lente, et au cours de laquelle l'innovation et de nouvelles opportunités sont possibles. Les phases Ω et α ensemble forment une boucle arrière imprévisible. La phase α mène à une phase r subséquente, qui peut ressembler à la phase r précédente ou être significativement différente (Holling 2001; Walker et al. 2004).

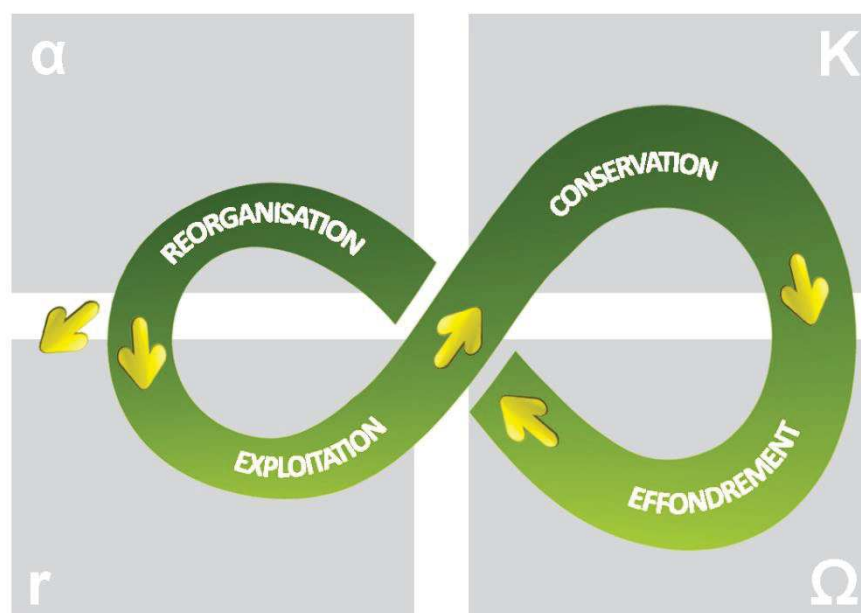


Figure 14 : Cycle adaptatif

Le cycle adaptatif est constitué de 4 phases : (r) phase de croissance ou d'exploitation ; (K) phase de conservation ; (Ω) phase d'effondrement ; (α) phase de (re)organisation.

Extrait de Gunderson and Holling 2002.

1.3.4 Interactions entre les échelles

Tous les systèmes, et en particulier les SSE, existent et fonctionnent à de multiples échelles d'espace, de temps et d'organisation sociale. Les interactions entre échelles sont d'une importance fondamentale pour déterminer la dynamique du système à une échelle focale particulière. Cet ensemble interactif d'échelles hiérarchiquement structurées a été nommé panarchie (Gunderson & Holling 2002).

La panarchie relie les cycles adaptatifs dans une hiérarchie imbriquée (Figure 15). Il existe potentiellement de multiples connexions entre les phases du cycle adaptatif à un niveau et les phases à un autre niveau. Deux liens importants sont appelés « révolte » et « mémoire ». Les niveaux inférieurs, plus rapides, inventent, expérimentent et testent, tandis que les niveaux supérieurs, plus lents, stabilisent et conservent la mémoire accumulée de la dynamique du système. De cette façon, les niveaux plus lents fixent les conditions dans lesquelles les niveaux plus rapides fonctionnent (Gunderson & Holling 2002).

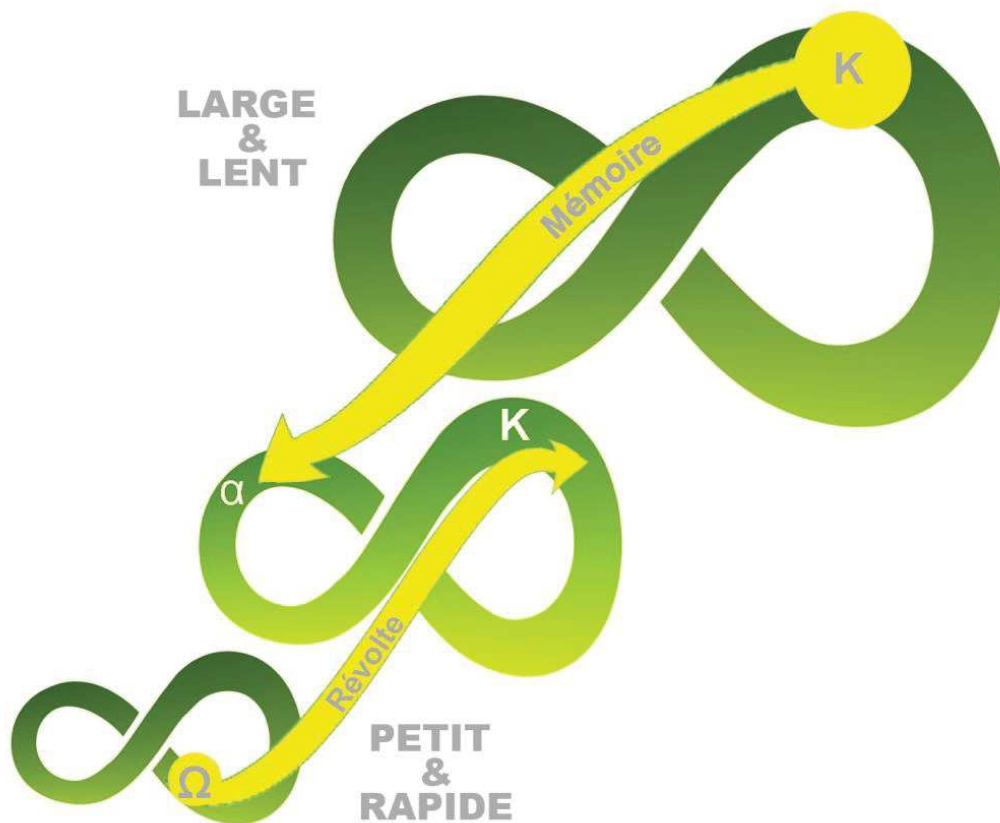


Figure 15 : Panarchies

Les niveaux inférieurs, plus rapides, inventent, expérimentent et testent, tandis que les niveaux supérieurs, plus lents, stabilisent et conservent la mémoire accumulée de la dynamique du système. Schéma repris de Gunderson and Holling 2002.

1.3.5 Capacité adaptative, adaptation et transformation des SSE

Les systèmes sont dits à forte capacité d'adaptation s'ils sont plus à même de se reconfigurer sans que leurs fonctions fondamentales ne changent de façon significative ou que les services écosystémiques ne déclinent. Un SSE dont la capacité d'adaptation est limitée

dispose d'un éventail restreint d'options et d'alternatives pendant les périodes de réorganisation et de renouvellement (Folke et al. 2003).

La capacité d'adaptation des systèmes écologiques est liée à la diversité génétique, à la diversité biologique et à l'hétérogénéité des mosaïques paysagères. La diversité biologique joue un rôle important dans le maintien des états de l'écosystème face au changement (Peterson et al. 1998). La diversité des configurations spatiales fournit également un autre type de diversité des réponses (Elmqvist et al. 2003). L'effet de la diversité sur la résilience dépend donc de l'organisation des espèces entre les groupes fonctionnels, de la diversité des réponses des groupes fonctionnels, des espèces à l'intérieur de ces groupes et des individus, de la configuration spatiale et de l'échelle des processus écosystémiques dans le temps et dans l'espace (Carpenter et al. 2006).

La capacité d'adaptation du système est conditionnée également par sa diversité sociale. La résilience dépend de la possibilité pour les populations humaines d'exprimer diverses valeurs économiques, culturelles et spirituelles (Bottom et al. 2009). Ces diverses valeurs humaines peuvent fournir la diversité de la réponse sociale dont les communautés humaines ont besoin pour s'adapter avec succès aux environnements changeants ou d'emprunter de nouvelles voies de développement (Senos et al. 2006; Turner et al. 2003). Par ailleurs, certains écosystèmes se sont détériorés en l'absence de pratiques culturelles qui contribuaient à leur entretien, comme l'abandon de la pratique des feux de prairie par les amérindiens d'Amérique du Nord (Ryan et al. 2013). L'existence de réseaux et d'institutions impliqués dans la gestion du SSE renforce également sa capacité adaptative. Ainsi le maintien de la diversité bio-culturelle réduit la vulnérabilité des systèmes aux chocs et favorise leur résilience et leur adaptation.

Selon Walker (2004), l'adaptation consiste à développer de nouvelles configurations socio-écologiques qui fonctionnent efficacement dans de nouvelles conditions, tel que le cas présenté ci-après des éleveurs de rennes en Sibérie confrontés à des changements climatiques et socio-économiques. La transformabilité du SSE, représente sa capacité à créer un système fondamentalement nouveau lorsque les structures écologiques, économiques ou sociales rendent le système existant intenable. La transformation est le processus de passage de l'état existant vers le nouvel état du système. Le nouveau système ainsi

transformé inclut de nouvelles variables d'état, exclut une ou plusieurs variables du système existant et opère généralement à d'autres échelles (Walker et al. 2004).

1.3.6 Quelques exemples d'étude de la résilience de SSE

A l'origine, les études de cas utilisées pour élaborer la théorie de la résilience ont décrit la dynamique d'écosystèmes relativement circonscrits et stationnaires dont les limites spatiales sont bien définies, comme les lacs, les savanes (Anderies et al. 2002), les zones humides (Gunderson 2001), les récifs coralliens (Berkes & Seixas 2005; McManus & Polsenberg 2004). Peu d'études de cas s'attachent à décrire la résilience de SSE centrés sur une espèce animale plutôt qu'un écosystème. Forbes (2009), en s'appuyant sur l'exemple des peuples Nenets éleveurs nomades de rennes en Sibérie, montre que les SSE s'adaptent aux changements à de multiples échelles, y compris les changements des régimes climatiques, économiques et géopolitiques. La fin de l'ère soviétique a engendré dans de nombreuses régions avoisinantes de la péninsule Yamal de fortes baisses des communautés humaines, de l'élevage du renne et des activités économiques. Mais les Nenets de la péninsule Yamal ont pu maintenir une population importante et des activités économiques, dont l'élevage du renne, en adoptant un système souple alliant un accès libre aux pâtures et aux routes de migration avec une propriété privée des troupeaux. La transformation croissante de la toundra vers un écosystème dominé par les graminées a également poussé les éleveurs à modifier leurs pratiques d'élevage et de nomadisme.

Bottom et ses collègues (2009) ont étudié le SSE du saumon du Pacifique (*Oncorhynchus spp.*) exploité par de nombreuses communautés et dont le cycle de vie s'étend des zones de frai en eau douce à la migration en haute mer. Le système est alors particulièrement complexe car il intègre de multiples échelles tant spatiales que juridictionnelles et leur cortège d'interactions. Le SSE est déterminé par des interactions à la fois entre les niveaux spatial et juridictionnel ou entre les échelles locale et globale. Des changements dans les conditions écologiques, économiques et géopolitiques qui échappent aux compétences ou au contrôle des institutions de gestion influent sur la résilience des écosystèmes du saumon. Ainsi, la valeur des devises, les marchés économiques et les politiques de croissance démographique et économique d'autres pays modifient l'état socio-écologique du saumon exploité par une communauté spécifique.

De fait, une génération qui surconsomme ses ressources locales et réduit la diversité sans créer de nouvelles possibilités élimine des options qui permettraient à la collectivité de s'adapter lorsque les conditions changent (Bottom et al. 2009). Selon Folke et Gunderson (2012), nombreux sont ceux qui se rendent compte aujourd'hui que les SSE dynamiques et complexes exigent des stratégies qui renforcent la résilience à long terme plutôt que de tenter d'atteindre une production optimale et de maximiser le gain à court terme dans des conditions supposées stables.

La résilience des systèmes sociaux-écologiques constitue un cadre d'analyse pertinent de la dynamique du système humain - éléphant sauvage - éléphant captif face aux changements au niveau global (libéralisation et croissance économique, changements sociaux, réduction de l'habitat, etc.) et local (nouvelles pratiques d'élevage, isolement des éléphants sauvages, conflits entre humains et éléphants etc.).

1.4 Problématique et approche méthodologique

1.4.1 Interactions sauvages-captifs : un objet hybride peu étudié et éludé par les acteurs

Le cas de l'éléphant d'Asie constitue un objet hybride au sens donné par Latour (1991). A la fois sauvage mais travaillant pour l'humain, dressé mais pas toujours dominé, considéré comme un membre de la famille de son cornac mais enchaîné, nuisible mais vénéré, l'éléphant d'Asie relève tout à la fois du naturel, du symbolique, du culturel, de l'économique et du politique. Ce statut hybride déstabilise, empêche une classification simple et normative et une prise en compte globale de sa complexité. Cela s'illustre dans la controverse pour nommer l'éléphant vivant aux côtés des humains comme nous l'avons vu, mais également au niveau des institutions. Dans les pays d'Asie, l'éléphant est classé soit comme un animal sauvage - relevant alors des ministères de l'environnement et des forêts - , soit comme un animal captif - et dépendant alors des ministères de l'Agriculture et de l'Élevage - , ce qui provoque controverses et confusions dans les prérogatives de chacun (Lair 1997). De la même façon, les ONG se posent en porte-paroles de l'un ou de l'autre. D'un côté, celles engagées en faveur du bien-être animal s'appliquent à améliorer les conditions de captivité des éléphants en remettant souvent en cause les pratiques traditionnelles d'élevage (Lainé 2017a). De l'autre côté, les ONG de conservation ont longtemps refusé d'aborder la question de ces éléphants vivant hors de la nature pour des raisons de valeurs

et d'éthique (Lainé 2015). Aujourd'hui les ONG de conservation reconnaissent l'importance de la prise en compte des populations captives, certes pour le rôle éventuel qu'elles peuvent jouer en termes de sensibilisation à la conservation de l'espèce, mais aussi et surtout pour les menaces qu'elles feraient peser sur la population sauvage (capture, trafic, compétition pour les ressources, risques épidémiologiques) (Hedges et al. 2018; Dublin et al. 2006; Hedges et al. 2005).

La recherche académique illustre aussi la difficulté à aborder de façon globale les relations entre l'éléphant captif, l'éléphant sauvage et l'humain. En effet, une abondante littérature en biologie, écologie ou sciences humaines et sociales traite séparément des populations sauvages ou captives, ou des conflits humains-éléphant sauvages, ou encore des relations humains-éléphants captifs. Peu d'études ont tenté de décrire et d'analyser les interactions complexes entre les humains, les populations sauvages et les populations captives en utilisant une approche interdisciplinaire et intégrative (Trautmann 2015; Locke 2013; Leimgruber et al. 2008), malgré l'importance reconnue des effets anthropiques sur la dynamique des populations animales exploitées et sauvages (Lebreton 2005), et la reconnaissance des animaux comme agents interactifs en sciences humaines et sociales (Descola 2004; Ingold 2000c).

1.4.2 Une approche interdisciplinaire

La nature hybride de l'éléphant d'Asie en fait un sujet d'étude à l'interface des sciences humaines et sociales et de la biologie. Nous avons choisi d'aborder la question des interactions entre éléphants captifs et sauvages en nous appuyant sur le cadre conceptuel de la résilience des SSE et les sciences de la conservation, ce qui impliquait une approche globale et interdisciplinaire.

Pour ce faire, nous avons choisi de privilégier trois champs disciplinaires : l'ethnoécologie, la dynamique de populations et la génétique des populations. La première permet une approche systémique de description de l'état du SSE et son évolution. Cette première étude permet d'éclairer les travaux des deux autres disciplines qui apportent une analyse plus spécifique des facteurs conditionnant le système, à court et moyen terme pour la dynamique de population, et à plus long terme pour la génétique.

Ce travail ne prétend pas apporter une vision exhaustive de l'ensemble des interactions et des facteurs déterminant le système humain - éléphant de village - éléphant sauvage, ni à l'échelle du Laos, ni encore moins à l'échelle régionale, mais entend contribuer à une meilleure compréhension des dynamiques complexes gouvernant ces interactions et des enjeux qui en résultent.

1.4.3 Les cas du Laos et du Myanmar comme modèles d'étude

Le Laos et le Myanmar présentent des conditions favorables à l'étude de la résilience des SSE humain - éléphant sauvage - éléphant de village pour plusieurs raisons.

Tout d'abord, ces deux pays abritent une population d'éléphants de village notablement importante par rapport à la population sauvage (cf. Figure 11). Le Laos et le Myanmar conservent également une utilisation traditionnelle de l'éléphant pour le débardage du bois et pratiquent un élevage extensif des éléphants de villages dans leur milieu naturel au contact des populations sauvages, pratiques qui ont disparues du reste de l'aire de répartition à l'exception de quelques zones en Inde du Nord et au Cambodge.

Les conditions socio-écologiques des deux pays présentent également plusieurs similitudes. Le Laos et le Myanmar disposent d'une couverture forestière de respectivement 52% et 41% (Stibig et al. 2014; Stibig et al. 2004), constituée principalement de forêts tropicales décidues humides et dans une moindre mesure de forêts tropicales décidues sèches soumises au régime des moussons (Fernando & Leimgruber 2011; Olson & Dinerstein 1998). La population du Laos est composée de 49 groupes ethniques différents. Ceux-ci sont généralement classés comme appartenant à quatre familles ethnolinguistiques : Lao-Tai (Tai-Kadai), Mon-Khmer (Austro-Asiatique), Hmong-Mien (Hmong-Yao, Miao-Yao) et Sino-Tibétain (principalement Tibéto-Birman) (Messerli et al. 2008). La famille ethno-linguistique Lao-Tai est dominante au niveau national (65 % de la population totale). La principale religion pratiquée est le Bouddhisme - 64% (Messerli et al. 2008). Au Myanmar, le gouvernement reconnaît 135 groupes ethniques : Birman (Bamar) 68%, Shan 9%, Karen 7%, Rakhine 4%, Chinois 3%, Indien 2%, Mon 2%. Le Bouddhisme est pratiqué par 85% de la population. Les indicateurs macro-économiques dressent aussi le portrait de deux pays dont le statut socio-économique est proche (Chan & Taylor 2013) : le PNB par habitant pour le Laos et le Myanmar était respectivement de 1 141 et 988 USD en 2010, l'espérance de vie

s'élève à 61 ans dans les deux pays, la part de la population rurale étant respectivement de 67% et 69% (The World Bank Group 2015). L'Index de Développement Humain du Laos s'élève à 0,586 (138^{ème} rang mondial), et 0,556 pour le Myanmar (145^{ème} rang mondial) (United Nations Development Programme 2016).

Si le Laos et le Myanmar partagent quelques similitudes dans leurs conditions écologiques et socio-économiques évoquées par ces quelques indicateurs, ils n'en demeurent pas moins marqués par une histoire, une culture, une société et un environnement distincts. L'élément principal qui justifie le choix de ces pays pour une analyse de la résilience du système humain-éléphant vient du fait qu'ils connaissent tous deux une phase de transition récente après des décennies d'isolement.

Après 1990, le cadre politique de la République Populaire Démocratique Lao a radicalement changé avec l'ouverture du pays à l'économie de marché, la libéralisation économique et le lancement de nombreuses réformes (Evrard & Pholséma 1997). De la même façon, la libéralisation politique et économique de 2011 à 2015 au Myanmar, suivie d'élections relativement démocratiques et du lancement de nouvelles réformes ont conduit à la levée des sanctions économiques américaines et à l'ouverture du pays sur la scène internationale (Prescott et al. 2017). Cette situation transitionnelle des deux pays offre donc un contexte particulièrement adapté à l'étude de la résilience d'un système socio-écologique soumis à des perturbations importantes. Les chapitres ci-après apportent des informations de contexte plus détaillées sur le Laos et le Myanmar.

1.4.4 Problématique de la thèse et organisation du manuscrit

Depuis des millénaires, l'éléphant joue un rôle important dans la culture, l'économie et la construction des pays asiatiques. Près d'un quart de la population de cette espèce emblématique et menacée est constituée d'éléphants dits captifs. Toutefois, les législations nationales comme les programmes de conservation ont tendance à traiter séparément les populations captives et sauvages. Au Laos et au Myanmar, les interactions entre éléphants sauvages et éléphants de villages perdurent. L'objectif de cette thèse est de qualifier et quantifier ces interactions afin de mieux comprendre leurs dynamiques et leurs rôles dans la survie de l'espèce.

Je m'interrogerai donc 1) sur les impacts potentiels de l'évolution du système socio-écologique humain-éléphant sur les interactions entre éléphants sauvages et éléphants de villages et 2) sur les conséquences de ces changements sur la relation homme-éléphant, les dynamiques de population et la conservation de l'espèce. J'adopterai le cadre méthodologique de la résilience des systèmes socio-écologiques pour estimer la capacité adaptative du système face aux bouleversements socio-écologiques majeurs à l'œuvre dans ces pays. Cela m'amènera à discuter des mesures de gestion permettant d'assurer la viabilité du système et de l'espèce, pour évoquer en fin de compte le processus de domestication de l'espèce et ses conséquences en termes de résilience.

Le manuscrit est organisé en trois parties principales :

- (i) J'adopterai tout d'abord un point de vue systémique pour décrire et analyser l'état du système traditionnel au Laos et son évolution récente à travers une approche ethnoécologique (Chapitre 2 - article 1).

Je décrirai l'évolution du système socio-écologique au Laos au cours des dernières décennies à partir d'une analyse intégrative des facteurs socio-écologiques et de leur dynamique. J'évaluerai les conséquences de cette évolution sur les interactions entre humains et éléphants, sur les pratiques d'élevage et sur les perceptions de l'espèce chez les propriétaires d'éléphants. J'étudierai également les changements qui en résultent dans la nature de la relation entre l'humain et l'éléphant au Laos.

- (ii) Dans un second temps, je prendrai un point de vue spécifique pour illustrer la capacité adaptative et la résilience du système en prenant deux exemples.

D'une part, j'étudierai la dynamique de la population d'éléphants de village du Laos en m'attachant à décrire les déterminants de la fécondité par une approche de modélisation bio-économique (Chapitre 3 – article 2). Ce chapitre permettra d'estimer la viabilité de la population en fonction de scénarios démographiques et socio-économiques qui intègrent la contribution de la population sauvage à la fécondité des femelles de village et les facteurs économiques incitant les propriétaires à faire de la reproduction.

D'autre part, je présenterai une étude de génétique des populations d'éléphants sauvages et de villages au Laos et au Myanmar afin d'estimer la diversité

génétique et la structuration des populations dans ces deux pays (chapitre 4 - article 3). Je discuterai la diversité génétique et la viabilité à long terme des populations d'éléphants sauvages et de villages dans un contexte de restriction des flux de gènes et de l'intérêt de considérer ces populations comme une unité de gestion commune.

- (iii) Enfin, je questionnerai en discussion (chapitre 5) la résilience et la capacité adaptative du système actuel au Laos au regard de ces résultats.

J'explorerai ensuite les voies possibles d'adaptation du système à travers une lecture critique du plan de conservation à 100 ans du Myanmar et considèrerai enfin l'hypothèse d'une transformation radicale vers un système dualiste de protection / domestication.

2 Approche ethnoécologique : évolution du système socio-écologique humain-éléphant au Laos



2.1 Objectifs et résumé de l'article 1

Les changements politiques, socio-économiques et environnementaux en cours au Laos ont fortement affecté les conditions de la cohabitation entre humains et éléphants. Nous avons mené une étude ethnoécologique pour évaluer la dynamique temporelle du système socio-écologique au Laos et ses conséquences sur les interactions entre les humains et les éléphants, les pratiques d'élevage et la perception de l'espèce chez les propriétaires d'éléphants. Combinée à une expérience de terrain sur le temps long, l'analyse de 52 entretiens semi-directifs a montré que le système socio-écologique traditionnel, basé sur les principes de l'accès commun aux ressources naturelles et du contrôle social sur la nature et les esprits, a conduit à une forme de pastoralisme de l'éléphant avec des interactions fortes entre les éléphants de villages et sauvages. Ainsi, les éléphants de villages sont relâchés la plupart du temps dans les forêts et friches avoisinant le village, souvent au contact de leurs congénères sauvages, et la reproduction est libre. L'émergence depuis les années 2000 de la marchandisation de la nature et de la division de l'accès aux ressources naturelles a conduit à la ségrégation des éléphants sauvages et à l'élevage intensif de leurs congénères captifs. Ainsi les forêts sont protégées par la loi, valorisées pour leurs services écosystémiques tandis que leur accès est interdit aux villageois comme aux éléphants de villages. Parallèlement, la ségrégation territoriale entre les zones dédiées à la conservation et les zones destinées à la production agricole a fait disparaître les pâtures communes. Les éléphants de villages sont désormais à l'attache, la reproduction est contrôlée et liée au paiement de la saillie. L'intensification du travail dans le débardage du bois puis dans le tourisme s'apparente à une forme d'élevage intensif proche du « ranching ». Ce processus de purification entre sauvage et non-sauvage a eu un impact sur la relation entre l'homme et les éléphants avec des perceptions et des stratégies d'élevage variables selon les régions.

Statut de l'article : Rejeté, invité à resoumettre à Human Ecology. Les deux principales consignes sont i) de resserrer la thématique de l'article, et de la discussion en particulier (nous avons choisi de focaliser sur le thème de la résilience) et ii) d'omettre la partie quantitative.

2.2 From cohabitation to segregation: evolving human–elephant relationships in a changing socio-ecological system in Laos

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2.2.1 Abstract

Human-Asian elephant relationships have been lasting for millennia based on a closed interlink between wild, captive elephants and their human masters. The ongoing and rapid political, socio-economic and environmental changes occurring in Laos have strongly affected the conditions of this cohabitation. We conducted an ethnological survey to assess how the socio-ecological system has evolved in Laos and its consequences on human-wild-captive elephant's interactions, elephant handling practices and perceptions of the species among owners. We show that the traditional socio-ecological system, based on the principles of common access to natural resources and social control over nature and spirits, led to a form of elephant pastoralism with closed interactions between captive and wild elephants. The emergence since the 2000s of nature commodification and the divided access to natural resources led eventually to the segregation of wild elephants and the intensive ranching of their captive congeners. This purification process has impacted the relationship between human and elephants with different perceptions through regional variations.

2.2.2 Introduction

The population of Asian elephants, *Elephas maximus*, ranges from 30,000 to 50,000 individuals (Hedges et al. 2005; Raman Sukumar 2006; Choudhury et al. 2008). It is in overall decline and classified as endangered by the International Union for Conservation of Nature (Choudhury et al. 2008). On one side, wild populations are threatened by habitat loss and poaching (Fernando & Pastorini 2011), while on the other side, the prevalence of human-elephant conflicts (HEC), mainly crop-raiding, leading to the occasional death of humans or elephants, is increasing all over the region (Perera 2009). One-quarter to one-third of the Asian elephant population are captive (Leimgruber et al. 2008; Rees 2003). Captive elephants were traditionally sourced from wild populations for at least 4,000 years (Lair 2002; Sukumar 2003a). They have been used as war animals, for cultural and ceremonial use, as draught animals for village works or the timber industry, and more recently in the tourism, thereby playing an important role in the construction of Asian nations, their identity, culture and economy (Lair 1997; Csuti 2006). Ban on capture has been implemented since the 1970s in most countries (Csuti 2006; Pimmanrojnagool & Wanghongsa 2002; Sukumar 2003a). The interrelations between wild and captive populations persist in most countries of the species range, notably through captive females reproducing with wild males. The abundant literature in biology, ecology or social sciences focused on either wild or captive populations, or human-wild elephant conflicts, or human-captive elephant relationships. Few studies attempted to describe and analyze the complex interactions between human, wild and captive populations using a multidisciplinary and integrative approach (Maurer et al. 2017; Trautmann 2015; Locke 2013; Leimgruber et al. 2008), despite the importance of human-made effects on exploited and wild animal population dynamics (Lebreton 2005), and the recognition of animals as active agents in social sciences (Descola 2004; Ingold 2000b).

Laos, historically known as *Lan Xang*, the “Land of a Million elephants”, shelters both wild and captive elephants with high levels of interactions between the two populations (Maurer et al. 2017; Suter et al. 2014). The wild population abundance ranges from 600 to 800 individuals, living mostly in isolated and fragmented forest areas (Khounboline 2011). Lao captive elephants were used as draught animals for domestic works to carry rice bags, fire wood or logs for building houses and shared the same habitat with their wild conspecifics. In

the last twenty years, most elephants have been employed in the logging industry. The intensification of elephants' workload has affected the fecundity of the population, leading to a sharp decline from 1,000 to 540 individuals (Maurer et al. 2017). In Lao language, captive elephants (*Xang ban*) are literally called "village elephants" where "*ban*" means village or home⁷. Emic interpretations reflect the cognitive and linguistic categories of the natives, whereas etic interpretations are those that have been developed by the researcher for analyses purposes (Harris 1976). In this article, we adopt the Lao terminology of "village elephants" instead of "domestic elephants" or "captive elephants" that is used in biology (Locke 2014). Wild elephants are called "*Xang pa*" where "*pa*" means forest. Wild and forest being the same word in Lao language, we use the terminology of wild elephants in this article. As recently shown in several studies in anthropology of nature and sociology of sciences, the dichotomy between wild and domestic, and more generally between nature and culture appears to not be universal (Descola 2013; Descola 2004; Ingold 2000b; Latour 1991). In Laos, the interpretation of wild and forest is historically illustrated by the opposition between the *muang* (district or city) and the *pa* (forest), a dialectical contrast rather than a strict dichotomy between domestic, civilized settlements and the wild, untamed forests (Singh 2009). The *pa* is a place of backwardness that lacks social order, but is also a source of desired natural resources. The *muang-pa* dialectic interlinks natural and social worlds emphasizing the social process of the domestication of the wild *pa* into the civilized *muang* (Singh 2009). Similarly, the coexistence of two worlds, the village (*man*) and the forest (*pa*) has been described among Khamti people, a Tai ethnic group living in north-east India and related to Lao-Tai ethnic groups of Laos, allowing constant and dynamic interactions between the village and forest elephants (Lainé, in press). The perception towards the forest, wild and village elephants has shaped their relationships with elephant owners and caretakers.

Human-animal relations are set into a particular conjunction of ecological and social relations (Ingold 1980). Socio-ecological systems are not static, they change over time and are intrinsically dynamic (Liu et al. 2007). People and their environment interact reciprocally and form complex feedback loops. (Liu et al. 2007). For instance, changes in hunting and livestock husbandry practices following political upheaval in Kyrgyzstan and Republic of

⁷ A signification close to domestic which comes from "domus", i.e. house / home in latin.

Macedonia led to modifications in the socio-environmental context and in the nature of human-wolves interactions (Lescureux & Linnell 2013). Ultimately these changes contributed to changes in the perception towards the species and its coexistence with local communities (Lescureux & Linnell 2013).

Similarly, after 1990, the political framework changed radically in Laos with the opening of the country to the market economy and economic liberalization (Evrard & Pholséma 1997). Land reform, and more precisely the individualization of land rights and the systematic zoning and mapping of forests, became a precondition for agricultural intensification (Ducourtieux et al. 2005). Concurrently forest cover declined from 70% of land use in the 1940s to 41.5% in 2005, with an acceleration since the 1990s (Robichaud et al. 2009; Vongsiharath 2009), affecting both wild and village elephants' dwelling. Besides, elephant husbandry practices shifted from traditional village work to logging then tourism in less than three decades (Suter et al. 2013).

The relationship between human and elephant has been lasting for millennia (Sukumar 2003a), based on a tight interlink between wild and village elephants. The rapid political, socio-economic and environmental changes occurring in Laos for few decades should have strongly affected the conditions of this particular cohabitation. Our study builds on an integrative analysis of socio-ecological factors and their dynamics to investigate the potential impact they have had on the relationship between human, wild and village elephants. We assess how the socio-ecological system evolved in Laos the last decades and what consequences these changes have had on human-wild-village elephant's interactions, elephant handling practices and perceptions of the species among elephant owners. We also investigate the resulting changes in the nature of the relation between human and elephant in Laos. To do so, we first analyse the symbolism of the species for village elephant owners and their caretakers, called mahouts. Then we describe the traditional socio-ecological system based on the principles of common access to natural resources and social control over nature and spirits. We enquire how the emergence since the 2000s of nature commodification and the divided access to natural resources has led to a new socio-ecological system. We finally show the effect of these changes on human-wild-village elephant's interactions and perception of the species.

2.2.3 Material and methods

2.2.3.1 Study area

The Lao People's Democratic Republic, or Laos, is a mountainous sub-tropical country located in the Indochinese peninsula. About seventy percent of its geographic area is made up of mountain ranges, highlands, plateaux, and rivers cut through. The highest peak is the 2,800 metre Phou Bia (Savada & Whitaker 1995). 83% of its population is living in rural areas at low densities (Ducourtieux et al. 2005). Village elephants are privately owned in Laos. Ownership is shared by 3.6 people on average, usually from the same family (Suter et al. 2013). Traditionally, owners are also in charge of caring and working with their elephant. In this case the owner is also a mahout. A minority of owners also employ mahouts and do not perform husbandry tasks. For clarity, we use the word mahout for employees that do not own the elephant. Time-sharing is the most common arrangement among co-owners. Both working duties and profits are shared according to their agreement. Village elephants have nomadic working behaviours. Their owner can travel across the country upon working opportunities in logging or tourism for months or years. Most village elephants belong to owners from the Sayaboury province.

2.2.3.2 Data collection

This study is based on an intensive ethnographic survey conducted for 5 weeks starting in November 2015 by the first author who lived in Laos for 15 years and learnt Lao language. During the intensive survey, we used semi-structured interviews to explore (1) knowledge and perception of the species, (2) handling practices and their (3) interactions with wild elephants, as well as (4) the future of mahoutship and elephants in the country (see interview guide in Appendixes 8.1.1). Additional questions and topics were addressed in the course of the discussion on specific points of interests or because of the respondent's willingness to talk about this subject. Questions were adapted and some topics were not addressed for respondents that did not own elephant, such as officials, monks, retired owners or training masters. Some questions or sub-topics were not addressed because of lack of time or misunderstanding, or reluctance from the respondent to answer. This method was chosen to allow respondents to provide broad range of answers on complex

issues such as their perceptions and practices, with as little influence as possible from the investigator (Huntington 2000).

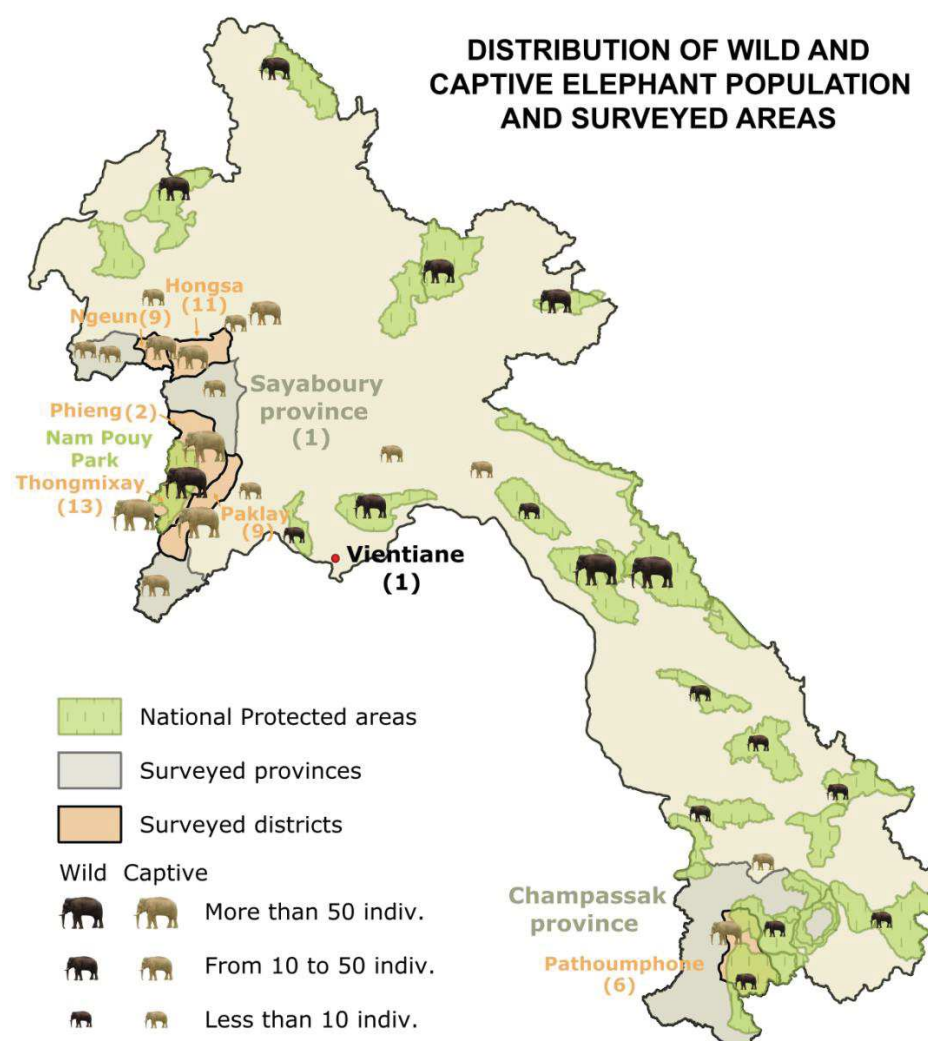


Figure 16 : Distribution of wild and captive elephant population in Lao PDR and surveyed areas
Numbers in brackets indicate the number of interviews conducted in this area. Adapted from Maurer et al., Scientific Reports 2017. Map has been designed with QGISversion 2.14.0-Essen (www.qgis.org) and Photoshop version 9.0 (www.adobe.com). Protected areas shape files are downloaded from The World Database on Protected Areas (WDPA), IUCN and UNEP-WCMC (2017), available at: www.protectedplanet.net.

Interviews typically lasted for 30 minutes or more and were usually conducted in the field, next to the elephant resting place. Sampling was done using a stratified method based firstly on the district of residence and secondly on ownership status of the respondent. We conducted a total of 52 interviews. In the Sayaboury province, we interviewed 11 respondents from Thongmixay district, 11 from Paklay and Phieng, 11 from Hongsa and 9 from Ngeun district (Figure 16). We also conducted 6 interviews in the southern province of

Champassak. Pathoumphone district in Champassak province was sheltering more than a hundred village elephants by the end of the XXth century. Today, only 20 village elephants remain there. We interviewed elephant owners (40), mahouts (8), officials (2) from the Ministry of Agriculture and Forestry at national level and from Sayaboury province, and one monk living in a village known for its elephant keeping tradition. Because elephant handling is mostly a male activity, we had only one female respondent. Interviews were conducted in Lao language by the first author, recorded on a Zoom H1 handy recorder, and fully translated into French and English. All methods were carried out in accordance with the guidelines for anthropological surveys, and in accordance with the legal requirements of France and the National Center for Scientific Research (CNRS) institutional protocols for research (Baude et al. 2006). All informants provided informed verbal consent before participating in the interview.

2.2.3.3 Data analysis

In addition to manual text analysis and extraction of relevant sentences, the corpus of translated interviews was coded *a posteriori* using an open list of codes into MaxQDA software version 12.3.2. For instance, a respondent may say that his elephant was used for 'logging' and/or 'tourism'. Each time the respondent mentioned 'logging', the 'logging' code was assigned to the corresponding part of the interview. Codes were aggregated into topics, e.g. 'work of the elephant'. One respondent often mentioned the same code several times during the interview. For each respondent, the number of occurrences of this code was discretized. Therefore 'n' indicates the number of occurrences of a specific code over the corpus. We also indicated the total number N of respondents that provide at least one answer or code over one specific topic.

To detect and represent underlying structures in our multidimensional data set, we performed a Multiple Correspondence Analysis (MCA). MCA is relevant for analysing patterns in relationships among several categorical data such the codes used in our study (Abdi & Valentin 2007). MCA allows identifying groups of respondents with similar profiles in their answers and the associations between different codes. We selected topics of interests and with the highest contribution scores for the MCA (see detailed list in Appendixes 8.1.2). Typical MCA outputs are biplots showing multiple codes and/or individuals in a low-

dimensional space, so that the proximity in space indicates similarity of codes and/or individuals (Le Roux & Rouanet 2010). Labels on biplots were displayed only for codes with highest degree of association between variable codes and a particular axis (squared cosines). MCA was performed with the R (R Core Team 2017) package FactoMineR (Lê et al. 2008).

2.2.4 Results and analysis

2.2.4.1 A human animal

The close relationship between elephants and humans is very much alive in some areas of Laos, such as the Sayaboury Province. Although the perception of the species by mahouts and elephant owners is affected by their husbandry practices, it is rooted into a long history and tradition of coexistence between humans and elephants.

First, the elephant differs from other animals in its humanlike capacities. According to respondents, the elephant is much closer to mankind because of its ability to understand the language of humans (n=15) and to learn and acquire knowledge. The respondents indicated that the communication between human and elephant is mostly verbal, even though the elephant cannot speak (n=9). Beyond the recognition of specific cognitive skills, the elephant's ability to understand language is a shared feature with humanity:

"Other animals do not know the language of humans. The elephant is like people (Xang beb khron), a human animal (sat khron). He knows the words (hu kwam)."
(#53, Ngeun)

The proximity between humans and elephants is reinforced by elephant's faculties to remember and execute orders, including complex ones. The elephant is able to do what is asked (n=6) and work (n=8).

Respondents also quoted its big size (n=11), strength (n=3) and intelligence (n=6). In this context, it is worth noting that the word "big" (*nyay*) has two meanings in Lao language. It refers to the size, '*sat nyay*' means a big animal and also to the social status, '*phu nyay*' being used for important people or elites (Singh 2012). In that way, the elephant is given a social status deserving fear and respect. Two respondents also mentioned the ability of elephants to kneel down. The Lao tradition commands to kneel down before a person of a

higher rank. Therefore, the elephant's ability to kneel down before its master, a king or the Buddha image, gives this species huge respect.

It seems obvious for respondent #53 that the elephant is a "human animal" (*sat khron*). Like humans, the elephant is in-habited by *kwan*, souls or vital spirits, that need to be re-integrated in its body at the occasion of a *sukwan* ceremony. Their absence may provoke diseases, misfortune or let the wild spirits (*phi pa*) take over. Wild spirits are a powerful attraction for the elephant to escape and return to the wild. Therefore, the master of *sukwan* ceremony is invoking the elephant's souls, asking them to leave the wild and re-integrate the village community:

"Precious New Year's Eve, we recall your soul. Let's welcome it. [...] Whether your soul follows ancient traditions and comes back, or get lost in the deepest part of the vast forest. [...]. I'm gonna call and bring back the soul of the precious and courageous elephant. Let it return to the men's village. [...] Let all your 32 souls return." [Extracts from a ritual entitled "Ceremony for welcoming the soul of my elephant, by monk (novice) Heun from Ban Phoun Leuï village", (Keovanthin n.d.)].

Lao people believe that a person has 32 souls. Is the elephant so closed to humanity that it has the same number of souls? Another respondent thinks so:

"Elephant and human are similar because of their knowledge, even if the elephant is a little weaker than human. The elephant has got 200 souls, human 220." (#17, Thongmixay)

At the end of the *sukwan* ceremony, participants hold cotton threads that conduct and share vital forces in a joint network:

"The master of food aligns dishes. There is the left master and the right master, in this order. [...] Everyone holds a thread: elephant - human, elephant – human ... and so on, without interruption." (Keovanthin n.d.)

These cotton threads also symbolize the special bond that links elephants with their human masters. The symbolism of the elephant among owners and mahouts has been nourished by the complex human-animal relationships and interactions that have developed over time.

2.2.4.2 *From a traditional socio-ecological system based on the cohabitation between humans and elephants*

The traditional way of handling village elephants and the perception of the species by respondents' elders ascribed a socio-ecological system based on two main principles: 1) a common access to natural resources and 2) the social control over nature and spirits.

2.2.4.2.1 *Common access to natural resources*

By the end of the 20th century, dense forest was estimated to cover 47% of the national territory with only 5% of agricultural land (Vongsiharath 2009). At that time, Laos sheltered large populations of wild and village elephants sharing the same habitat, with respectively 4,000 and 850 individuals (Santiapillai 1993b). Elephant owners and mahouts' livelihoods were mostly based on subsistence economy and relied largely on forest resources (Sirivongs & Tsuchiya 2012).

Elephants used to be part of the family heritage (*Xang moladok khopkwa*). The elephant's lifespan being roughly equal to that of Lao people (50-60 years), the owner's family and the elephant genealogies were often parallel. Ownership and workload were shared among family members. Elephants were used for light village work such as firewood or rice bags transportation or dragging logs for the house construction. Otherwise, elephants were released most of their time. Traditionally village elephants did not feed from cultivated fodder but foraged in the forest or bush surrounding the village. Mahouts visited them once a month. Elephants were either completely free (*poy*), or partially restricted with hobbles (*catyae*) on the front legs or a chain (*so*) that the elephant was dragging away. The choice of the release mode depended on the animal behaviour and the distance to crops. Males and "naughty" elephants were usually restrained with hobbles to avoid escape, attacks on humans or crop damages. Such extensive herding was possible thanks to large forest areas where elephants could browse freely and sustain themselves. Families therefore accumulated their wealth through the workload of their elephant for domestic uses, with no or low cost thanks to their free-ranging abilities and free reproduction within the village herds or through cross-mating with wild males.

2.2.4.2.2 Social control over nature and spirits

The dialectic between the wild and the domestic, between untamed natural resources and village prosperity described by Singh (2012) provides a suitable framework to explain the perception of the species among elephant owners and mahouts. Indeed, these elephant masters are engaged in a perpetual attempt to harness and control the wild nature of their elephants.

Lao people distinguish wild (forest) elephants (*Xang pa*) from their captive (village) congeners (*Xang ban*) but 71% of respondents (32/45) considered that village and wild elephants were the same species. Interestingly, the further respondents live from areas of current wild presence, the more different the species are considered to be (Thongmixay and Paklay, 1/11 each, Hongsa 2/11, Champassak 2/6, Muang Ngeun 5/9). When we asked what these differences were, we noticed 24 answers referring to physical attributes with no clear consensus, such as the head and/or the ear being either bigger or smaller. Otherwise, 20 answers were related to the coexistence with humans (wild do not live with humans, wild do not work, wild do not have scars, etc.) and 19 answers concerned behavioural differences (wild attack or run away in the presence of humans).

Two elephant owners from Hongsa and Thongmixay referred to a Lao tale about the origin of wild elephants:

“In ancient times there were only domestic elephants. An elephant was born and could not be caught. He fled into the forest. It's a tale. Before, we did not tie elephants with a rope. They were free. This elephant remained free for 3 months and could not be caught. He became a wild elephant [...] and bred in the forest. [...] So, we captured some wild elephants, brought them back and raised them. They know language like our elephants.” (#44, Hongsa)

This popular cosmogony illustrates the dualist view between the civilized world, where humans have been brought with their domestic companions, and the forest or wilderness that shelters afterwards some fugitives. More specifically, these stories illustrate the paths between the village (*ban*) and the wild or the forest (*pa*). Elephant owners do not conceive domestic or wild as immutable status. Among 24 answers, 13 indicated that wild elephants can become village elephants after capture and training, with the exception of big or

aggressive elephants that cannot be captured and tamed easily. Seven respondents also added that a wild elephant needed to be released from its wild spirits to become captive.

In addition, the elephant status is not inherited from its genitors. Indeed, even if the female's owner can claim ownership on its progeny, the calf is considered a village elephant only from the moment it is trained and lives with humans, whether its father is a wild or a village elephant. Finally, the taming of an elephant appears as a mix of breaking-in technics and shamanist rituals aiming at clearing the elephant from its wild spirits:

"A calf that hasn't been taught yet doesn't belong to us. It still belongs to the forest... It is wild. The spirits of the forest (phi pa) are not those of the village (phi ban). If the shaman doesn't hit hard enough to scare them away, the elephant dies. [...] Once the shaman has taken care of the spirits, it's okay, it's a village elephant." (# 35, Hongsa)

The domestic status is transient and the path to domestication is reversible. Indeed, 11 respondents confirmed known cases of village elephants returning back to the wild. Decades ago, village elephants were released in the forest over long periods of time and could meet with wild ones. It was not uncommon for them to escape and follow their wild congeners, especially gestating females. The latest known case of a village elephant never retrieved was 5 years ago. For eight respondents, such escaped village elephants became fully wild and forgot the language of humans, whereas six respondents considered that they still remember the language. Two respondents also noticed that their wild spirits came back. Knowing the language and ownership that is transmitted from the mother to its calf are therefore only prerequisites. The status of forest or village elephant is eventually a question of perpetuating the control over spirits.

The socio-ecological system that governed the interactions between elephant owners and the species was historically based on a principle of cohabitation, habitat and resources being shared and controlled by the community (Figure 17). The two last decades have seen major changes in these ecological and socio-economic factors.

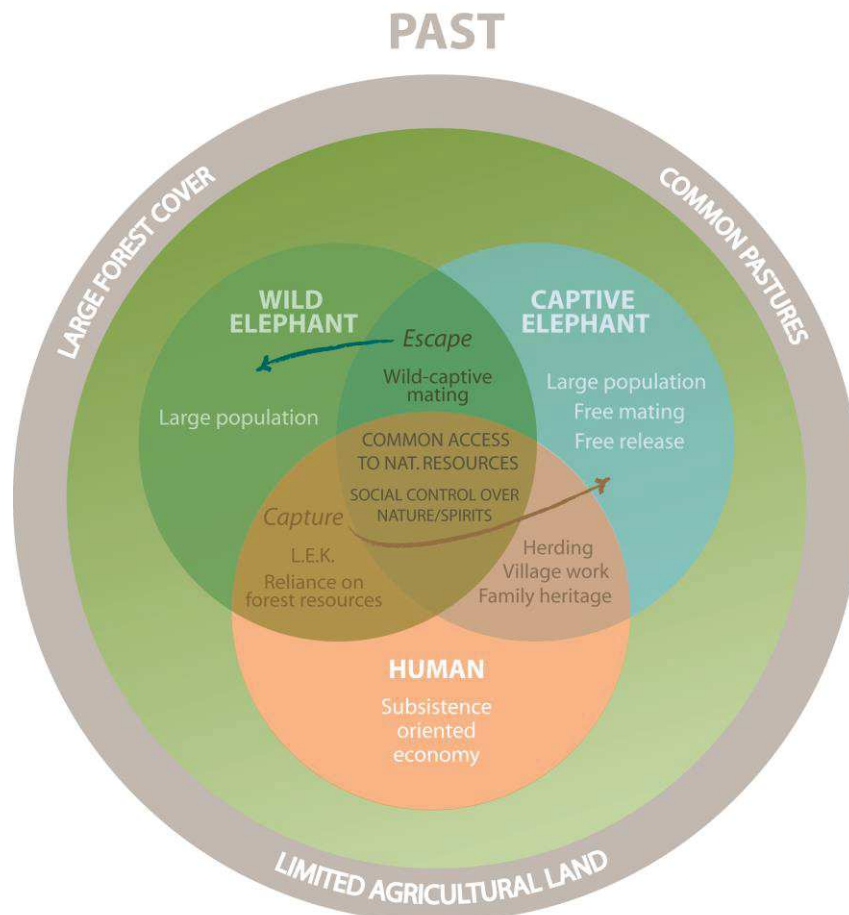


Figure 17 : Traditional socio-ecological system governing interactions between human and elephants

2.2.4.3 Towards a new socio-ecological system based on segregation between humans, village and wild elephants

Since the 1990s and the opening of the country to the market economy, Laos has been engaged in a major social, economic and ecological transition under a process of neoliberalisation. According to Liverman (2004), neoliberalisation lead to the commodification of natural resources, assigning prices and values to natural commodities and allowing their trading within a free market. The commodification process also spreads to environmental externalities such as the valuation of protected forests for their ecosystem services (Castree 2003), and government policies induce a divided access to natural resources (Ingold 1980) or territorialisation, that refers to the partitioning of resources and landscapes in ways that control, and often exclude local people (Igoe & Brockington 2007). Such territorialisation is best illustrated in Laos by the privatization of land and the establishment of national protected forests. These changes induced a major shift in the paradigm founding human-elephant relationships and strongly impacted village elephant

husbandry practices as well as management and perception of wild elephant, as detailed hereafter (Figure 18).

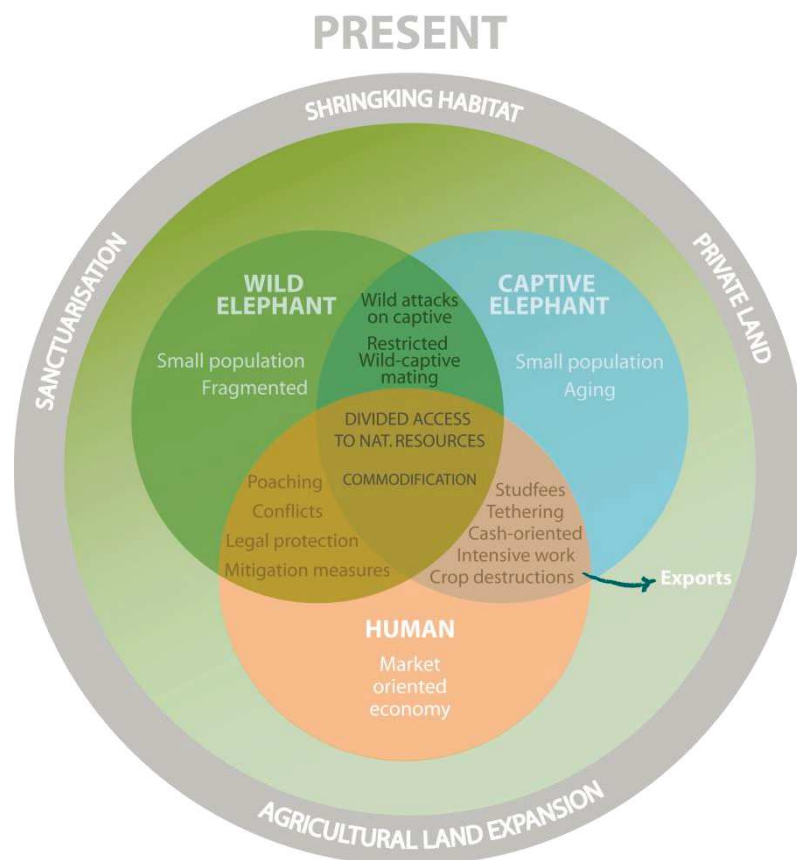


Figure 18 : Current socio-ecological system governing interactions between human and elephants

2.2.4.3.1 Commodification and income generating activities

The development of timber quotas in the 2000's urged some people to invest in an elephant. Nine respondents indicated having bought their elephant with the intention of working for the logging industry:

"There used to be a lot of timber quotas and you could quickly earn money. That's why, I bought an elephant, besides there's not much expenses [to handle an elephant]." (#27, Paklay)

Six respondents even sold and bought several animals, changing radically the status of the elephant from a full member of the family to a production investment. Thereupon, elephants were priced on a market basis depending on offer and demand variations (Maurer et al. 2017).

The development of the forestry industry for export has disrupted elephant handling practices. From occasional village work, the elephants turned to become beasts of burden employed full-time by the timber industry. Their workload slightly increased during the last two decades until the government recently decreased timber quotas, letting many elephants jobless. 13 respondents confirmed their workload decreased during the last 2 years. Most elephants do have now mixed activities, depending on opportunities and periods of the year (Table 2).

Occupation		Yearly workload	
Mostly inactive	3	Superior to 8 months	17
Breeding	7	4 to 8 months	16
Logging	27	Inferior to 4 months	8
Occasional logging	1	Total workload	41
Village work	17		
Tourism	8		
Occasional tourism	4		
Tourism abroad	2		
Total occupation	69		

Table 2 : Type of work done by elephants (N=48 elephants) and workload (N=41 elephants)
Most elephants have mixed activities upon season or opportunities.

Part of the village elephants are now reconverted in the tourism industry, especially around Luang Prabang, a UNESCO heritage city, located far from their native region. But tourism does not have the capacity to employ all village elephants. Approximately a hundred of elephants are employed by the tourism sector, some of them temporarily, as tourism is a seasonal activity. Private companies also buy village elephants to operate their businesses, turning a family heritage into a mean of production. Nowadays owners who do not make an income from their elephant workforce consider selling, exporting or renting them to foreign countries for tourism or circus purposes:

“Right now my elephant is in China. I hired a young man from the village to take care of it and I visit them every 3 months. In Hongsa, there are 11 elephants that left together.” (#41, Hongsa)

The process of commodification also strongly impacted breeding practices. The female long gestation and weaning period is not compatible with intensive workload. Therefore, owners have to make an economic choice between selling their calf after weaning or earning an alternative income from logging during the three-years gestation and weaning period (Maurer et al. 2017). During the last two decades, most owners preferred the incomes generated by their elephant work, resulting in a drastic decrease in the village elephant population. However, the constant rise in elephant prices recently led growing number of owners to conclude it is more profitable to breed their elephants. Thus, seven respondents declared breeding their female elephant for the purpose of selling the calf. During the survey, we met eight respondents with pregnant females, six of them living in Thongmixay district closed to Nam Pouy National Park, and two from Hongsa and Ngeun districts. Thongmixay elephant owners dislike males and prefer to sell them or the calves to other districts, making their living from breeding their females with wild males. Elephant owners from the north of Sayaboury province (Hongsa and Ngeun) still perpetuate a tradition of breeding their females with village males but face difficulties in finding village mates. Indeed, male elephants are not available due to their working commitments and their owners are now asking for expensive stud fees. With the payment of stud fees, commodification has extended to village elephant gametes. Nowadays, most elephant owners confess they did not successfully bred their elephants during the last decade (n=35/48), including 30 of the owners who had never bred their elephants (Table 3):

Breeding history		<i>Including pregnancy during the survey</i>
Never mate (males)	17	
Nulliparous (females)	13	
At least 1 calf	18	
Total	48	
Last 10 years breeding success		
No breeding during last decade	35	
Breeding last decade	13	
Total	48	

Table 3 : Village elephants breeding history and status

A minority (n=18/48) of elephants have a successful breeding history.

When considering the last decade only, the proportion is even lower (13/48).

Finally, this tendency to optimize breeding appears quite similar to ranching-like economy as defined by Ingold (1974). From a natural increase in animal capital, breeding becomes an economic activity based on the financial interest of the owner to breed his female. These changes in breeding practices did not stem only from the commodification of elephants, but also arose because of a shift from commons to a divided access to natural resources.

2.2.4.3.2 Divided access to natural resources

Commodification has been accompanied by the division and privatization of natural resources preventing free release of elephants in or close to the forest and free pairing among village mates.

With the increase of agricultural lands (rice fields, gardens, commercial crops or tree plantations) and the systematic mapping and privatization of forest land, suitable pastures are difficult to find. Elephants are pushed further away from the village. The reduction of grazing areas is becoming a major issue for elephant owners. More elephants are now inactive but owners cannot release them. Elephants must be tied to a tree and moved twice a day, often at distances over several kilometres from the village (see Figure 37 in Appendixes 8.1). As a result, elephants are always chained (n=26), and release is not possible (n=18), usually because they are too many gardens and fields around (n=28) that could be damaged and create conflicts with local communities. The permanent tethering of village elephants isolated one from each other also impairs their mating.

However, 19 respondents still release their elephants during a part of the year. In Champassak district, females are released in wetlands during the monsoon period. Thongmixay district also offers favourable conditions for such releases. This district is located in a remote area, landlocked between the forests along the Lao-Thai border and the Nam Pouy national park. As shown on the map drawn by local mahouts (Figure 19), village elephants regularly encounter their wild congeners allowing pairing with wild mates.

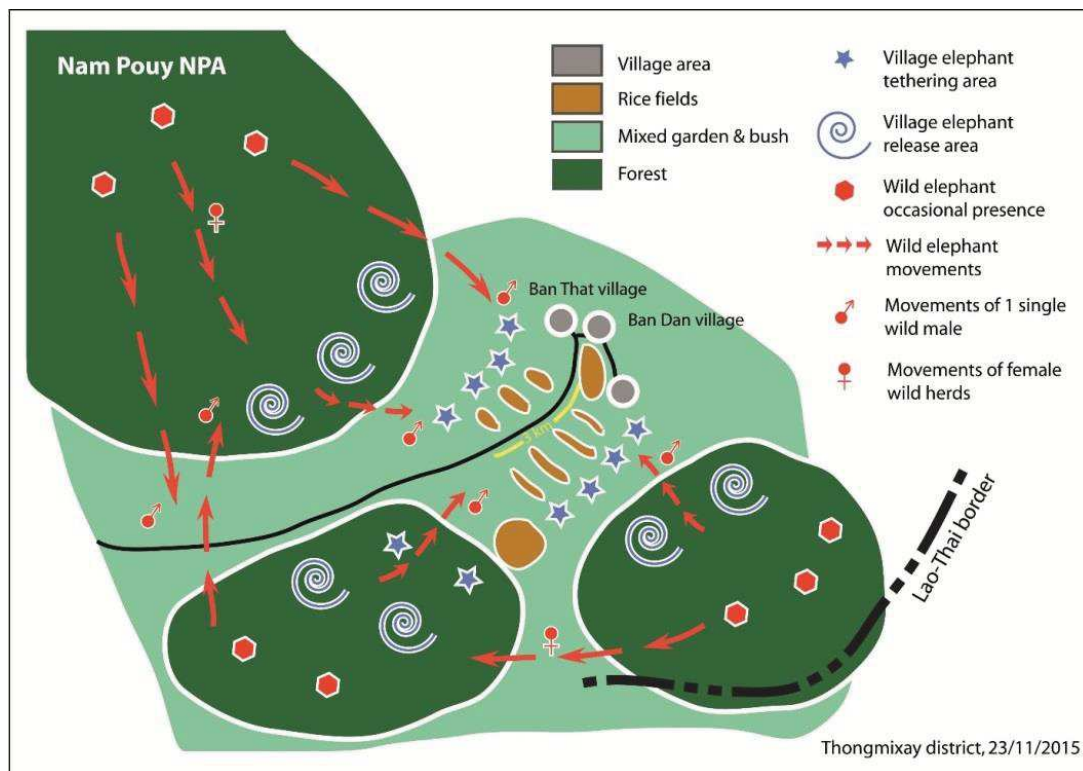


Figure 19 : Map of elephant keeping areas in Thongmixay

Village elephants are either kept attached next to the village fields or released in surrounding forests where they can occasionally meet wild elephants. Arrows show the movement of wild females' herd or a single wild male that is coming every year to mate with village female elephants.

Elephant owners switched from a pastoralism-like system, where their wealth was made of animal capital, to a ranching-like economy based on the accumulation of monetary capital from the elephant/mahout employment by the logging or tourism industries or the sale of calves. Incomes generated rely on the existence of a market where elephants do have a price and their employment vary upon demand. Breeding is controlled and elephants are tethered most or all of their time.

2.2.4.3.3 Human-Wild-Village interactions drive the perception of the species

The principle of a divided access to natural resources has reshaped human-elephant interactions (Figure 18). Village elephants are mostly tethered and have no or restricted contacts with wild ones. Nowadays, village elephants could not escape in the forest anymore because their owners do not want to lose their animal (n=11), so: *"we tied their legs"* (#57, Ngeun) and *"this animal is worth a lot of money. If it escapes, we will get him back."* (#49, Ngeun). Besides, *"there are no more large forests"* (#33, Hongsa). Nowadays, wild-village elephants' interactions only occurred around the Nam Pouy national park, where wild males impregnate village females from Thongmixay. But respondents from the surrounding

districts of Paklay and Phieng, who own males for logging purposes, complained about wild elephants' attacks on their animals.

Wild elephants are now protected by law and their capture is illegal. Authorities and NGOs promote a policy of sanctuarisation of the Nam Pouy National park, with the objective of banning villagers, mahouts and village elephants from accessing this protected forest, leading eventually to what Ghosal et al. (2013) consider a process of purification of nature without humans nor village elephants.

However, wild elephants do not stay permanently within the boundaries of the protected area, and regularly raid agricultural fields and commercial crops nearby. Wild elephants destroying crops have been mentioned by 19 respondents and nine respondents stated that wild elephants are dangerous for people. The rising conflicts between human and elephants are now a major concern for conservation programs, which focus on reducing threats to elephants, including:

“[the] loss of habitat as a growing [human] population results in encroachment into its ancestral home. As this occurs, elephants may wander from the forest onto farmers' land, destroying crops and damaging property, leading to human-elephant conflict. [...] Poaching too remains a serious problem [...]. [The program] focuses to restore, maintain and increase the population of Asian elephant within Nam Pouy. To do this, increased monitoring and data collection on wild elephants is conducted, guidelines for land use management are being set out, and illegal human activity is tackled by the increase and effectiveness of patrols” (WWF-Laos website).

The coexistence between wild and village elephants is still perceived as globally possible, especially for female owners. 15 respondents (N=27) considered that wild and village elephants could live together (Figure 20) with a majority of respondents from Thongmixay and Hongsa, while seven respondents indicated that only females can live with wild elephants, five of them originating from Paklay-Phieng. Among negative perceptions, most respondents, irrespective of their district of origin, stated that wild elephants destroy crops and attack people, while mainly Phieng-Paklay respondents added that wild elephants attack village ones. Mostly Champassak and Thongmixay respondents considered that coexistence between humans and wild elephants is not a problem.

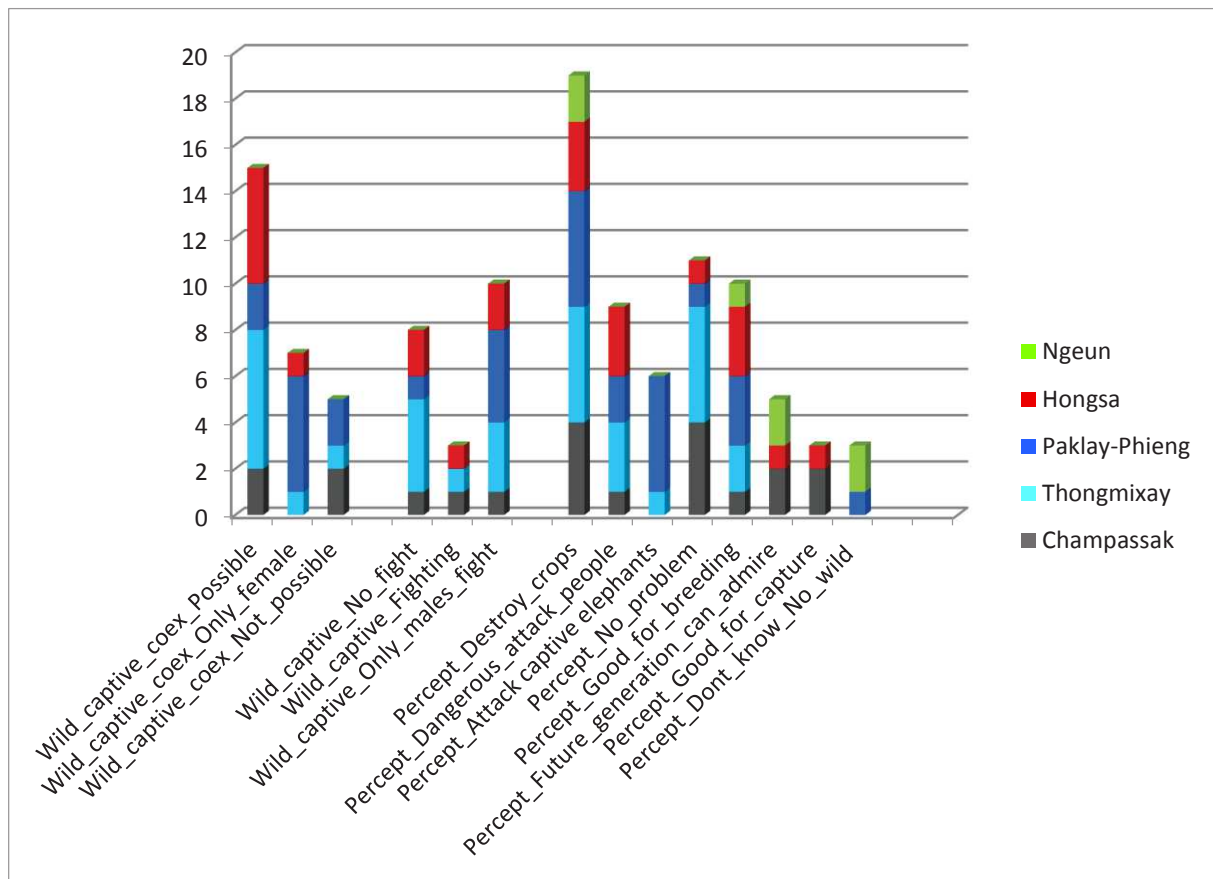


Figure 20 : Perceptions and coexistence between wild, village elephants and humans

Number of answers per code is given on the Y-axis. Colours indicate the respondents' district of residence. The three first codes are related to the perceived coexistence between wild and village elephants. The next group deals with the potential fights between wild and village elephants. The last group of codes gathers the different perceptions of wild elephants for the respondents.

Thus, the perception of coexistence seems to depend on the elephant activity (breeding or logging) and the distance to wild elephants. For example, an informant from Thongmixay who owns a pregnant female sired by a wild elephant explained how local people avoid conflicts in their village:

“Usually there is no problem when the wild male approaches the village because we know where it is and we don't go there. Village elephants are moved to places where villagers don't go because the male is attracted by females. [...] If females were tied up near gardens, plantations or places where villagers collect forest products, the wild male would come in and do damages and we would be responsible for the damage because the female was there.” (#11, Thongmixay)

In contrast, his colleague from Paklay-Phieng, engaged in logging activities, was afraid of the presence of wild elephants:

“Last year a wild elephant came. We were afraid, so we watched the females during the night. We'd also like to have babies, but we're afraid the male will hurt our females. We've seen this happening before.” (#27, Paklay)

An elephant owner from Ngeun district explained the importance of conserving wild elephants but not in his district because of crop destructions:

“In this region, there are more drawbacks than advantages [to have wild elephants] because there are many properties and fields. But elsewhere, there can be many advantages. We must conserve wild elephants. But here, we shall preserve village ones so that young people can watch them in the future.” (#57, Ngeun)

Nowadays, most if not all elephant owners have to deal with the commodification and the divided access to natural resources. But the shift from a mode of cohabitation to one of segregation has not resulted in a uniform change in husbandry practices and perceptions. Respondents adopted various strategies to address changes in socio-ecological factors.

2.2.4.4 A transitional state with various answers to socio-ecological changes

From Thongmixay female owners that breed their elephant with wild males to Paklay owners engaged in logging activities, the answers to socio-ecological changes seem variable. We seek to characterize land-uses, husbandry practices and perceptions to enquire for specific profiles and livelihood strategies among respondents. To detect and represent the underlying structure behind respondents' discourses, we used a Multiple Correspondence Analysis (MCA). The MCA three first axes explained 42.7% of the overall variance, with the first dimension explaining 20.6%. We rely on the two maps built with axes 1 and 2 and axes 1 and 3 to draw a portrait of interactions with, and perceptions of elephants within the study population. Inspecting map 1-2 (Figure 21), the most discriminating variables were linked to village elephants' pasture management. Owners 'partially releasing their elephants' were located on the top-right corner, whereas elephants being 'always chained', 'release is not possible' because of 'too many gardens' were on the bottom-left corner of the map. The respondents' profiles were also discriminated by their elephant reproductive status. 'Pregnant' females, elephants with 'at least 1 calf' and with a 'successful breeding history during the last 10 years' were strongly discriminating (bottom-right). Finally, respondents

considering that wild elephants were ‘not a problem’ were located on axis 2 (top-right). Now, map 1-3 (Figure 22) mainly highlighted answers linked to the coexistence between village and wild elephants and their perception among respondents. The top-left corner aggregated respondents considering that wild and village elephants fight, coexistence between them was not possible and wild elephants did attack their animals. To a lower extent, supplementary variables such as the elephant sex and elephants being ‘bought’ or ‘inherited’ also structured the profiles of answers (see Appendixes 8.1.2 for further details).

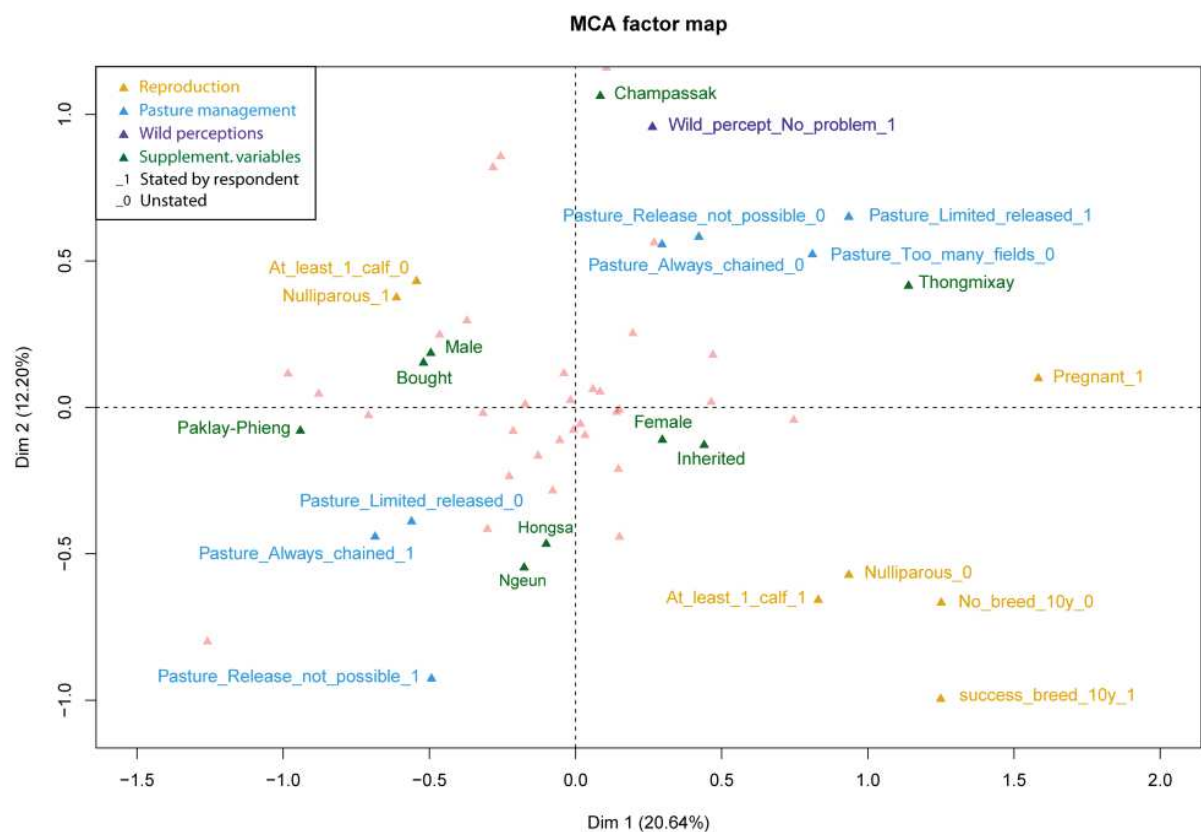


Figure 21 : Factor map showing modalities with the 15 highest contributions on dimensions 1 and 2
Colours indicate the answers' general topic. Labels followed by _1 show the contribution of a modality stated by respondents. For instance, Pasture_Limited_released_1 (top right) is given for respondents that indicate releasing their elephants part of the year, otherwise Pasture_Limited_released_0 (bottom left) was scored. Stated and unstated modalities of a variable are roughly symmetrical on the chart.

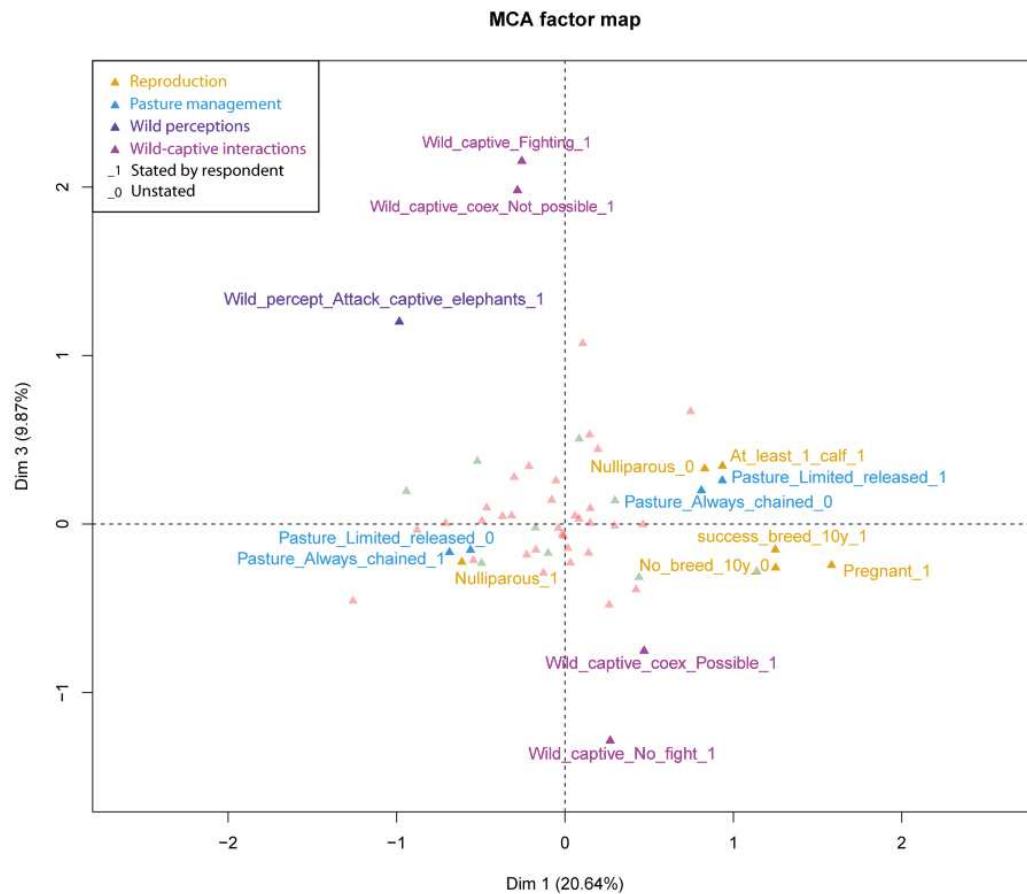


Figure 22 : Factor map showing modalities with the 15 highest contributions on dimensions 1 and 3

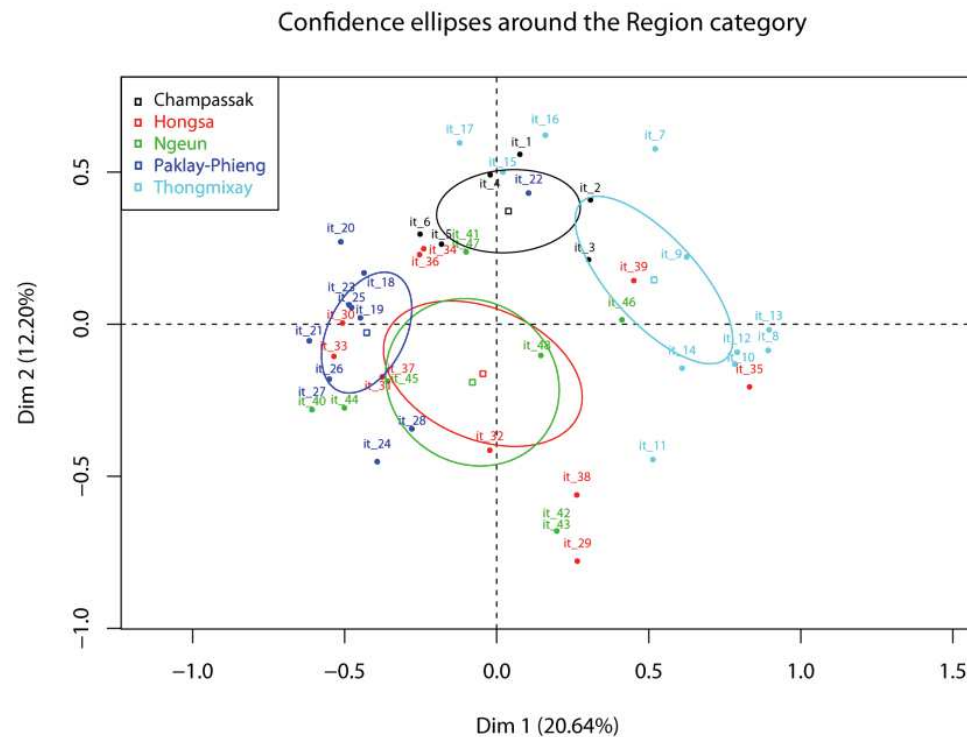


Figure 23 : Map of individuals with 95% confidence ellipse around the respondents' region of residence.

General structures or profiles can be deduced from this analysis. First, pregnancies were strongly linked with the practice of village elephants' release and a positive perception of the wild elephants and village-wild interactions. To the contrary, owners of bought male elephants had more negative perceptions of the wild and coexistence was seen as problematic. These elephants did not have a successful breeding history. The type of work (logging, village work, tourism) and the workload were not so informative in the framework of the MCA, probably because of the workload decrease following the government timber quotas reduction due to wood rarefaction and national conservation policies.

The map of individuals by district allowed drawing four main profiles of answers according to the local conditions (Figure 23).

- (i) "The breeders": Thongmixay district hosted six of the eight pregnant females. They did release their captive elephants and had direct interactions with the wild ones. Their perception was positive. The three respondents from Thongmixay (it_16, 17, 18) who were located further from this cluster were male owners. Thus, Thongmixay owners specialized in breeding their elephants.
- (ii) "The loggers": a second cluster is made of Paklay-Phieng districts that are located on the other side of the Nam Pouy protected area. They did have occasional interactions with wild elephants but considered them more negatively. They saw wild elephants as preventing them from working. They preferred males, and usually bought them for logging purposes.
- (iii) "The traditional elephant handlers": Hongsa and Ngeun districts shared similar profiles. They are located far from the wild presence area in a highly farmed region where release is no more possible. Their answers were more diversified. These two districts are known for their tradition in handling village elephants including their breeding among village mates. Most of them had a successful breeding history, but only few respondents were currently breeding (two males and two females). Some respondents also showed profiles more similar to Paklay-Phieng districts with owners looking for an intensive productivity of their elephant workforce, including elephants working in the tourism sector in Laos or abroad. Their perception of wild elephants was positive, and coexistence was seen as possible. Even if they recognized that wild elephants destroy crops, they deemed wilds are good for

breeding and should be conserved as a heritage, but not in their backyards. However, these 'traditional elephant handlers' were facing major changes in their elephant management practices.

- (iv) "The capturers": finally, Champassak province is known for being 'wild elephant capturers'. They did release their elephants seasonally but had no breeding history for decades. Capture is banned, and wild elephants are found far away in remote forests. Their perceptions were positive, since wild elephants are good for capture, somehow good to think in the sense of Levi-Strauss (1966), as being capturable, even if captures don't occur anymore.

Our MCA results illustrate the current transition from a rather traditional holist system to a more modern dichotomic one, but with respondents choosing different alternatives facing similar challenges. Some have chosen to optimize their incomes through tourism or breeding, while many owners did not find suitable ways to feed and keep their elephants, neither breeding them nor founding employment in logging or tourism. As a result, the village elephant population did not appear self-sustaining and many owners tried to sell their elephants, even abroad. In addition, the young generation did not seem interested in such a hard work. Once Lao mahouts and elephant owners were living close to the forest where they could harvest resources for their livelihood. Nowadays, they have been dispossessed from accessing these natural resources because of land privatization or state-led legal protection. In addition, it appears that their children preferred living in cities and disliked their parents' heritage:

"Young people don't like this job, it's hard to go into the forest. They all went to school, they went away from here and they don't want to come back. They want to be employed. I'm old now, if a buyer comes in, I'll sell my elephant to him." (#07, Champassak)

2.2.5 Discussion and conclusion

We illustrated the on-going gradual shift of the Lao elephant-human socio-ecological system from a pastoralism-like to a ranching-like mode of production. These changes are ascribed to the evolution of the socio-ecological conditions and impact the perception of the species among elephant owners and mahouts.

Socio-ecological systems are subject to both endogenous and exogenous, ecological and socio-economic changes. The prevalence of socio-economic drivers over ecological dynamics, the development of market oriented economies and globalization, the privatization and changes in land management have been highlighted as the main drivers of recent shifts in socio-ecological systems (Lambin & Meyfroidt 2010). Our results highlight the socio-economic and ecological conditions which are driving the change from a pastoralist to a ranching mode of production observed in village elephant handling in Laos.

2.2.5.1 *From hunting to pastoralism*

Using the example of arctic reindeer herders, Ingold (1974) emphasized the relationships between the system of ecological relations linking the human population with herds and pastures, and the system of social relations governing access to the land and to animals. Ingold described the conditions prevailing the changes from a hunting economy to pastoralism and ranching. Historically the tradition of elephant handling is more akin to the hunting economy described by Ingold, as capture was once the main source of captive stock repletion. Sandersen (1879) acknowledged that:

“it would not answer from an economic point of view to breed elephants in India, as, before they were of a useful age — fifteen years — they would have cost more than would suffice to capture a number of mature wild ones, ready for work.” (1879: 61).

In India especially, the low reproductive potential of village elephants resulted in the establishment of wild elephant reserves and their protection by law to ensure a sustainable access to this resource. Therefore, the capture of wild elephants contributed to the persistence of the species as part of a land ethic governing land-uses patterns and relations among interests (Trautmann 2015). However Sandersen also added that:

“in parts of Burmah and Siam it is said that [village elephants] are bred in a semi-wild state, and with little expense. The females there are shackled and left at large in the forests during the non-working months, where wild males have access to them. But in Burmah fodder is plentiful, and the young stock cost nothing till taken up for sale”. (1879: 61)

Such extensive management was made possible because of the specific ecological, social and economic conditions prevailing in Burma or Laos at that time.

The economy of elephant handling in South-East Asia could be seen as a form of pastoralism. Pastoralism or herding is usually associated with a relationship of domination of humans over animals, which is questionable in regards to the relative autonomy of village elephants. Indeed, alternative forms of herd management based on animal autonomy and an alternance of separation and control periods have been described in northern Asia (Stépanoff et al. 2017) that share similarities with traditional elephant handling in Laos.

Ingold (1980, p. 237) listed prerequisites for a pastoralism economy, namely: 1. Animals are convertible into basic raw materials or workforce for domestic consumption (no commodification), 2. capable of self-reproduction, 3. identifiable with forbears and progeny, 4. of relatively low reproductive potential, 5. tolerant of crowding, 6. capable of supporting itself in nature, all of these criteria being verified in the Lao traditional elephant handling mode. The pastoralism mode of production is based on a common access to pasture with an exclusive right of disposal from the owner. Families are engaged in a spiral of accumulation (Ingold 1980) through the natural reproduction of their herd, aiming at providing workforce for domestic use in a subsistence economy. A market for elephants used to exist under a pastoralist economy, but this market concerned mainly the sale of incremental increase in animal stock, where the owner could resort to a one-off sale of an animal or its calf to cover specific needs (Ingold 1980).

2.2.5.2 From pastoralism to ranching

In Laos, the socio-ecological system and elephant husbandry have evolved in recent years to a ranching-like economy. This mode of production is based on the existence of a market, not only for elephants and their workforce, but for all factors of production such as mahout labour and pastureland. Therefore ranching does introduce a formal principle of divided access to pastureland (Ingold 1980). In Laos, the state implemented a land tenure reform leading to the privatization of forests and agricultural lands that impacted the way of life of mahouts and village elephants alike. At least this situation compels village elephant owners to adopt a more intensive form of husbandry - as observed for other animals in Mongolia (Marchina 2017) - and tether their elephants. As land is divided and privatized, it now

constitutes the scarce resources of the system. The owner is then engaged in a spiral of accumulation of profits, where the ultimate goal is not to increase the animal stock but the profits (Ingold 1980). The owner should optimize his number of elephants according to market prices and available resources, especially human (mahout) labour costs and landpastures. As a result, the village elephant population dynamics under ranching economy relies more on socio-economics parameters than on ecological factors and the population of elephants is eventually minimized. The development of tourism camps holding village elephants is particularly illustrative of these changes. Elephants have been moved to semi-urban areas accessible for tourists, far from their traditional habitat and their wild congeners. They are usually fed by cultivated fodder and sometimes kept in stables. Elephants are under continuous supervision of their mahouts. Permanent guarding and fodder supplementation induce high costs that are hardly bearable during the low tourism season or in the event of crises such as a pandemic, financial or political crises that affect tourist frequentation (Duffy & Moore 2010). Ingold (1980) also mentioned that ranching economy entails a strict control over reproduction and the selection of specific traits while pastoralists favour the animal wild qualities. Indeed, males and aggressive elephants are highly disliked in tourism, contrary to logging. Therefore, the socio-ecological transformation also induced radical changes in the human-village elephant interactions, with an apparent shift from rather indirect negative action with some autonomy for the elephant towards more direct positive actions, restraining autonomy and increasing control (Haudricourt 1969) over food, reproduction and work (Ingold 2000a). Mahouts employed in the tourism sector are mostly young and inexperienced (Suter et al. 2013). Non-traditional mahouts lack of traditional knowledge to care, cure and control their animal. Vanitha et al. (2009) showed that elephants handled by non-traditional mahouts cause higher rate of casualties and deaths among the public or their own mahout. Traditional medicine or reproductive behaviour knowledge are also replaced by veterinary skills especially in tourism camps. Similar to other Asian countries, traditional knowledges and the art of mahoutry are dying at a fast rate (Vanitha et al. 2009; Lair 2002). The loss of know-how and the absence of technical innovations (Ingold 1980) threaten the long term sustainability of this new intensive and specialized mode of husbandry. Indeed captive breeding techniques and artificial insemination are not mastered yet.

As a result, the fate of village elephants becomes highly contingent to prices and market trends. Once the elephant was a family heritage, but now it is restricted to a national heritage marketized for its tourism potential. The sanctuarization of forest and wild elephants, their proxy commodification through ecosystem services (Castree 2003) and the real commodification of their village congeners are also disrupting the traditional socio-ecological system. Moreover, it seems hazardous to base the survival of a species with complex socio-ecological factors on the solely ability of self-regulating market to find long term equilibrium (Martin et al. 2016; Sullivan 2011).

2.2.5.3 Land sparing, segregation and divergence

Besides, the on-going confinement of wild elephants into protected areas also impacted the perception of the species. As we have seen among elephant owners, the use of wild elephants as a breeding reservoir favoured villagers' tolerance towards potential conflicts. Furthermore, a deep knowledge of wild elephants behaviours allowed villagers to anticipate potential conflicts and implement local mitigation measures such as the choice of village females tethering locations to avoid attracting wild males in farmed or populated areas, showing once again the importance of traditional knowledge for human – elephant relationships. On the contrary, elephant owners who do not find any interests in wild presence complained about human-wild elephants conflicts. The raising segregation between the village and wild pools illustrates the land sparing or zoning approach promoted by many governments, international institutions and NGOs as a paradigm for conservation and conflict reduction (Fischer et al. 2014; Linnell et al. 2005). Forest is no more perceived as a biophysical system but as a legal demarcation that governs rights and obligations, coercitive and institutional conservation measures. Unfortunately, wild asian elephants transgress the legal and ontological boundary that separates forests and fields (Münster & Münster 2012). Protection measures are largely unsatisfactory for both wild elephants and local communities, leading to a process in which the state and international NGOs strengthen laws, penalties or patrols, while local communities ask for improving protection measures such as electrical fencing, alert systems, payment of compensations, etc.

Dichotomies between nature and society, local and global, economy and ecology prevents from handling the complexity of interrelations existing inbetween and favors processes of

purification (Latour 1991). In Laos, the social control over nature is replaced by a clear demarcation and purification process between the village and the forest poles. Thus deforestation can be regarded by Lao people as a sign of social improvement since civilized and prosperous (*chaleun*) areas are expanding (Singh 2009). However, the long term survival of wild elephants may be compromised by repeated poaching and encroachment of wild elephant habitat, genetic isolation, an increasing defiance towards the species and the alarming increase in conflicts between humans and elephants. The ontological dichotomy between the wild and village animal is getting stronger. Wild individuals are perceived more and more as a different species, living in a different habitat. The Lao terminology of village elephant refers to a vanishing socio-ecological-spiritual system. The terminology of “captive” elephants used in the first place by biologists and conservationists did not reflect the specific living conditions of Lao village elephants, but might finally reveal the ongoing changes in husbandry practices and human-elephant relations. Reinforced by the isolation from the wild pool, this process might be akin to the premises of domestication in the biologic sense, i.e. with control over reproduction and selection or its social acceptance, i.e. securing a more predictable supply of a resource of interest (Zeder 2015).

For years, the debates between pros and cons of captivity or domestication of Asian elephants and more globally between land sparing versus land sharing strategies, have led to many controversies. As suggested by Fischer et al. (2014), a potentially promising approach could be to assess ecosystems and agricultural landscapes as social–ecological systems and their potential benefits to livelihoods and biodiversity conservation. The coexistence between human, wild and village elephants should be discussed and managed globally as part of a socio-ecological system.

Compliance with Ethical Standards: All methods were carried out in accordance with the guidelines for anthropological surveys, and in accordance with the legal requirements of France and the National Center for Scientific Research (CNRS) institutional protocols for research. All participants provided informed verbal consent before participation.

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Conflict of Interest: The authors declare that they have no conflict of interest.

Data availability: Anonymised Data used in Multiple Correspondence Analysis is given in Supplementary Notes.

2.2.6 References article 1

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3 Approche dynamique de population : un modèle bio-économique pour estimer la viabilité de la population

Η επιβίωση των ελεφάντων στο Λάος είναι θέμα οικονομίας

LA CROIX

Des « congés maternité » pour sauver l'éléphant du Laos

PA 02000-500000, 14 JUL 2017 2 0105T

Pré **Centre Services** le 31/12/2017 à 20h07

Afin de limiter la charge démographique des éléphants au Laos, des chercheurs français proposent la mise en place de y compris d'observer le point d'entrée des éléphants pendant la longue période de gestation des éléphants domestiques.

Des chercheurs réclament des «congés maternité» pour les éléphants

For AIT: <http://www.sciencedirect.com/locate/0005-0719> = 2 November 2017 A 06:30

Une population d'éléphant

Ensuring the survival of elephants in Laos: A matter of economics
 Jennifer L. Smith, DVM, DABVP, DABVP-IM

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in the capital city of Laos, Vientiane, Laos, which are under a process of construction. The old French Museum is on the left.

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Scientific Reports

...ρήνι στο Λάος, η ενετακποίηση της του φόρτου εργασίας των
περίοδος κώσης του ελέφαντα (22 μήνες), που ακολουθείται από 2 χρόνια απασαίτη του απογαλακτισμού,
κάθισα την αναπαραγωγή ασυμβάστη με την εργασία. Επιπλέον, η εξαγωγή ελεφάντων του Λάος σε

3.1 Objectifs et résumé de l'article 2

Depuis une vingtaine d'années, l'intensification du travail des éléphants dans les camps de débardage de bois a provoqué une forte chute de la fécondité. En effet, la longue gestation (22 mois) et la période d'allaitement ne sont pas compatibles avec le travail des femelles. Les propriétaires considèrent alors la reproduction comme un manque à gagner de près de 3 ans et préfèrent les revenus générés par le travail de leur éléphant. Dans ce chapitre, nous analysons les dynamiques de la population d'éléphants de villages du Laos en nous attachant à décrire les déterminants de la fécondité. Nous proposons différents scénarios socio-économiques de gestion de la population et analysons leurs effets dans le futur.

Nous avons construit un modèle bio-économique pour quantifier les effets des stratégies socio-économiques sur la viabilité à long terme de cette population. Nous montrons que la fécondité est impactée en premier lieu par la dynamique de la population sauvage à travers la reproduction entre femelles de villages et mâles sauvages. En second lieu, le taux de fécondité dépend de l'intérêt financier des propriétaires à faire de la reproduction. Ainsi, le modèle prévoit que la fécondité devrait augmenter en réponse à l'augmentation rapide du prix des éléphants. A terme, la population d'éléphants de villages atteindra une limite asymptotique dont le niveau dépend de la dynamique de la population sauvage. Une politique de compensation du manque à gagner pendant la période de gestation, ou « congés maternités », permettrait de dissocier la démographie de l'animal des contraintes et fluctuations économiques. Enfin, si le gouvernement Lao ne met pas un terme aux exportations d'éléphants vers des pays tiers, la population disparaîtra.

Cette étude interroge sur les effets de la marchandisation sur la survie de l'espèce et replace les interactions entre populations d'éléphants sauvages et de villages au cœur des politiques de conservation de l'espèce.

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<https://www.nature.com/articles/s41598-017-13907-x> , Annexe 8.3

3.2 Wild-captive interactions and economics drive dynamics of Asian elephants in Laos

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3.2.1 Abstract

The interactions between wild and captive populations of Asian elephants (*Elephas maximus*) persist in most countries of the species distribution, notably through the reproduction between captive females and wild males. However, these complex interactions have been poorly studied, despite their relevance for conservation of this endangered species. Laos has a centuries-long tradition of raising Asian elephants. Besides being cultural icons, captive elephants are inextricably linked to economics through their work in forestry. Using an ecological-economic model, we investigated the effect of socio-economic strategies on fecundity of the Lao population whose dynamics is shaped by human practices. We demonstrated that fecundity is impacted by: i) the dynamics of the wild elephant pool through mating of captive females by wild males, and ii) the financial incentive of elephant owners to breed their animals. As a result, we expect fecundity to rise in response to increases in elephant prices. The captive population will tend towards an asymptotic limit determined by the wild pool growth rate. However, the population will tend to extinction if exports continue. Our ecological-economic approach, by accounting for economic incentives, allows us to predict new equilibria that can serve as a baseline for designing sustainable management strategies for the species.

3.2.2 Introduction

The population of Asian elephants, *Elephas maximus*, is in overall decline and classified as endangered by the International Union for Conservation of Nature. Total population abundance ranges from 30,000 to 50,000 individuals; however, these figures are probably overestimates (Hedges et al. 2005; Raman Sukumar 2006; Choudhury et al. 2008). One-quarter to one-third of the population consists of captive elephants (Leimgruber et al. 2008; Rees 2003). Captive elephants were traditionally sourced from wild populations though bans on wild capture have been in place since the 1970s (Csuti 2006; Pimmanrojngool & Wanghongsa 2002; Sukumar 2003b). These so-called “domestic” elephants are, however, not a domesticated species and are similar to their wild counterparts in terms of genetics and behaviour (Lair 1997).

The interactions between wild and captive populations persist in most countries of the species distribution, mainly through reproduction between captive females and wild males. In Laos, India and Myanmar, captive females are released in the forest and pair with wild males (Sukumar et al. 1997; Lair 1997; Mar 2007; Thitaram, Somgird, Mahasawangkul, Angkavanich, Roongsri, Thongtip, Colenbrander, van Steenbeek & J. a. Lenstra 2010). Nearly 80% of calves born in captivity in Laos during the past decade are from wild genitors from the Nam Pouy Protected Area (V. Chanthavong, pers. comm.). In Myanmar, live capture of wild elephants has been used to sustain the captive pool. This practice may, however, pose a serious threat to the survival of the country’s wild population (Leimgruber et al. 2008). Elephant calves also have great appeal to tourists and, hence, are highly valued (Godfrey & Kongmuang 2009). With corruption, a lack of law enforcement, and deficient registration systems of captive individuals in many Asian countries, the incentive is high to illegally capture and smuggle calves to supply the tourism sector (Nijman 2014). As a result, the captive population partially relies on wild males for breeding, while the wild pool is threatened by illegal captures to supplement the captive pool. Both captive and wild pools also share common threats and conservation challenges, such as habitat destruction, poaching, increased conflicts with local human populations, and risks of inbreeding depression (Thitaram et al. 2010). Despite their relevance for the conservation of the species, the complex interactions between wild and captive pools have been poorly studied.

The understanding of Asian elephant demography and ecology has recently improved thanks to a longitudinal study of a large semi-captive population in Myanmar. For example, it has been shown how life histories could impact reproductive success, survival or senescence (Hayward et al. 2014; Robinson et al. 2012; Mumby et al. 2013a; Lahdenperä et al. 2014). Climate variations also impact age-specific survival of Asian elephants (Mumby et al. 2013b; Mumby et al. 2015). Besides survival, large variations in average fecundity rates have been observed in different populations across the region and over time, with a fecundity rate of 0.023 (2.3% of breeding females) in Laos (Suter et al. 2014), 0.083 in Myanmar (Mar 2007), and varying from 0.095 to 0.155 for a captive elephant population in India over the past century (Sukumar et al. 1997). No systematic assessment explains why the captive birth rates are highly variable and lower than birth rates observed in wild populations. It has been hypothesized to be the consequence of management and husbandry practices, which in effect place breeding secondary to work (Leimgruber et al. 2008).

The alteration of vital rates in the dynamics of wild-captive Asian elephant populations illustrates the intricacies of mixing natural and human-induced mechanisms (Lebreton 2005). Our objective was to assess the effect of these interactions on the viability of Asian elephant populations using an ecological-economic modelling approach with Lao populations as a case study.

Lao captive elephants are traditionally used as draught animals in the logging industry and share the same habitat as their wild conspecifics. In the last twenty years, the intensification of elephants' workload has affected the fecundity of the population, leading to a sharp decline from 1,000 to 540 individuals (Suter et al. 2014). The long gestation and lactation period for female elephants is not compatible with work (Leimgruber et al. 2008). Owners consider breeding to represent a loss of income for nearly three years and therefore avoid breeding their elephants, preferring the high incomes generated by the logging industry (Leimgruber et al. 2008). Meanwhile, the contiguous Nam Pouy wild population has experienced a sharp decrease from 400-500 individuals in 1990 to 60-80 in 2010 (Khounboline 2011; Santiapillai 1993a; Duckworth et al. 1999), further hindering the reproductive potential between wild males and captive females. Finally, the Lao captive population has also been affected by the withdrawal of individuals through the export of captive juveniles to third countries. These exports violate the Convention on International

Trade in Endangered Species of Wild Fauna and Flora (CITES) despite its ratification by the Lao government in 2014. While exports are highly regulated, the trade of captive elephants is unregulated on the domestic market (Norachack 2002).

To develop a demographic model incorporating economic constraints, we considered the processes impacting the dynamics of captive elephants with a focus on the determinants of fecundity. Therefore, we developed a model including three components: (i) a demographic component structured by sex and age, including the exports of living captive elephants, to estimate the captive population abundance at a given time; (ii) a wild elephant component to account for the wild male breeding potential; (iii) and an economic component to model the elephant owner's decision-making process. Finally, we defined several demographic and socioeconomic scenarios to investigate new ecological-economic equilibria that can serve as a basis to design sustainable management strategy for the species.

3.2.3 Results

3.2.3.1 Changes in breeding practices

Breeding practices radically changed since Laos transitioned to an open market economy in 1989. Traditionally, captive elephants were used for occasional village work while spending most of their time in small herds, grazing freely in the village surroundings. Mating of captive females with either captive or wild males was uncontrolled.

In 2015, we conducted 52 semi-structured interviews among elephant owners, keepers, and officials throughout the distribution of captive elephants in Laos – 41 out of 50 respondents indicated difficulties finding a captive mate. Among owners of females, the main reason given for the difficulty in finding a captive male was the absence of captive breeding males ($n = 21$ out of 43) because “there is no male nearby”, “males are kept far away”, “they (males) are engaged in logging and therefore not available for mating”, or “the few males living nearby” are “too young” or “sterile”. Two other reasons were given equally ($n = 11$): stud fees being too expensive, and their elephant being too tired for breeding. Owners of males indicated having difficulties finding a captive female for mating because “females are not available” ($n = 8$), “their male is too tired for mating” ($n = 8$), and “females owners do not want to pay stud fees” ($n = 6$).

Meanwhile 28 out of 42 respondents considered that mating with a wild male is easier than with a captive one, including all respondents (n=11) living at the edge of Nam Pouy park and having access to the wild pool. Such a mating system was easier because wild males are “available”, “free of their movements”, “in good health”, “not exhausted unlike the working captive males”, and “do not ask for stud fee payment”.

As a consequence, the reproduction of captive females depends mainly on the presence of wild males in Nam Pouy, and to a lesser extent, on the availability of a captive mate. Unlike in natural populations, the reproduction of captive females is density-dependent towards males.

3.2.3.2 How much does an elephant cost?

The captive population dynamics are also driven by the willingness of owners to breed their female. According to economic theory, owners maximize profits, and therefore have to make an economic choice between breeding their female or having them work in the logging industry. The owner estimates how much he can earn by selling a calf after weaning and compares these earnings with the foregone alternative income from logging during the three-year gestation and weaning period.

Our model incorporated the price of an elephant following supply and demand theory – that is, a product (i.e., elephant) is a function of its quantity (i.e., the population). Thus, the price of an elephant can be expressed in terms of the population size given by the demographic component of the model. We associated the sale price given by 26 owners who sold their elephants between 1994 and 2012, to the population size produced by the model at the time of sale. Elephant prices in constant USD were exponentially related to total population (all parameters being different from 0 with p-value < 0.035).

The price of an elephant in constant USD increased with the decrease in population (Figure 24). From 1990 to 2012, the increasing scarcity of elephants was accompanied by a rapid increase in sale prices exceeding 20,000 constant USD (Suter et al. 2013). This result illustrates that the relationship between quantity and price is consistent with economic theory. Lower populations (quantity available to the market) lead to higher prices, which

lead more owners to conclude it is profitable to breed their elephants rather than using them for logging.

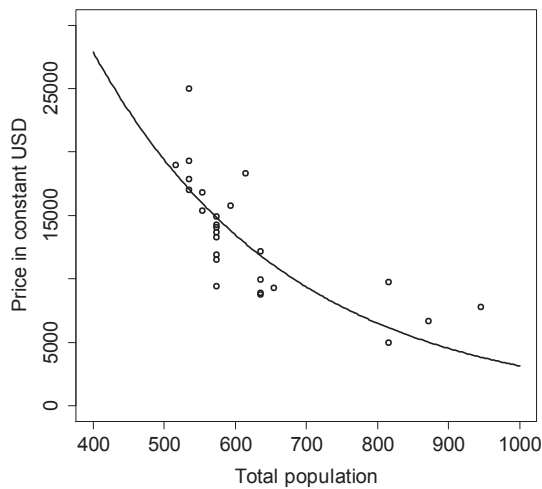


Figure 24 : Elephant price is a function of total population abundance
Prices are given in constant USD, base year 2000

3.2.3.3 Population projections depending on ecological-economic scenarios

Using our ecological-economic model, we investigated the impacts of economic and government policies on future trends in the captive population. The government may impact the population dynamics by revising its policy on the controversial export of elephants to third countries and by fighting illegal trade. The government could also reinforce its wild elephant conservation policy by enforcing the law and effectively protecting the Nam Pouy park wild pool. Finally, the government and private stakeholders could promote pro-birth policies for captive elephants (e.g., by compensating owners for foregone logging returns).

Based on the 2012 population census of captive elephants and on estimates of the Nam Poy wild population, we selected five scenarios that are representative of the different dynamics of the wild pool and levels of exports. All scenarios are based on a price-dependent domestic market. The reference scenario (i) showed the current level of exports of juveniles and a decreasing wild pool at a rate of 8%. The four other scenarios were based on an effective prevention of exports with (ii) a decreasing wild pool, (iii) a stabilized wild pool to investigate the effect of a conservation policy, (iv) a growing wild pool, and (v) a maternity-leave scheme that financially compensates owners for the loss of income during the breeding period. We ran all scenarios for a period of 100 years with stochasticity in the economic growth rate.

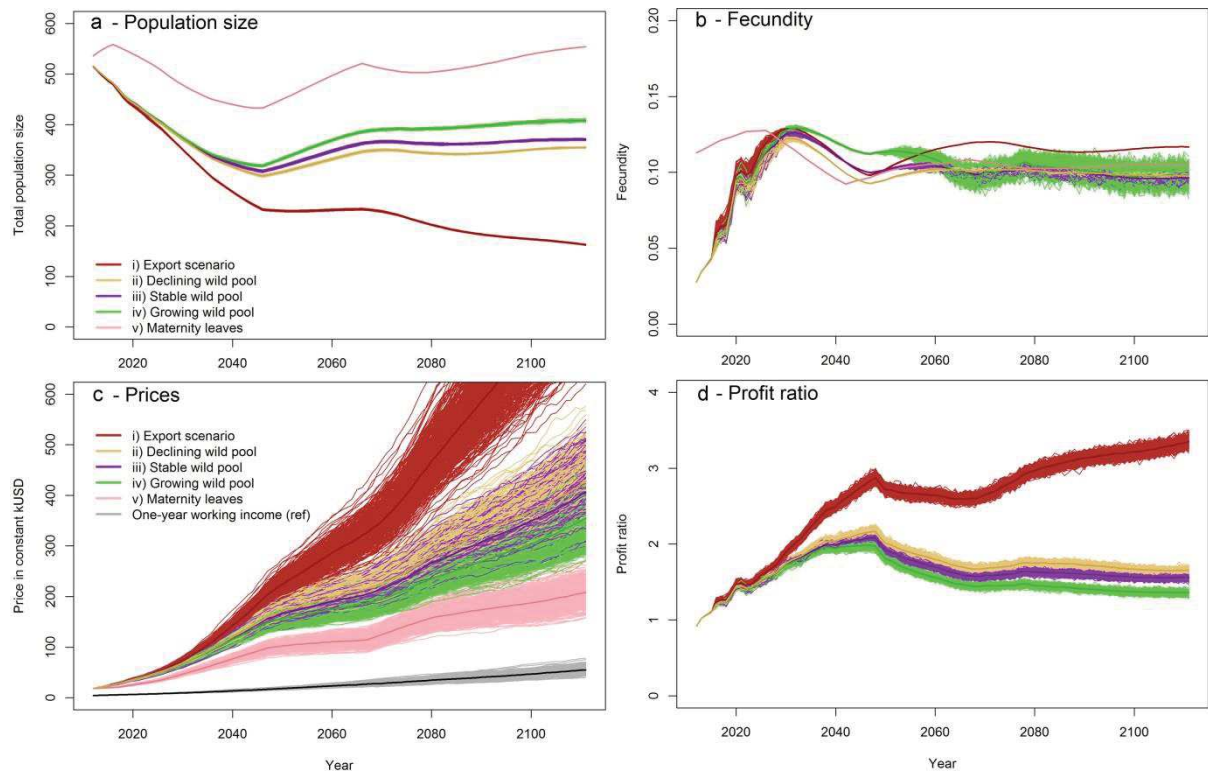


Figure 25 : Model projections depending on ecological-economic scenarios

Fig.a: Population estimates; Fig.b: Fecundity; Fig.c: Elephant prices in constant thousand USD;

Fig.d: Profit ratio. The different scenarios within each figure are:

- (i) Current level of exports and declining wild pool;
- (ii) No export and declining wild pool at a growth rate of 0.92;
- (iii) No export and stable wild pool;
- (iv) No export and growing wild pool at a growth rate of 1.03;
- (v) Maternity-leave compensation scheme with no export and declining wild pool.

The median value of the 500 simulations is shown in contrasted color. The gray line in Fig.c shows one-year working income as a reference. Fig.d does not show the profit ratio for the maternity-leave scenario (v) as it tends to infinity.

Whatever the scenario, the population decreases during the first 35 years until it recovers from the transient and unstable structure observed in 2012 (Figure 25a). If current export practices continue (i), the population decline slows, but tends to extinction over the long term with an estimated population of 10 individuals after 480 years. If exports are prevented, the population reaches an asymptotic equilibrium that depends on the dynamics of the wild pool. After 100 years, the captive population reaches an abundance of 355, 371 and 408 individuals for a decreasing (ii), stabilized (iii), or growing (iv) wild pool. Maternity leaves (v) are the only scenario allowing the population to exceed 2012 abundance with 554 individuals. In this case, compensating the owners' loss of income counteracts the prevailing effect of economic incentives on elephant fecundity.

The population decrease due to exports (i) tends to sharply pull prices upward (Figure 25c), reaching prices over 800,000 constant USD. The population increases for the other scenarios equalize prices from USD 206,000 [s.d. 20,000] (scenario v) to USD 428,000 [s.d. 39,000] (scenario ii). Consequently, the profit ratio (Figure 25d) stabilizes respectively at 1.36 [s.d. 0.02] (iv), 1.56 [s.d. 0.02] (iii) and 1.65 [s.d. 0.03] (ii). The rising prices in the export scenario (i) brings the profit ratio to 3.35 [s.d. 0.05] after 100 years. As maternity leaves cover the loss of income, profit ratio of scenario (v) tends to infinity.

Fecundity rates (Figure 25b) follow the same growing trend as the profit ratio, but are constrained by density dependence in reproduction (see Methods 3.2.5.5 Figure 29). Export scenario (i) displays the higher fecundity rate of 0.117 followed by the maternity leave (v) fecundity rate 0.105. The fecundity rates in the three other scenarios (ii to iv) are approximately 0.095.

3.2.3.4 Changes in demand for elephants

Because we study elephant population dynamics, we built an economic model centered on supply. Variations in supply, the total population, explain price fluctuations given that demand for elephants is proportional to supply. We investigated the effect of a change in demand by applying a 25% decrease and increase in elephant prices. If demand fluctuates over time, using fixed rates allowed us to define a maximum interval bounding the total population estimates under supply and demand equilibrium (Figure 26).

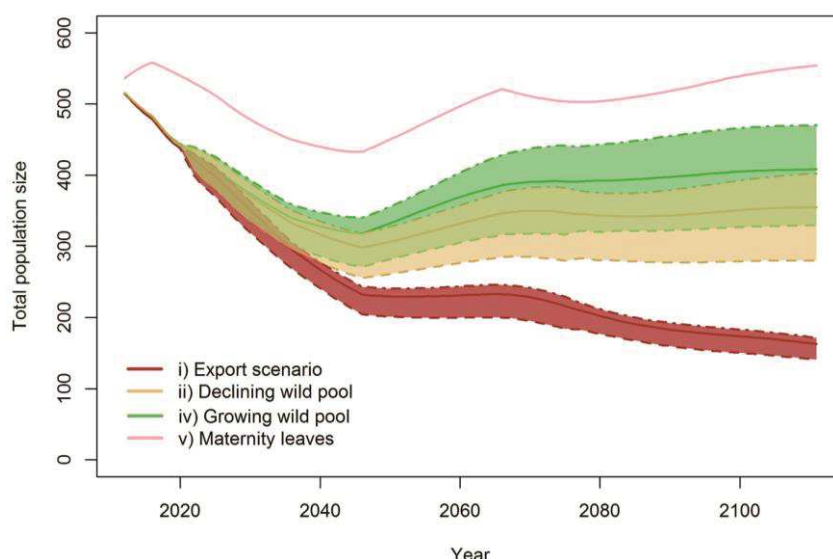


Figure 26 : Population estimates under various scenarios of demand variation

(i) Current level of exports and declining wild pool (ii) No export and declining wild pool at 8% per year (iv) No export and growing wild pool at 3% per year (v) Maternity-leave compensation scheme with no export and declining wild pool. Dot-dashed lines give the total population size for demand increase (upper estimate), dashed lines the total population size for demand decrease (lower estimate) and plain lines the total population size with constant demand (as shown in Figure 25a). Demand variations do not affect maternity-leave scenario (v).

In the export scenario (i), population estimates range from 141 to 172 for a 25% decrease and a 25% increase in demand for elephants. The declining (ii) and growing (iv) wild pool scenarios have respective population estimates of 280 to 402 and 330 to 470. Once again, population size in the maternity-leave scenario (vi) is not affected by the variation in demand.

3.2.3.5 Elasticity analysis

We projected the population out 20 years in each scenario and calculated the elasticity of the resulting population growth rate to model parameters (see Appendixes 8.2.3). The parameter showing the highest elasticity (0.033) is the wild pool growth rate (grw) for the growing wild pool scenario (iv). It decreases to 0.021 for the stable wild pool scenario (iii) and 0.005 for the declining wild pool (ii), export (i) and maternity-leaves (v). The female export rate shows a medium-range elasticity (0.012) for the export scenario (i) while it is null for all other scenarios. All other parameters show similar elasticities whatever the scenario with Maximum fecundity and Sex ratio at a rate of approximately 0.03. Elasticity to female survival rates decline continuously from 0.03 to zero. Elasticity to male survival shows much

lower values with a maximum of 0.007 for the 35 years age class. Other model parameters had an elasticity rate lower than 0.001, including all economic parameters.

3.2.4 Discussion

No study has investigated the effects of socio-economic strategies on the fecundity of an animal population whose dynamics are shaped by human economic practices. We demonstrate that fecundity of captive elephants is impacted by: i) the dynamics of the wild elephant pool through mating of captive females by wild males, and ii) the economic incentives of elephant owners to breed their animals. As a result, we expect fecundity to rise again gradually in response to the rapid increase in the price of elephants. The captive population will tend towards an asymptotic limit determined by the dynamics of the wild pool. In any case, the population will tend to extinction if the government does not stop export practices at current rates. Elephant exports, mostly to Chinese zoos and tourism enterprises, threaten the survival of the Laotian population.

Our model illustrates the strong interactions between the wild and captive pools. The value of captive elephants for conservation have been recognized, not only because of their numbers and the threat that their capture could pose to wild pools, but also for their potential roles in reintroduction, patrolling, human-elephant conflict mitigation, and scientific research (Lair 1997; Dublin et al. 2006). Beyond the risks of extinction of wild populations, we showed that wild pool dynamics directly impact the survival of the captive population through crossbreeding. The elasticity analysis confirms the influential contribution of a stable or growing wild pool to the growth of the captive population. The Nam Pouy wild pool was modelled using a geometric growth rate, based on published data (Khounboline 2011; Santiapillai 1993a; Duckworth et al. 1999); however, these data are scarce and approximate. A better estimate and monitoring of the abundance of this population would reinforce the recognition of how dynamics of the wild pool affect the demography of the captive pool. For the time being, it seems urgent to strictly protect the wild populations and consider organizing new wild-captive breeding areas in Laos. Policy-makers should also consider the side-benefits of a strict conservation strategy for wild elephants in regards to the cultural and economic role played by captive elephants.

Our ecological-economic approach also emphasizes the impacts of human practices on the dynamics of the captive elephant pool. Several models have been developed to search for potential balance between ecological and economic dynamics. Most of these models favored a macroeconomic approach – searching for a global equilibrium between total profit maximization and population survival (Horan & Bulte 2001; Rakotoarison 2009; Timmermann et al. 2014). In our case, we directly linked fecundity with owner profit maximization. In the absence of reliable macroeconomic data, this microeconomic approach allowed us to model the owner’s decision-making process and study its impact on species’ demography. However, our elephant price dataset was derived from data for a population between 530 and 900 individuals. Therefore, the estimated price of elephants in a population of less than 200 individuals remains questionable, being far from the original data range. This was one reason we limited our projections to 100 years.

As shown by our model, changes in handling practices have long-term effects on population structure and dynamics. In 2012, the population was already transient and unstable, with a strong bias in favour of adults over 20 years old (see Figure 31 in Methods 3.2.5.10). As a result, the model indicates it will take 35 years before the population grows again. Long-lived species, such as the Asian elephant, are highly sensitive to population inertia (Koons et al. 2007), with long periods before the population may recover from any change in a vital rate. Further investigation of such transient status and its consequences on elephant population dynamics are needed. But our model demonstrates that the commodification of captive elephants and its accompanying changes in handling practices have probably dominated the ecological and biological dynamics of this population, such as shown by the short-term elasticity analysis (see Appendixes 8.2.3).

Our maternity-leave compensation scheme provides additional insights into the conservation questions surrounding captive and semi-captive populations. If owners are compensated for their loss of income during breeding, the steep economic trade-off between using an elephant for breeding versus work is removed, the elasticity of all economic parameters being null under this scenario. By covering the opportunity cost of breeding, the maternity-leave scheme we analysed allows the population to exceed its 2012 abundance. Such a policy could be funded either by a tax on elephant incomes or directly by the tourism industry, for which calves are highly prized. Because the tourism industry is also

a buyer of elephants, supporting such population growth would also put downward pressure on elephant prices (Figure 25c).

Overall, our ecological-economic model may not explicitly predict the size of the elephant population in a century. It rather provides a framework for policy-makers, conservationists and managers to anticipate the impacts of socio-economic determinants and their policies—such as exports, or wild elephant conservation—on the fate of the population. Moreover, the interactions between captive and wild pools should be further investigated as they set in motion poorly understood demographic, genetic, epidemiological, economic and socio-cultural processes that strongly influence the species' population viability.

3.2.5 Methods

3.2.5.1 Study Species and Area

Laos has a centuries-long tradition of raising Asian elephants (Khounboline 2011). Most captive elephants live in remote areas and are used to extract logs in the forestry industry (Suter et al. 2013; Lair 2002). After their daily working hours, they are tied to trees where they can forage by themselves and are moved twice a day by their keepers. Keepers also often release their elephants in the forest for a few months while the keepers are engaged in rice farming (Lassausaie et al. 2015). Most of the country's captive elephants live in Sayaboury province (Figure 27), which also hosts the Nam Pouy National Park (Lat: 18°12' – 18°58'N, Long: 101° 04' – 101°32'E) – home of the second largest wild population in the country (Lassausaie et al. 2015; Suter et al. 2013; Khounboline 2011).

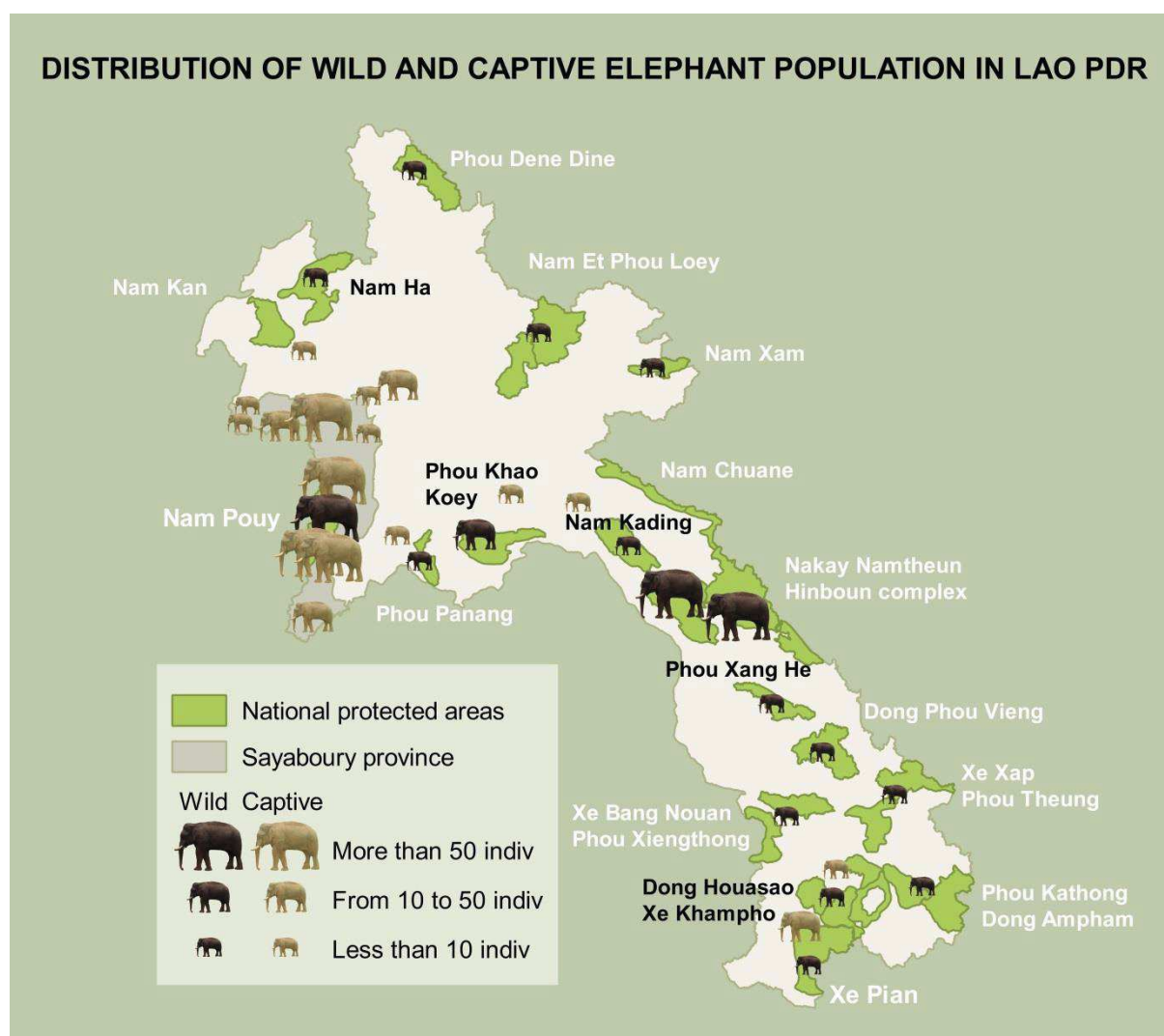


Figure 27 : Map of captive and wild elephant populations in Lao PDR

Map has been designed with QGIS version 2.14.0-Essen (www.qgis.org) and Photoshop version 9.0 (www.adobe.com). Protected areas shape files are downloaded from The World Database on Protected Areas (WDPA), IUCN and UNEP-WCMC (2017), available at: www.protectedplanet.net.

3.2.5.2 Population data

Since 2006, the Lao Care and Management Program (LECMP) of the Department of Livestock and Fisheries of Lao PDR has implemented a national campaign to register all captive elephants. Captive elephants are microchipped by the LECMP. Their records, including name, microchip number, sex, age, physical description, medical history, ownership details and location, are saved in a database. Data are updated twice-yearly during LECMP veterinary care visits. We used the data on captive populations structured by sex and age extracted from the database with the year 2012 as a reference (Suter et al. 2014). Data on the Nam Pouy wild elephant population from 1990 to 2012 were extracted from the literature

(Khounboline 2011; Santiapillai 1993a; Duckworth et al. 1999). More details on the data used throughout are provided in Appendixes 8.2.4.

3.2.5.3 Trade in captive elephants

Captive elephants are privately owned in Laos. Domestic trade is allowed after the payment of a tax to local authorities (Norachack 2002). Elephant prices are driven by demand on the domestic market. Domestic sales or re-sales do not change the size of the population unlike exports. CITES Convention does not allow international trade in elephants. Despite its ratification by the Lao government in 2004, the export of living elephants continues. Juvenile females illegally cross the border into Thailand and China (Lair 1997). National authorities also export young elephants in the form of "rentals" or diplomatic gifts (Suter et al. 2014). Being either legal or illegal, exports are considered as permanent, individuals are permanently removed from the domestic population.

3.2.5.4 Breeding practices in Lao PDR

We studied mahout (elephant handler) practices and their impacts on wild-captive interactions using ethno-ecological methods. The topics covered in this study included the perception of the species and its wild-captive status, the description of husbandry practices, including working, temporary releasing, breeding and interacting with the wild pool, and the respondent perception of the future. In particular, this study described the free-grazing and husbandry practices in Laos that are potentially interfering with the wild elephant pool, and described the mating systems between captive mates. The breeding practices observed during the ethno-ecological study served as a basis to model the drivers of captive population fecundity. We presented in chapter 2 the global results of the ethno-ecological study.

In 2015, we conducted 52 semi-structured interviews among elephant owners, handlers, and officials throughout the distribution of captive elephants in Laos. Interviews were conducted in Lao language by the first author, recorded on a Zoom H1 handy recorder, and fully translated into French and English. All methods were carried out in accordance with the guidelines for anthropological surveys (Baude et al. 2006), and in accordance with the legal requirements of France and the National Center for Scientific Research (CNRS) institutional

protocols for research. Research protocol has been approved by Montpellier University. All participants provided informed verbal consent before participation. Sampling was done using a stratified method based on the district of residence and ownership status of the respondent. We coded answers using MaxQDA software.

3.2.5.5 Demographic model for the captive population

We developed a population model composed of a two-sex and 55-age-class matrix to account for the sexual dimorphism in vital rates and sex-specific animal handling practices (Figure 28).

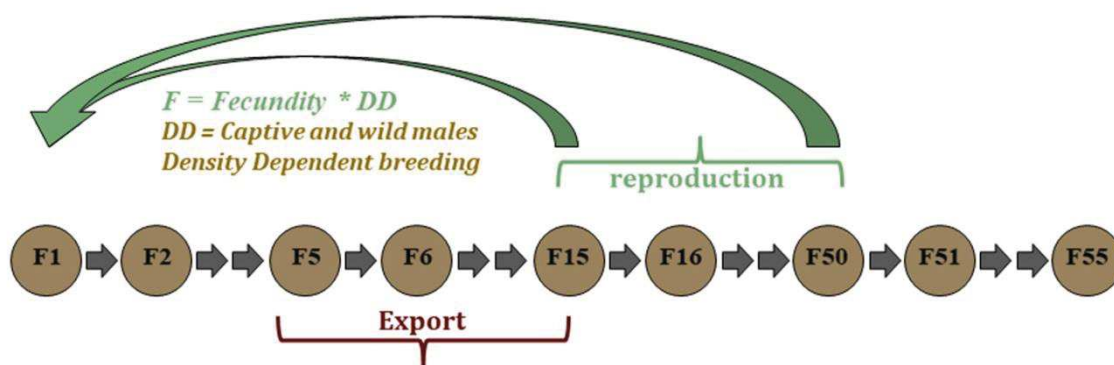


Figure 28 : Life cycle of captive females

Survival

Demographic data from Laos did not allow estimation of survival rates. We used sex- and age-specific survival rates for a semi-captive elephant population in neighboring Myanmar that shares similar working practices (Mar 2002). Survival is given per year from age 0 to 55 with sf^n the female survival at age n and sm^n the male survival (see data in Appendixes 8.2.4).

Exports

From a population perspective, exports to foreign countries are considered permanent migration. We apply an export function to survival for individuals aged 5 to 15 years with $sf^n (1-ef)$ for females and $sm^n (1-em)$ for males. We defined 2 scenarios: a ban on exports (ef and em equal 0) and the reference scenario showing the current level of exports. Since females are preferred to males due to their docility and reproductive potential, the respective rates for ef and em are set to 0.04 and 0.01 for the reference scenario.

Birth

Yearly recruitment is given by the product ($sf^0 sr d F$) for females aged from 15 to 50, with sf^0 the female survival before their first year, sr a balanced sex ratio at birth, d the density dependence function and F the fecundity function, described hereafter. The same formula is used for males with sm^0 as the male survival rate.

Density-dependent reproduction

As captive males are engaged in logging activities, many owners of females do not find male mates. Working males are chained to a tree during their resting time and are therefore not available for mating. A prior breeding agreement between female and male owners is therefore required. But female owners found the costs of stud fees too expensive and male owners are reluctant to engage their males in mating because mating is time-consuming and believed to reduce a male's working strength. Most births therefore result from mating between a captive female and a wild male from Nam Pouy Park. When the breeding process depends on external factors, such as the availability of captive males or the presence of a wild mating pool, the fecundity function is weighted by a coefficient d (Legendre et al. 1999). We introduced a density-dependent reproductive function in relation to the proportion of the mating pool (Sundelöf & Åberg 2006) where the probability for a captive female to reproduce is dependent on the ratio of the number of breeding males from the captive and wild pools to the number of captive breeding females:

$$d = \frac{1}{1 + e^{-b \frac{Nm}{Nf}}} \quad (1)$$

with Nf the number of captive females of breeding age (15 to 50 years), Nm the number of captive breeding males from 30 to 55 years plus the estimated number of wild males living in Nam Pouy Park, and b the stretching exponent of the function. The parameter b allows the growth of the function to be adjusted. In the case of this long-lived polygynous species, we set the stretching exponent to 2. Thus, for a given population of 200 reproductive females and 20, 60 or 100 breeding males respectively, fecundity will be affected by a coefficient d equal to 0.57, 0.71 or 0.92, illustrating a steep decrease in the reproductive potential due to the unavailability of males (Figure 29).

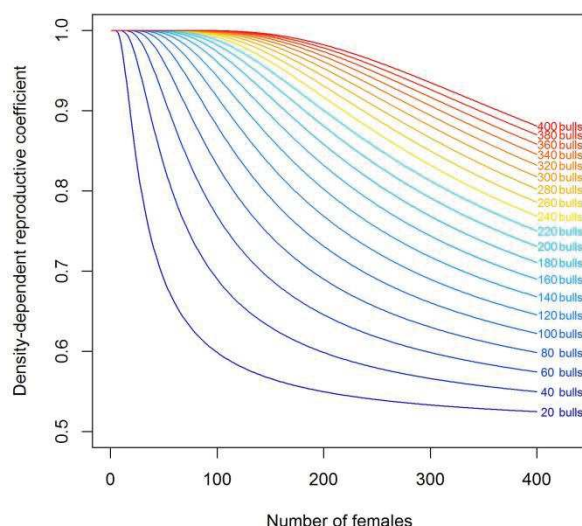


Figure 29 : Density-dependent reproductive coefficient depending on the number of females.

The density-dependent reproductive function is plotted for several male breeding stock levels: from 20 males (blue line) up to 400 (red line), at 20-male intervals. For a given male stock (one line in the chart), the density-dependent coefficient decreases when the number of females increases, meaning that fecundity is negatively impacted by the excess of females relative to breeding males.

3.2.5.6 Population dynamics of the wild pool

The reproduction of captive females depends partially on the Nam Pouy wild pool, as explained above. Given the limited information available on this population, we model the change in Nam Pouy wild population using a population growth rate $wm(t+1) = grw \times wm(t)$, with $wm(t)$ the total population at time t ($wm0 = 68$ the population at time 0) and grw the yearly average growth rate of Nam Pouy population. We select three different growth rates to explore how wild elephant conservation policies could impact the captive dynamics: an increasing wild pool at a rate of 3% per year, a stable wild pool, and a declining wild pool at a rate of 8% per year. This annual decrease of 8% reflects the sharp decline of this population over the last 20 years (see data in Appendixes 8.2.4).

3.2.5.7 Economic decision-making

According to microeconomic theory, owners tend to maximize profit. Because breeding is not compatible with female elephants working, elephant owners make an economic choice between having their female elephants breed or work. Thus, our economic model assumes owners maximize expected profits by choosing whether or not to breed their females, where the expectation arises because owners do not know future elephant prices or logging income with certainty. This decision framework implies a decision rule where owners will

choose to breed up until the expected net present value of breeding exactly equals the opportunity cost of breeding (i.e., foregone timber income). This is equivalent to choosing to breed until the profit ratio (2) is equal to or greater than 1.

At any point in time, the owner compares how much they could receive in net present value by selling a calf after weaning ($Price_{t+3}$), knowing that the survival at 3 years ($surv_3$) is 0.75, with the alternative income from logging during the 3 years. The profit ratio P is therefore:

$$P = \left[surv_3 * \frac{Price_{t+3}}{(1+r)^4} \right] / \left[\frac{Inc_t}{1+r} + \frac{Inc_{t+1}}{(1+r)^2} + \frac{Inc_{t+2}}{(1+r)^3} \right] \quad (2)$$

with $r = 10\%$, the discount rate that takes into account the time value of money or the risk aversion for agricultural projects in Asian developing countries (Fisher et al. 2011; Tomish et al. 2001; Markandya & Pearce 1991). Thus, a profit ratio greater than 1 implies there is an economic incentive to breed females, whereas a profit ratio less than 1 implies that the opportunity cost of foregone logging profits is too large to justify breeding. More information on owners' price estimation methods are given in Appendixes 8.2.2. Finally, the costs related to each activity do not appear in the calculation of the profit because they are limited – elephants are foraging freely in Laos, and the cost of guarding is identical with or without a calf. As a result, feeding and labor costs of the two alternatives do not influence the marginal decision to breed or not.

All monetary values, including incomes and profit, have been converted to constant US dollars (USD) in the year 2000 using the methods of Williamson (Williamson & Officer 2010) in order to correct prices for the high inflation in Laos.

Price and Income

According to supply and demand theory, the price of an elephant can be expressed in terms of the population size given by the demographic components of the model. From the ethno-ecological study conducted among 26 owners who sold elephants between 1994 and 2012, we assigned each reported price to the population estimate given by the model at the time of sale. Elephant price in constant USD follows an exponential relationship:

$$Price = v_1 e^{v_2 population} \quad (3)$$

with v_1 (Est.= 119200, $t = 2.234$, $p = 0.035$) and v_2 (Est.= - 0.003633, $t = - 4.697$, $p < 0.01$).

Working incomes are estimated from IC Suter's 2011 survey (Suter et al. 2013) among 133 elephant owners and keepers, which indicated that average income was equivalent to 4,070 constant USD (i.e., 6.11 times the constant per capita Gross Domestic Product (GDP)). Economists generally use GDP per capita as an indicator of changes in household incomes (Boarini & Johansson 2006).

To estimate prices and incomes after 2012, we applied an average economic growth rate (eco_t) to the owner income and price of an elephant according to the long-term GDP projections from the Asian Development Bank (Asian Development Bank 2011). Moreover, we added stochastic variation to the projected economic growth rate following a normal distribution with mean 1 and a variance of 0.01. Thus, from 2012 and forward, prices at time t equal: $Future\ prices_t = Reg(price_t) \prod_{j=1}^t eco_j * N(1, 0.01)$, with $Reg(Price)$ the price function (Equation 3). Income at time $t+1$ is given by $Income_{t+1} = Income_t * eco_t * N(1, 0.01)$.

3.2.5.8 Linking fecundity with elephant owners' profit

Fecundity is driven by the financial incentive of owners to breed their elephants instead of having them work. When working income exceeds that of breeding (profit ratio $P < 1$), the incentive to breed is low and fecundity is minimal or opportunistic (f_{min}). Fecundity increases as profit increases up to a maximum (f_{max}) set by the biological constraints of the species (Figure 30). Thus, we model fecundity (F) as a logistic function:

$$F = f_{max} \frac{1}{1 + \left(\frac{f_{max}}{f_{min}} - 1 \right) e^{-P\sigma}} \quad (4)$$

where P is the profit ratio (2). The function is bounded respectively by f_{max} the maximal fecundity and f_{min} the opportunistic fecundity. The parameter σ is used to fit the steepness of the function (Verhulst 1845) so that fecundity is maximized when the profit ratio equals 2. We retained a profit ratio of 2 for f_{max} to account for the most extreme case in breeding arrangements (i.e., where all owners consider it profitable to breed their females). Such a rate is a strong incentive for any owner able to pair his female with a wild male. However, the owner of a captive sire usually claims a maximum of one third of the calf value or calf

ownership as stud fee, leaving 2/3 of the calf price to the female's owner (Netvalue = 2/3). In this case the profit for the female's owner should be positive if:

$Price * surv_3 * Netvalue \geq \sum_{t=1}^3 Inc_t$ (derived from Equation 2), or profit ratio $P \geq 2$. As a result, parameter values used in our model are $fmax = 0.155$ (Sukumar et al. 1997), $fmin = 0.02$ (Suter et al. 2014), and $\sigma = 3$.

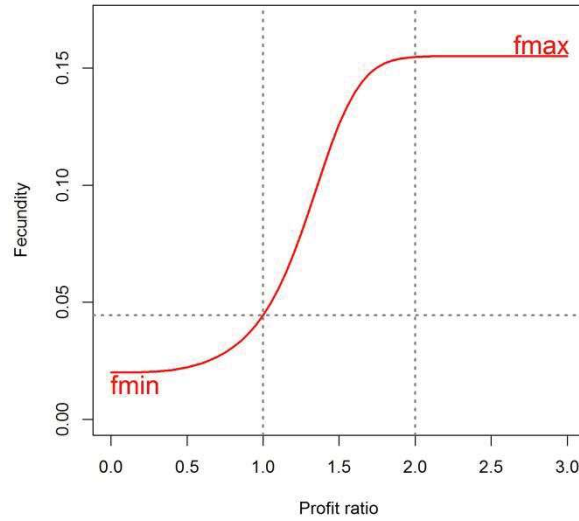


Figure 30 : Fecundity as a function of the owner's profit

Profit is the ratio of the calf's selling price to the income generated by the foregone work. Fecundity is maximum when breeding generates twice as much as working.

3.2.5.9 Sensitivity and Elasticity analysis

The sensitivity analysis allows studying the effect of variation in the model parameters on the population dynamics as measured by their asymptotic growth rate (λ). The asymptotic population growth rate, calculated as the dominant eigenvalue of the matrix, is calculated using the R popbio package (Stubben & Milligan 2007). We used elasticities instead of sensitivities because these metrics take into account the unit in which the demographic parameters are measured and thus make comparisons possible between these parameters.

The elasticity (EL) of parameter α is given by $EL(\alpha) = \frac{(\lambda' - \lambda)}{\lambda(1 + \Delta\alpha)}$ where λ' is the new value of λ after applying a variation Δ to the parameter α .

3.2.5.10 Model calibration

To calibrate our model, we projected the population over 20 years starting from a stable structured population of one thousand individuals in 1992 and compared its demographic

structure with the observed structure in 2012. Population abundance reached 530 individuals, consistent with 2012 estimate of 527 individuals. Moreover, the population structure is highly transient and unstable. A strong bias is observed in favor of elephants over 20 years old and a deficit of females in the 20-29 years age class resulting from our hypotheses (sharp drop in fecundity and export of juvenile females during the last twenty years). The population structure derived in the model (Figure 31) cannot be distinguished from the structure inferred from the 2012 census data (Chisq = 13.6, df = 11, p = 0.25). All analyses were performed with R version 3.2.3 (R Core Team 2017).

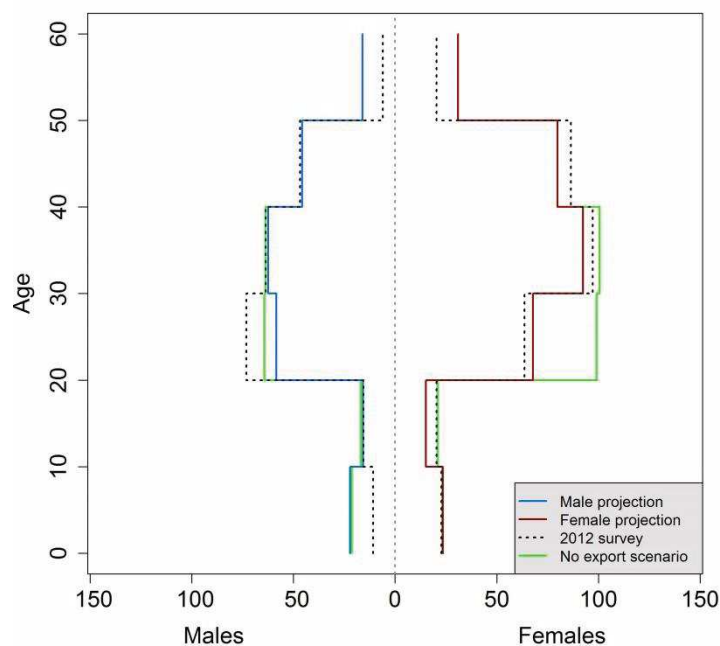


Figure 31 : Age pyramid of captive elephants in 2012

Dotted lines show the number of males and females given by the 2012 census. Solid lines indicate the results of the model projection for year 2012. The green line shows the structure of the population in absence of export, confirming the effect of this practice on the number of females aged from 20 to 30 years.

Data Availability

All data generated or analysed during this study are included in this published article (and its Supplementary Information files – Appendixes 8.2).

3.2.6 References article 2

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Author contributions statement

G.M. and O.G. designed the study. V.C. and G.M. collected the data. G.M. built the model and analysed the data with O.G. and B.R. G.M. wrote the paper with contributions from O.G. and B.R. All authors reviewed the manuscript.

Competing financial interests

The authors declare no competing financial interests.

4 Etude de la structure génétique des éléphants sauvages et de villages au Laos et au Myanmar ; implications en termes de conservation



4.1 Objectifs et résumé de l'article 3

Cette étude vise à estimer la diversité génétique et la structuration génétique des populations d'éléphants sauvages et de villages au Laos et au Myanmar et à discuter de leur viabilité à long terme dans un contexte de restriction des flux de gènes. La réduction de la taille des populations d'éléphants sauvages, leur fragmentation et leur isolement entraîne des risques élevés de perte de diversité génétique et de consanguinité (Frankham et al. 2004). Par ailleurs, il a été montré que, de façon générale chez les animaux et plantes domestiqués, l'élevage en captivité induit une baisse de la diversité génétique et conduit à une divergence génétique avec le pool sauvage (Frankham et al. 2004). La comparaison de la structure génétique entre éléphants sauvages et éléphants de villages vise à tester l'hypothèse d'une différenciation limitée au niveau régional, du fait des pratiques de capture et du maintien des flux de gènes lors de la reproduction. Ce chapitre s'inscrit dans l'analyse des facteurs de résilience du système socio-écologique humain - éléphant de village - éléphant sauvage introduit au chapitre 2. En particulier les changements de pratiques d'élevage, la ségrégation des éléphants de villages et l'isolement des populations sauvages peuvent affecter la diversité génétique et réduire la capacité adaptative (au sens de Folke 2003) du système.

Le génotypage de 122 échantillons sur 11 marqueurs microsatellites a permis de montrer que (i) la diversité génétique était modérée à élevée selon les marqueurs sur l'ensemble des populations testées, (ii) le niveau de consanguinité était faible sinon inexistant, (iii) la différenciation génétique était faible entre le Laos et le Myanmar et non significative à l'intérieur de chacun des pays, (iv) les éléphants nés de femelles de villages ne se différenciaient pas significativement de ceux capturés sauvages.

Face aux risques de perte de diversité et d'augmentation de la consanguinité due à l'isolement des populations, ces résultats suggèrent de considérer les populations d'éléphants sauvages et de villages du Laos et du Myanmar comme une unité de gestion commune. Une telle approche globale et inclusive permettrait de maintenir le plus efficacement la diversité génétique de l'espèce en favorisant les flux de gènes. Cependant les stratégies de conservation actuelles tendent au contraire à restreindre les interactions entre les populations sauvages et captives, ce qui peut menacer à terme la diversité de la

population d'éléphants de villages et limiter son potentiel de conservation en particulier dans le cadre de programmes de réintroduction.

Statut de l'article : en préparation.

4.2 Genetic structure of wild and captive elephants across Laos and Myanmar with implications for management

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4.2.1 Introduction

The Asian elephant (*Elephas maximus*) is an iconic species with strong cultural relationships with humans (Sukumar 2003b; Vidya 2016). Asian elephant populations are in overall decline and classified as endangered by the International Union for Conservation of Nature (IUCN). The total number of elephants has been reduced by at least 50% over the past three decades (Bandara & Tisdell 2004; Hedges et al. 2005; Choudhury et al. 2008). The total population estimates vary between 30,000 to 50,000 individuals, although these figures are considered as overestimates (Hedges et al. 2005; Raman Sukumar 2006; Choudhury et al. 2008). Populations are affected by loss of habitat and fragmentation, human–elephant conflicts, and poaching for ivory (Sukumar 2006; Dublin et al. 2006; Hedges et al. 2005). An estimated 14,500 to 16,000 elephants live in captivity or semi-wild conditions (Leimgruber et al. 2008; Sukumar 2003b). They are generally used by the logging industry or work in villages, in tourism or do representation in temples (Sukumar 2003b; Dublin et al. 2006).

Myanmar is home for 2,000 wild elephants living in expansive and relatively intact forest areas with low human densities (Leimgruber et al. 2011). There are about 5,000 captive elephants of which 3,000 are owned by the government and 2,000 are privately held (Anon 2017a). These elephants are semi-captive and work for the timber industry. At night, captive elephants forage in the forest unsupervised. There, they encounter tame and wild conspecifics (Lahdenperä et al. 2016). Since a decade, Laos is regularly reported to host a population of 600-800 wild elephants (Anon 2017a) living mostly in isolated populations. However an expert workshop (Hedges et al. 2008a) identified five main populations : Nakay 132 individuals [120,149], Nam Pouy <100, Se Sap <30, Nam Ha <20 and Nakai-NamTheun <10, and small groups of isolated individuals. Laos also shelters 450 captive elephants used in the logging industry and more recently for tourism. Most Lao captive elephants live in Sayaboury province. In Thongmixay district, captive females are released part of the year so that they can mate with wild males from the Nam Pouy protected area. They contribute 80% of the captive births in the country (Maurer et al. 2017- chapter 3).

Since centuries, elevated levels of gene flow have been maintained between the captive and wild stocks. Most captive elephants have been caught from the wild to supplement the captive population (Lair 1997). In Laos and Myanmar, captive elephants still share the same

habitat as their wild congeners and interact regularly. Captive females still mainly mate with wild males (Maurer et al. 2017- chapter 3). Gene flow from the captive stock to the wild stock also exist, to a lesser extent, through the release or accidental escape of captive elephants into the wild or through mating of captive males with wild females (Lair 1997; Thitaram et al. 2010). Captive elephants are traded throughout their native country and have nomadic work assignments. Their owners move across the country for months or years according to working opportunities in logging or more recently for tourism (chapter 2). Historical reports also mention trade between countries over larger distances. According to Lair (1997), there have been three main centres for capturing and then selling wild elephants - Bengal, Ceylon, and Pegu (lower Burma). These centres, beyond trading captured individuals of their own abundant wild stocks, also imported animals for resale from similar centres elsewhere.

Phylogeographic studies have been conducted to investigate the origin and evolution of *Elephas maximus*. A large-scale study has shown some degree of nuclear differentiation from the Indochinese peninsula up to northern India, concomitantly with the coexistence of two mitochondrial divergent lineages (Vidya et al. 2009; Vidya et al. 2005). Mitochondrial DNA does not accurately reflect the diversity and viability of a population, as nuclear DNA is the main determinant of phenotypic variation and evolutionary potential (Vidya et al. 2007; Griffiths et al. 1999). In elephants, as in most mammals, males are more dispersive than females. It has been suggested that male-mediated gene flow could limit nuclear genetic differentiation, so that any persistent mtDNA geographic structuring does not reflect nuclear population structures. Contrasting patterns of differentiation between mitochondrial and nuclear DNA have been shown in Northern Indian elephants, suggesting female philopatry, male dispersal and hence male-mediated long distance gene flow (Vidya 2016). While Asian elephants exhibit large home ranges (50 – 1000 km²; Sukumar 2006), male dispersal patterns and distances are not yet clearly understood (Vidya & Sukumar 2005b).

Several studies based on microsatellite markers have investigated genetic diversity within geographically restricted areas in Laos (Ahlering et al. 2011), Vietnam (Vidya et al. 2007), Cambodia (Gray et al. 2014), China (Zhang et al. 2015), Myanmar (Kusza et al. 2018), Sumatra (Moßbrucker et al. 2015), Nepal (Flagstad et al. 2012) or at the country level such as in Thailand (Thitaram et al. 2010) or for the whole island of Borneo (Goossens et al. 2016).

Some of these studies aimed at estimating local population sizes using a capture-mark-recapture methodology and/or assessing social organization based on non-invasive genotyping of dung samples. The different studies have been based on different sets of microsatellite markers including highly polymorphic ones, preventing any global investigation of genetic variation across wider geographical ranges. Apart from India and Sri Lanka, no study has been undertaken across several countries using a large panel of microsatellite markers, and this is especially true for the Indochinese-Burma biogeographic region. The Indochinese-Burma region is home of the largest unfragmented ranges of elephant habitat, hosting either large (>1000 individuals) or small (<1000 individuals) populations (Leimgruber et al. 2003). If India and Sri Lanka shelter higher numbers of individuals separated into distinct populations in a more restricted habitat range, the Indochinese-Burma unfragmented habitats have a high potential for long-term conservation and maintenance or recovery of large wild elephant populations (Leimgruber et al. 2003).

Here, we conducted a population genetics study of Asian elephants from Laos and Myanmar using microsatellite markers on a total of 122 individuals, and estimated the genetic diversity and population structure of the captive and wild genetic pools across these two countries. We investigated whether the high level of differentiation found in mtDNA with the coexistence of two lineages, was confirmed by nuclear DNA. Finally, we discuss the long-term genetic diversity and viability of Lao-Myanmar populations in the context of restricted gene flows and the benefit of considering Lao and Myanmar captive and wild populations as a common Management Unit (MU). A management unit is defined as a set of populations presenting only very limited, if any, differences in allele frequencies at nuclear or mitochondrial loci, regardless of the phylogenetic distinctiveness of the alleles (Moritz 1994).

4.2.2 Methods

4.2.2.1 Study sites

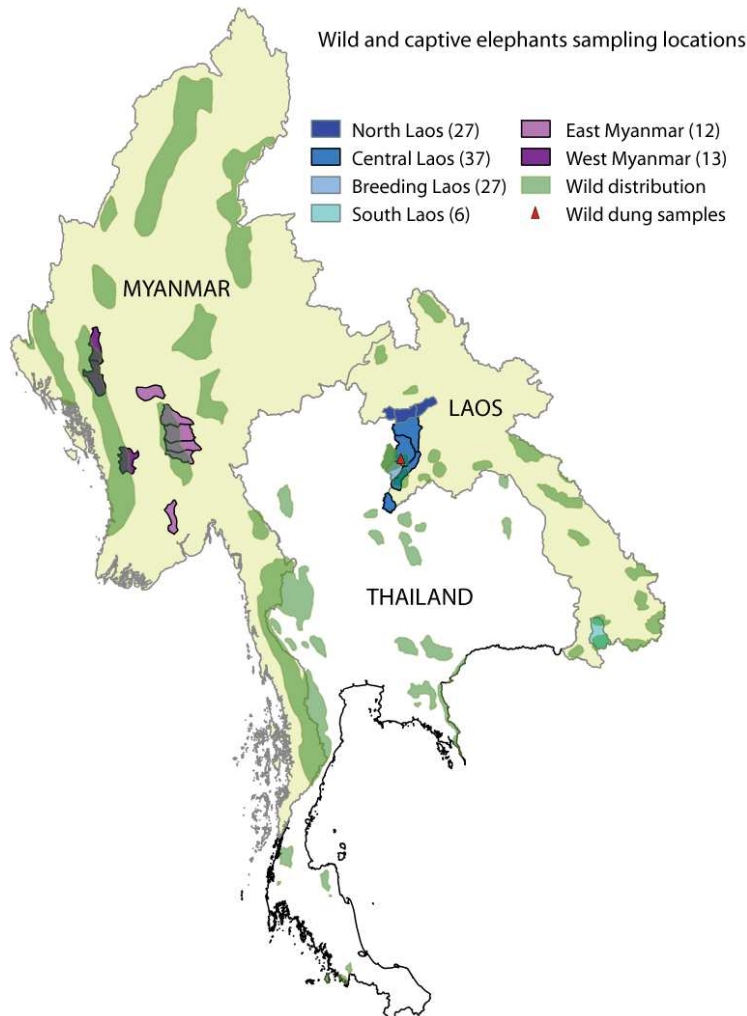


Figure 32 : Wild elephant distribution and sampling sites in Laos and Myanmar

The map was designed with QGIS version 2.14.0-Essen (www.qgis.org). Between parentheses is the sampling size for the genetic analyses.

Myanmar and Laos represent a main part of the Northern Indochina Subtropical Moist Forests, a large ecoregion extending across the highlands of northern Myanmar, Laos, Vietnam and most of southern Yunnan Province (Olson & Dinerstein 1998). Monsoon forests distributed over a mountainous landscape provide a broad range of habitat conditions from deciduous savanna woodland to montane evergreen forests. This ecoregion has the second highest richness value for mammals in Asia and host large populations of Asian elephants (Olson & Dinerstein 1998).

4.2.2.2 Sample collection

A total of 124 captive elephant blood samples (Laos – 99 and Myanmar – 25) were collected across the two countries at the occasion of veterinary controls organized by respectively the Lao Elephant Care and Management Program (Department of Livestock) and the Myanmar Timber Enterprise (Figure 32). Among the 25 Myanmar samples, 18 originated from captive born and 7 from wild caught elephants. Approximately 2 ml of blood were stored in 5 ml tubes filled with 95% ethanol or on FTA cards (Whatman). Samples were stored at room temperature before export. Sixteen samples of wild elephant dung were collected by WWF-Laos rangers in the Nam Pouy protected area. For each sample, approximately 10 g of fresh dung (<48 hours) was collected into 25 ml propylene tubes filled with 15 ml of 90° ethanol. Samples were stored at room temperature before export. Finally, approximately 10 ml of purified DNA extracted from 18 blood samples of Bornean elephants were provided by the authors of Goossens et al. (2016).

4.2.2.3 Export

An authorization to export samples was issued by the Lao department of Forest resource management, Lao-Cites management authority (# 0424 - 09/03/2017). An authorization to import biological samples has been issued by French veterinary services, ministry of Forest, Agriculture and Environment (registration number 2017043, 17/03/2017). All samples have been sent to the CEFÉ laboratory (Montpellier, France) for extraction and genotyping.

4.2.2.4 Laboratory

DNA was extracted from blood and dung samples upon delivery at CEFÉ. To minimize the possibility of contamination, extractions were performed in a laboratory designated exclusively for the extraction of DNA from non-invasively collected samples. Negative controls were processed concomitantly to insure non-contamination of reagents. DNA was extracted using QIAamp DNA Stool Mini Kit protocol modified as follows: overnight incubation at 55°C for the dung samples preserved in ethanol; overnight digestion of lysis with Buffer ASL and proteinase K at 55°C.

The purified DNA was eluted into 50 µl of elution buffer and stored at -20° C. We carefully selected 11 loci after testing an initial panel of 29 different markers based on their

polymorphism, amplification yields and non-ambiguous reading from blood samples. The selected loci were: EMU03, EMU07, EMU08, EMU11, EMU12, EMU14, FH60, FH94, FH103, LafMs05, LA2 (Nyakaana & Arctander 1998; Comstock et al. 2000; Eggert et al. 2000; Kongrit et al. 2008). Monoplex PCR were carried out for loci FH94, EMU08, EMU12 in 10 µl volumes, using 2 µl DNA, 0.2 µM of each primer, Qiagen Taq 1x and water. Multiplex PCR were carried in 10 µl volume using DNA 2µl, 0.2 µM of multiplex primers, Qiagen Taq 1x and water. The PCR consisted of an initial denaturation step at 95°C for 15 minutes, followed by 30 cycles of three steps: denaturation at 94°C for 30 seconds, followed by annealing for 90 seconds, and extension at 72°C for 1 minute. A final extension was performed for 30 minutes at 60°C. PCR products were electrophoresed, along with the internal size standard GS500LIZ, in an ABI 3500XL 24-capillary-array Genetic Analyzer (Applied Biosystems) in the Genseq-CEMEB Facility in Montpellier. PCR and genotyping were repeated 3 times for dung samples. Genotypes were scored using the GeneMapper software version 4.0 (Applied Biosystems). The observations listed by Fernando et al. (2003) were followed as guidelines for scoring alleles from electrophoregrams.

4.2.2.5 Data analysis

The frequency of null alleles, scoring errors and allelic dropout in the overall microsatellite data set were investigated using MICRO-CHECKER 2.2.3 (Van Oosterhout et al. 2004). Deviations from Hardy–Weinberg (HW) within loci and linkage equilibrium (LE) between loci were tested separately for each population using Fisher’s exact tests as implemented in GENEPOP 4.4 (Rousset & Raymond 1995). The number of alleles per locus (N_a), observed (H_o) and expected (H_e) heterozygosities, per-locus F_{is} , pairwise F_{st} values and analysis of molecular variance (AMOVA) were calculated in ARLEQUIN v.3.5.2.2 (Excoffier & Lischer 2010). Evidence of a recent population bottleneck was assessed using a test for heterozygosity excess (Cornuet & Luikart 1997) and a graphical test to detect mode shifts in allele frequency distributions (Luikart et al. 1998). Stepwise and two-phase models of mutation and 1000 randomizations were implemented in the program BOTTLENECK v.1.2.02 (Luikart and Cornuet 1999). Structuring into distinct populations across Laos and Myanmar and wild/captive individuals was investigated using Bayesian clustering as implemented in STRUCTURE v. 2.3.4 without spatial information (Falush et al. 2003). STRUCTURE was used under a model assuming admixture and allowing for correlation of allele frequencies

between clusters. We run models with and without population affiliation (Hubisz et al. 2009). We conducted ten runs for each value of $K = 1-8$ and each run consisted of a 10,000 burn-in followed by 100,000 iterations. The most likely value of the number of clusters was assessed using STRUCTURE harvester (Earl & vonHoldt 2012).

4.2.3 Results

4.2.3.1 Genetic diversity

We obtained 122 complete genotypes out of the 124 blood samples. Two samples presented missing data at respectively 2 and 8 loci and were excluded from further analyses. Both the Lao and Myanmar populations presented high levels of genetic diversity with a mean number of alleles per locus of respectively 5.8 (sd 2.4) and 5.3 (sd 1.7) over the 11 loci (Table 4). Mean number of alleles was similar to previous results from Cambodia and Thailand (Gray et al. 2014; Thitaram et al. 2010), but lower than the 8.1 average allelic richness found in a Lao wild population (Ahlering et al. 2011). We found moderate to high levels of observed heterozygosity depending on locus, ranging respectively for the two countries from 0.39 to 0.84 and 0.48 to 0.84. All loci agree with Hardy-Weinberg expectations. There was no evidence for large allele dropouts. Null alleles may be present at locus EMU08 in the North-Laos population and FH94 in the Myanmar-East population (12 samples). Null allele presence has been previously reported for loci FH94 and LA2 (Gray et al. 2014). No significant linkage disequilibrium was observed between pairs of loci across all sites (Fisher's method).

LAOS						MYANMAR				
Locus	Num. gene copies	Num. alleles	Obs. Het.	Exp. Het.	HW exact test p-value	Num. gene copies	Num. alleles	Obs. Het.	Exp. Het.	HW exact test p-value
EMU8	194	4	0,392	0,427	0,212	50	3	0,560	0,474	1,000
FH60	194	5	0,660	0,751	0,164	50	5	0,800	0,780	0,516
FH94	194	7	0,722	0,800	0,047	50	5	0,520	0,757	0,089
LafMs05	194	6	0,588	0,573	0,751	50	5	0,560	0,566	0,402
EMU07	194	11	0,835	0,826	0,655	50	9	0,840	0,856	0,557
EMU14	194	6	0,804	0,772	0,375	50	7	0,800	0,756	0,726
FH103	194	3	0,515	0,517	0,910	50	4	0,720	0,634	1,000
LA2	194	5	0,649	0,611	0,863	50	4	0,480	0,455	0,767
EMU03	194	4	0,639	0,656	0,725	50	4	0,680	0,633	0,939
EMU11	194	4	0,649	0,599	0,281	50	5	0,680	0,602	0,942
EMU12	194	9	0,526	0,595	0,178	50	7	0,720	0,749	0,535
Mean	194	5,82	0,634	0,648		50	5,27	0,669	0,660	
s.d.	0	2,40	0,128	0,126		0	1,74	0,123	0,130	

Table 4 : Parameters of genetic diversity in Asian elephants

Samples from Laos (N= 97) and Myanmar (N = 25).

The BOTTLENECK analysis showed that there was no consistent or strong signal for a departure from mutation drift equilibrium. The Wilcoxon test showed no evidence of heterozygosity excess under either the Two Phase Mutation Model or the Stepwise Mutation Model. The allele frequency distribution showed the expected L-shaped distribution. Therefore, no sign of a recent bottleneck event was revealed by our analysis. Thus, the panmixis hypothesis and an apparent absence of selection were supported by our analyses among and within sites.

4.2.3.2 Population structure

Analysis of Molecular Variance indicated that most of the variance is found within individuals (96.1 %) with limited, though significant, separation between the 2 countries. The pairwise Fst value of 0.026 between these 2 groups was significant ($p < 10^{-3}$, see Appendixes 8.4.1). Between sites, the highest but moderate level of Fst was observed between the Laos-South and Myanmar-East sites at 0.068 (Figure 33). The Myanmar-East site was significantly different from all four Lao sites, with Fst values ranging from 0.029 to 0.068, but not from Myanmar-West. Myanmar-West differed significantly only from the Breeding and the North-Laos sites (0.063, $p < 0.027$). No statistically significant Fis value was found at the site level.

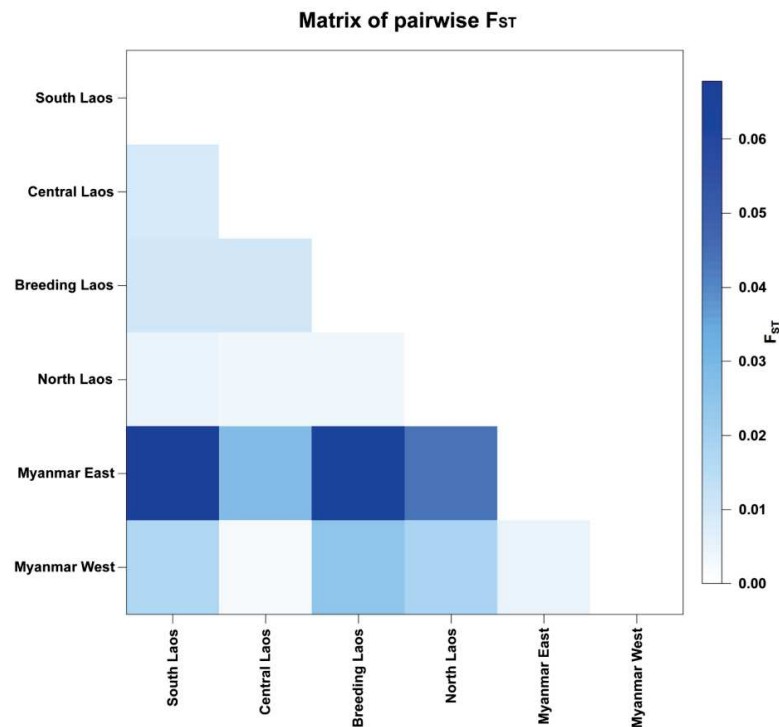


Figure 33 : Population Pairwise Fst matrix

Bayesian clustering analysis of microsatellite genotypes using STRUCTURE with no prior information did not evidence any clear structure, despite log-likelihood $\ln P(X|K)$ and the difference in the number of clusters Delta K values both suggesting $K=2$ (Appendixes 8.4.2). However, when using the 6 sampling locations as priors, STRUCTURE clearly segregated the two Myanmar sites from the four Lao ones, confirming the presence of a limited genetic differentiation into a Laos and a Myanmar gene pool as suggested by pairwise Fst analysis (Figure 34a). To better discriminate the Lao-Myanmar gene pools and avoid any misinterpretation of $K=2$ since ΔK cannot be calculated for $K = 1$ (Evanno et al. 2005), we further tested the genetic sub-structure of the Lao-Myanmar pools by adding control genotypes from 18 Bornean elephants (*Elephas maximus borneensis*), a population which is believed have been isolated for 15-18,000 years (Sharma et al. 2018). Pairwise Fst values between the Borneo samples and our study populations ranged from 0.31 to 0.35, confirming a strong differentiation with the Lao-Myanmar group. Regarding population structure, both simulations, with or without LOCPRIOR options, indicated 3 genetic clusters with Borneo on one side and a difference in the frequency of assignation of individuals to cluster between elephants originating from Lao and Myanmar on the other side (Figure 34c). Furthermore, we tested if the origin of Myanmar elephants, whether captive born or wild

caught, instead of their sampling location, affected the population structure. We found that wild born individuals could not be differentiated from the captive born ones within Myanmar while retaining together a weak differentiation from the Lao populations (Figure 34b).

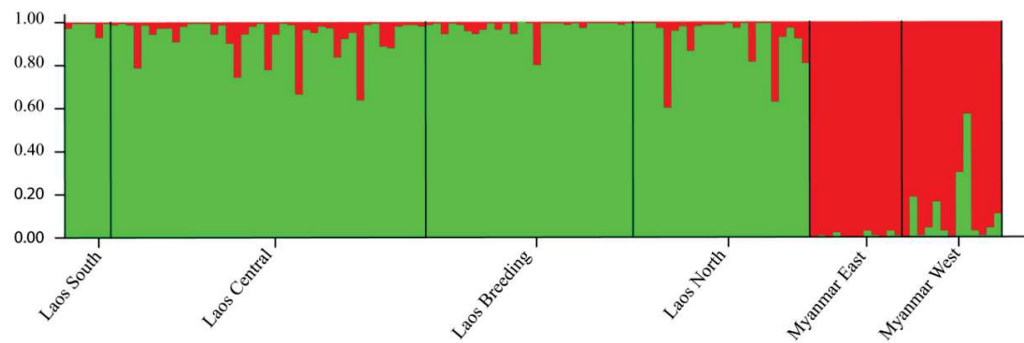


Figure 34a) Model-based structuring (K=2) of Lao-Myanmar populations using sampling location prior

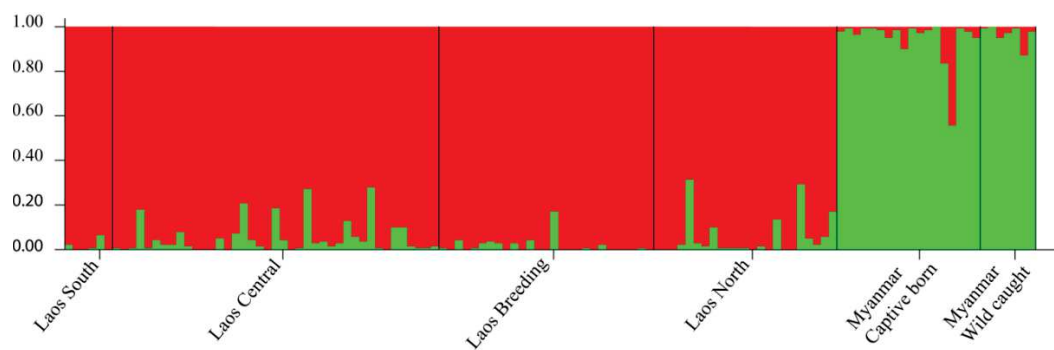


Figure 34b) Model-based structuring (K=2) of Lao-Myanmar populations using sampling location in Laos and captive born versus wild caught priors for Myanmar.

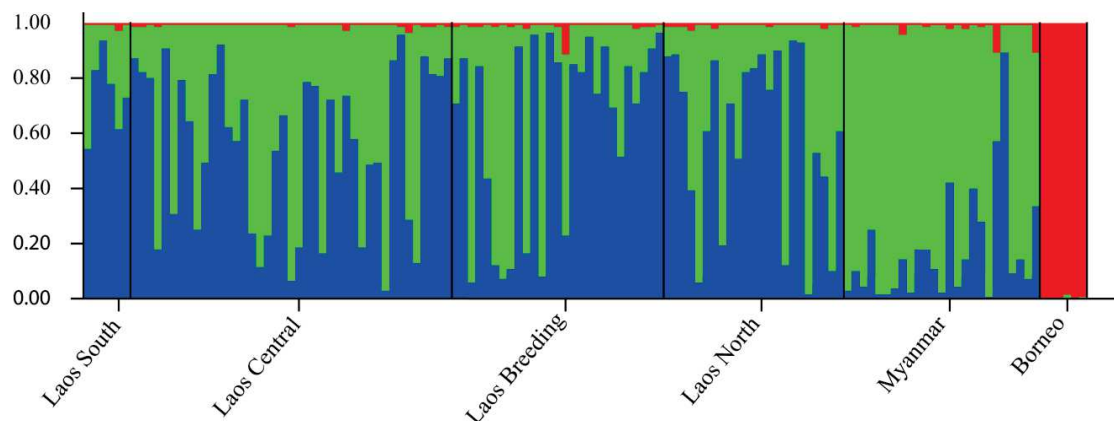


Figure 34c) Model-based structuring (K=3) of Lao, Myanmar and Borneo populations without prior location

Figure 34 : Individual assignment probabilities of Asian elephants to genetic clusters using the model-based program STRUCTURE (Falush et al. 2003)

4.2.3.3 Genotyping of non-invasive samples from dung and its comparison with genotyping using blood

Dung samples were collected from both captive and wild elephants. Among the 16 dung samples from Lao wild elephants, 8 were scored for at least 5 loci. Genotyping success rate reached 50% of the total number of samples based on a single extraction followed by 3 PCR replicates. Locus FH94 did not amplify, EMU08 and EMU012 were found monomorphic and presented missing data. These were the 3 loci whose amplification profiles were the most ambiguous and difficult to read in the blood samples. We directly observed allelic dropouts in 3 dung samples of captive elephants for which we also collected blood. Four loci were found in Hardy-Weinberg disequilibrium (FH60, EMU07, EMU14, EMU11). Mean number of alleles (2.8) and observed heterozygosity (0.38) were much lower than respective levels observed in blood samples from surrounding captive populations, despite the perpetuating uncontrolled mating between captive females and wild males. As a result, the genetic structure and diversity could not be reliably compared between captive and wild elephants from Laos when using blood on one hand and non-invasive genotyping from dung on the other.

We further investigated the potential difference between genotypes obtained from blood and non-invasive samples using the Bornean elephant population dataset provided by Goossens et al. (2016) as an example. We genotyped 18 individuals over our 11 loci using DNA extracted from blood and tissue of Bornean elephants provided by Goossens and colleagues. We found only 6 genotypes out of the 18 individuals, consistent with Fernando et al. (2003) findings of 5 unique genotypes over 15 of the same DNA samples using 5 other loci. Goossens and colleagues also shared raw data of 224 genotypes obtained after extraction from dung samples for which we have 6 loci in common (EMU03, EMU07, EMU08, EMU11, EMU12, EMU14). Over these 6 common loci, the Observed Heterozygosity in dung samples from 4 different locations ranged from 0.16 to 0.44, while for blood samples H_o was scored at 0.088. Expected heterozygosity in dung ranged from 0.21 to 0.48 compared to 0.095 for blood. Mean number of alleles was also lower in Bornean blood samples (1.50) than in any other population (2.00 to 4.17).

4.2.4 Discussion

We genotyped 122 captive elephants from Laos and Myanmar. Both countries showed moderate to elevated levels of genetic diversity as measured by microsatellite loci with a number of alleles per locus varying from 3 to 8.7, observed heterozygosity per locus ranging from 0.48 to 0.86 and a low degree of inbreeding, if any, consistent with a study using blood samples from Asian elephants in Thailand (Thitaram et al. 2010) and Myanmar (Kusza et al. 2018). Pairwise F_{st} values and Bayesian clustering showed a weak differentiation between a Lao and a Myanmar gene pool but not between groups of individuals within each country. The use of the sampling location as default information has been shown to allow the correct inference of population clustering and ancestry when the sets of data used present weak structure signals that cannot be detected by basic models available for STRUCTURE (Hubisz et al. 2009). Wild caught and captive born elephants from Myanmar did not differ significantly, showing that the captive and wild populations in Myanmar are homogenous. The molecular divergence of the Bornean population shown by a mitochondrial haplotype unique to the island (Fernando, T N C Vidya, et al. 2003) is also supported by nuclear differentiation in allele frequencies and the presence of two alleles that were not found in the Lao-Myanmar group. Genotyping of 16 non-invasive samples from wild elephant dung yielded incomplete genotypes that did not allow any simple comparison between the wild and captive pools of individuals in Laos. However, results from dung samples should be treated with caution due to the small number of samples and missing data. It is likely that there are allelic dropouts in these genotypes, as we only made 3 PCR replicates. Mean number of alleles (2.8) and observed heterozygosity (0.38) were much lower than respective levels observed in blood samples from surrounding captive populations, despite the perpetuating uncontrolled mating between captive females and wild males. Considering the permanent gene flow between wild and captive elephants in this region of Laos, and the non-differentiation between wild caught and captive born elephants in neighbouring Myanmar, it further supports the idea of incomplete genotyping of the wild samples due to genotyping errors in non-invasive samples.

4.2.4.1 *Genotyping reliability of samples from dung*

Amplification success rates of DNA extracted from dung appear to be highly variable. For instance, Gray et al. (2011) mentioned an average amplification success across all loci and samples of 68%, with considerable variation among collection teams, ranging from 50% to 97%, while Moßbrucker et al. (2015) reported an average amplification rate of 78% and Flagstad et al. (2012) 68%. The age of the dung samples (a few hours up to a few days) is crucial to successful amplification, though the sensitivity of primers at individual loci also plays a role (Vidya & Sukumar 2005a). We carefully selected 11 loci after testing an initial panel of 29 different markers based on their polymorphism, amplification yields and non-ambiguous reading from blood samples. The low amplification rate, missing data at some loci and allelic dropouts observed in our dung samples probably resulted from the age of dung for which we did not have reliable information, rather than the sensitivity of our primers. The reliability of genotypes obtained from non-invasive samples has been widely discussed (Vidya & Sukumar 2005a; Fernando, T. N C Vidya, et al. 2003; Buchan et al. 2005) with attempts to assess genotyping errors due to polymerase slippage, allelic dropouts, null alleles, spurious alleles or contamination. Specific collection, extraction, amplification and scoring protocols have therefore been recommended to minimize such bias (Fernando, T. N C Vidya, et al. 2003). Queirós et al. (2015) noticed that researchers tend to select the most polymorphic markers (which are also the most difficult to score correctly) while working on non-invasive DNA, leading to overestimation of the genetic diversity. Possible sources of overestimation in genetic diversity from wild elephant dung samples have already been mentioned (Goossens et al. 2016; Ahlering et al. 2011).

Comparing our data obtained from blood samples with results from other studies using non-invasive sampling, we observe that heterozygosity of the Nakay wild elephants in central Laos (0.75; Ahlering et al. 2011) was higher than our estimate (0.63) or the one of Fernando et al. (0.48; 2003) across Laos. All of the 5 loci shared between our study and the Ahlering study (EMU03, EMU07, EMU12, EMU14, FH95) showed a higher number of alleles in dung samples than detected in blood samples of a captive population in central Laos presenting a similar number of individuals. Locus EMU07 showed the largest variation with Ahlering scoring a total of 15 different alleles, while we found only 10 in the Lao Central population

and 12 when considering the whole dataset from both countries. This higher number of alleles may be due either to errors in allele size scoring or to lower genetic diversity in captive elephants in Laos. The data from Myanmar suggests that there is no reduction in genetic diversity of the captive stock. Further, our results for Laos comparing dung samples and blood samples are similar to those obtained for Bornean elephants. Indeed, for Borneo a larger number of alleles were detected in dung samples than in blood samples. We conclude that genotyping using dung samples readily leads to errors in allele size scoring, and hence in the different estimates that can be made using these genotypes.

Based on these observations, we may add some recommendations to the detailed protocols previously defined. Amplification success rates should be systematically mentioned in any study, as a prior indicative of the genotyping quality of the samples. Markers should be tested beforehand on a large panel of blood/dung samples, taking advantage of the large and genetically similar captive populations across the region. Any marker showing null alleles, possible slippage, allelic dropouts or slightly ambiguous scoring from blood samples should be avoided in non-invasive genotyping studies. While some highly polymorphic markers could be useful in the framework of capture-mark-recapture protocols, genetic diversity inferred from these studies should be assessed using a restricted panel of markers chosen for their reliability and representativeness of Asian elephant genetic diversity across the region.

4.2.4.2 Threats due to genetic isolation

Our study showed that population differentiation was weak using nuclear DNA over 1500 km from South Laos to central Myanmar, confirming the hypothesis of male locational dispersal and male-mediated gene flow observed in Northern India (Vidya 2016). Captive and wild pools could not be differentiated in Myanmar, and this is probably also the case in Laos. Similarly Thitharam et al. (2010) concluded that the captive pool genetically represents the wild one in Thailand. Over the past decades, habitat loss and fragmentation have broken up many of the larger habitat patches into smaller patches that now support small isolated herds of wild elephants (Dublin et al. 2006) especially in Thailand and Indochina (Hedges et al. 2008b). Wild elephant populations are affected by population size reduction, fragmentation and gene flows disruption leading to high risks of rapid loss of diversity and

inbreeding. The captive stock is exposed to similar threats. The traditional extensive form of captive elephant management is disappearing. Seasonal release of captive elephants that, once enabled breeding among captive females and wild males, is restricted because of agricultural land expansion or access ban in protected areas (chapter 2). Captive elephants are increasingly kept in suburban areas isolated from their wild congeners. Fecundity is also impeded by the limited availability of captive breeders (Maurer et al. 2017 - chapter 3).

Small effective population sizes at local level will automatically lead to loss of genetic diversity, and current levels of heterozygosity cannot be upheld on the long term (Frankham et al. 2004). Unlike the Bornean population that viably sustains high level of inbreeding, wild and captive populations from the Indochina-Myanmar complex have never been selected on their resistance to inbreeding. They should therefore be highly sensitive to inbreeding depression. Low nuclear diversity has been revealed in a tiny remnant herd of 12 elephants in Vietnam showing the signature of a recent population bottleneck, leading to close monitoring of possible physical signs of inbreeding depression (Vidya et al. 2007). Consequently, the maintenance of gene flow within a large pool of individuals is of paramount importance for the conservation of these isolated herds. Based on the weak genetic differentiation, if any, and similarity in alleles frequencies at nuclear loci (Moritz 1994), we recommend to consider the wild and captive pools of individuals from Laos and Myanmar as a global homogeneous Management Unit (MU) in the design of conservation strategies and management actions at local and sub-regional levels. The geographical demarcation of this MU should be further investigated by adding samples originating from neighbouring countries. The challenge is to determine whether the area ranging from peninsular Malaysia, Thailand, Cambodia, Vietnam, Laos, Myanmar, China and up to northern India constitutes a genetically homogeneous genetic unit in elephants.

4.2.4.3 Maintaining gene flows

The potential value for conservation of a large population of captive elephants has been recognized (Dublin et al. 2006). If captive populations are to form reservoirs or insurance populations to support the survival of isolated wild populations, then it is important that their genetic diversity is representative of extant diversity in the wild (Sato et al. 2017). There will likely be more translocation of elephants in the future as moving elephants,

especially small pocketed herds, will become a necessity as part of meta-population management programs (Anon 2017a). However, translocating wild elephants has proved to be risky as it often results in Human Elephant Conflicts (HEC). Solving the inbreeding problem by releasing wild elephants will increase HEC (Anon 2017a). Semi-captive elephants that are used to live and feed in their natural habitat can ultimately play the role of ‘temporary’ migrants into inbred wild populations avoiding the risks associated with the translocation of wild individuals. In this context, the captive elephant diversity should be actively managed over the long term. However current management actions focus on monitoring the captive population in order to reduce the threats that illegal captures could pose to wild elephant populations (Dublin et al. 2006). Potential deleterious alleles in wild populations may become more prevalent in captivity. Also, morphological and behavioural changes due to captivity may finally alter the wild population following reintroduction of captive individuals (Hedges et al. 2018; Frankham et al. 2004). As a consequence, current conservation strategies tend to restrain the interactions between the wild and captive pools. However, these strategies may eventually threaten the diversity of the captive pool and in the long term limit its conservation value for the species. Our results did not demonstrate any evidence of such effects on the Myanmar captive population but show that the pool of captive elephants has a potential role in maintaining gene flows, and we encourage others to explore this role further.

4.2.5 Conclusion

Wild and captive populations of Asian elephants have been closely interlinked for millennia. Today both pools are exposed to similar threats such as poaching, habitat destruction, isolation and potential loss of diversity. Governments, managers and conservationists should favour cooperation and a global approach considering the potential of a unique management unit extending from Laos to Myanmar and probably even wider. Captive and wild pools should be managed using an inclusive and global approach to maintain the species’ abundance and genetic diversity. Finally, researchers should further investigate the structure and range of management units using methodologies that will allow better cooperation and exchange of data between them. To do so, the definition of a common set of microsatellite markers would greatly improve the understanding of Asian elephant population genetics. Increased regional cooperation and standardization in population

management and genetic studies of European carnivores is advocated (de Groot et al. 2016). Similar strategies should be implemented for the Asian elephant. The use of SNPs and genetic markers associated with next-generation sequencing should be developed as they can easily be compared between studies and laboratories and are less sensitive to DNA degradation.

Author contributions statement

G.M., F.K and O.G. designed the study. V.C., J.L., Z.M.O and G.M. collected the samples in Laos and Myanmar. G.M. and MP.D. performed laboratory work, G.M. and F.K. performed analyses, G.M. wrote the paper with contributions from F.K., F.K. and O.G. revised the manuscript.

4.2.6 References article 3

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5 DISCUSSION

L'objectif de cette thèse était de qualifier et quantifier les interactions entre éléphants sauvages et captifs afin de mieux comprendre leurs dynamiques et leurs rôles dans la survie de l'espèce. Nous avons analysé l'évolution récente du SSE homme-éléphant et les conséquences de cette évolution sur les relations humain-éléphant, les dynamiques de populations et la conservation de l'espèce au Laos en particulier. Dans la suite, nous discutons des conditions de la résilience de ce système et explorons différents scénarios d'évolution de ce système à l'avenir en nous interrogeant sur le possible processus de domestication de l'espèce.

5.1 Evolution des interactions éléphants sauvages-éléphants de villages au Laos et élargissement aux autres pays de l'aire de répartition de l'espèce

5.1.1 Interactions éléphants sauvages et éléphants de villages au Laos

Nous avons montré que la division et la marchandisation récentes des ressources naturelles ont entraîné une diminution des interactions et une ségrégation croissante entre les populations d'éléphants de villages et leurs congénères sauvages au Laos (chapitre 2). D'une part, la population d'éléphants sauvages décline et subit de fortes pertes de son habitat. Ceci a conduit le gouvernement à promouvoir une politique de sanctuarisation des populations sauvages dans des aires protégées, interdisant l'accès aux hommes comme aux éléphants de villages. D'autre part, les forêts secondaires et les jachères où pâturaient les éléphants de villages ont diminué. Les éléphants sont maintenant enchaînés la plupart du temps, voire parqués aux abords des villes et des centres touristiques, restreignant d'autant leurs interactions avec les populations sauvages. L'intensification du travail des éléphants dans l'industrie du bois et plus récemment dans le tourisme a renforcé par la même la mise à l'attache des éléphants de villages et l'abandon de la pâture libre. Nous avons ainsi montré la prévalence à court terme des conditions économiques sur la dynamique de la population des éléphants de villages, et le rôle à long terme des interactions sauvage-village à travers la reproduction croisée (chapitre 3). Nous avons également montré que le système était en phase de transition au Laos, les propriétaires adoptant différentes stratégies en réponse à

ces nouvelles conditions socio-écologiques. Dix répondants nous ont indiqué que leur éléphant était en contact régulier ou occasionnel avec des éléphants sauvages, tandis que 14 répondants ont indiqué que leur éléphant n'était jamais en contact avec des sauvages. Enfin, nous avons montré dans le chapitre 4 que les populations d'éléphants sauvages et de villages présentaient les mêmes niveaux de diversité génétique et constituaient une unité de gestion homogène au sens génétique. Ainsi, les interactions entre éléphants sauvages et éléphants de villages perdurent au Laos même si elles ont fortement diminué au cours des dernières décennies.

5.1.2 Interactions éléphants sauvages et captifs dans la région

Aucune analyse détaillée sur les interactions entre populations sauvages et captives d'éléphants n'a été conduite dans les autres pays de l'aire de répartition. Cependant, des tendances peuvent être déduites des différentes études publiées à ce jour sur les populations sauvages et/ou captives. Nous illustrerons brièvement les différentes situations existantes en prenant l'exemple de quatre pays : le Myanmar, l'Inde, la Thaïlande et l'Indonésie.

A l'instar du Laos, le Myanmar pratique toujours un élevage traditionnel d'éléphants en semi-captivité employés principalement par l'industrie forestière. Le débardage du bois est toujours pratiqué à large échelle au Myanmar, sous l'égide de la Myanma Timber Entreprise (MTE), entreprise d'état dépendant du Ministère de l'Environnement et des Ressources Naturelles, qui possède près de 3 000 éléphants. Deux mille éléphants supplémentaires appartiennent à des propriétaires privés auxquels le ministère octroie des quotas de bois selon un système similaire à celui pratiqué au Laos. Ces éléphants vivent dans des camps forestiers, ils sont relâchés après leur travail et pâturent librement. Chaque année, les éléphants de MTE sont libérés complètement pendant les quatre mois les plus chauds. La reproduction n'est pas contrôlée par les cornacs et la plupart des naissances sont dues à la saillie de femelles captives par des mâles sauvages (Lahdenperä et al. 2016). Enfin, le Myanmar a interdit en 1995 la capture d'éléphants sauvages pour compléter la population captive, mais a continué à capturer des éléphants sauvages dans le cadre de résolution de conflits humains-éléphants. Le mode d'élevage en semi-captivité et le système socio-écologique observés au Myanmar semblent correspondre à la situation existant au

Laos il y a quelques années, avant que le pays n'opère la transition décrite dans le chapitre 2. Le Myanmar se différencie des autres pays, comme nous allons le voir ci-après, par le niveau et le maintien des interactions entre ses populations sauvages et captives.

La plupart des autres pays ont entamé une transition vers un système fortement dualiste. L'Inde, qui compte les plus importantes populations sauvages et près de 3 000 éléphants captifs, présente de fortes disparités régionales en termes d'interactions sauvages-captifs (Baskaran et al. 2011; Vanitha et al. 2011). Le nord-est abrite la deuxième population sauvage (près de 9 000 éléphants) et la principale population d'éléphants de villages (1 500 individus, 55%) appartenant principalement à des propriétaires villageois engagés, comme au Myanmar et au Laos, dans le débardage du bois au sein de camps forestiers. Cette exploitation traditionnelle maintient des interactions importantes entre éléphants sauvages et captifs, même si l'interdiction récente du débardage par le gouvernement remet en cause cette situation (Lainé 2013). Le sud de l'Inde abrite la principale population sauvage (14 000 individus) et la seconde population captive (environ 900 individus, 25%) mais celle-ci est beaucoup plus isolée des populations sauvages car employée principalement dans des camps de tourisme ou des temples.

La ségrégation entre populations sauvages et captives semble beaucoup plus avancée en Thaïlande. D'une part, l'évolution des conditions socio-écologiques telles que le développement des surfaces agricoles et le développement économique en général, ou la sanctuarisation des aires protégées, a précédé celle du Laos ou du Myanmar de plusieurs décennies. En particulier, l'interdiction de l'exploitation du bois dans les années 90 a bouleversé l'économie des éléphants captifs. De nombreux propriétaires se sont retrouvés sans ressources. À l'extrême, certains propriétaires ont été conduits à mendier avec leurs éléphants dans les rues de Bangkok (Lair 2002). Aujourd'hui, la quasi-totalité des éléphants captifs est employée dans des camps touristiques éloignés des zones de présence des éléphants sauvages. Depuis peu se développent des camps touristiques, appelés sanctuaires, proposant aux touristes d'observer des éléphants captifs en semi-liberté (Kontogeorgopoulos 2009). Toutefois, la localisation de ces camps ne permet pas de maintenir le lien traditionnel entre éléphants captifs et sauvages. La faible natalité et la forte demande de l'industrie touristique a induit un commerce illégal d'éléphants capturés sauvages en provenance du Myanmar voisin (Nijman 2014). Enfin, la Thaïlande a

expérimenté la réintroduction à l'état sauvage d'éléphants captifs. Un total de 104 individus a été relâché avec des résultats contrastés liés en particulier aux comportements de ces éléphants : défaut de socialisation intra-groupe, raids sur les cultures, etc. (Thitaram et al. 2015).

Enfin, l'Indonésie n'a pas de tradition d'élevage des éléphants mais l'île de Sumatra compte 467 éléphants sauvages capturés à la suite de conflits avec l'homme.



Figure 35 : Position relative de 5 pays représentatifs sur un gradient décroissant des interactions entre éléphants sauvages et captifs

Si les situations varient selon les 12 pays de l'aire de répartition de l'éléphant d'Asie, la dynamique des systèmes socio-écologiques humain - éléphant sauvage – éléphant captif tend globalement vers un dualisme et une ségrégation croissante entre ces derniers (Figure 35). Les systèmes traditionnels sont confrontés à de nouveaux enjeux qui remettent en question leur pérennité.

5.2 Résilience du système socio-écologique humain-éléphant

Nous reprenons le cadre conceptuel de la résilience des systèmes socio-écologiques présenté au chapitre 1.3.2 pour évoquer l'évolution des dynamiques socio-écologiques au niveau régional et historique, puis l'envisager dans le cas du Laos contemporain.

5.2.1 Conditions du retrait ou de la persistance des éléphants, une approche historique

Sur l'ensemble de l'Asie, le nombre total d'éléphants capturés depuis le 16^{ème} siècle est estimé entre deux et quatre millions. Au cours du 20^{ème} siècle, Sukumar (2003) estime que plus de 100 000 éléphants d'Asie ont été capturés pour le travail et la représentation dans les temples et les zoos. Trautmann (2015), à travers une approche d'histoire environnementale, revient sur les conditions du retrait ou de la persistance des éléphants d'Asie en comparant les conditions qui prévalaient en Chine et en Inde en particulier. En Inde, l'utilisation d'éléphants pour la guerre, puis comme animaux de bât pour les travaux

forestiers, a entraîné la création de réserves d'éléphants sauvages et leur protection légale afin d'assurer un accès durable à cette ressource. L'exemple de la Chine illustre, quant à lui, les effets de l'absence de mesures de conservation des éléphants sauvages. Alors que les rois indiens protégeaient les éléphants sauvages, même contre l'intérêt de leurs agriculteurs, en Chine, les rois avaient tendance à éradiquer les grands animaux sauvages des forêts, dont l'éléphant, afin de rendre ces forêts plus sûres pour l'humain et de les convertir en terres agricoles. D'une manière plus générale, Trautmann oppose une économie basée sur la valorisation des ressources naturelles en Inde, à une économie orientée vers la mise en valeur du foncier par le travail en Chine. Par conséquent, selon Trautmann, les besoins de captures d'éléphants sauvages ont contribué à la persistance de l'espèce en Inde dans le cadre d'une éthique de la terre (« Land ethic ») gouvernant les schémas d'utilisation des terres et les relations d'intérêts (Trautmann 2015). Aujourd'hui, l'Inde compte près de 60% de la population sauvage totale et les réserves d'éléphants de jadis correspondent aux parcs naturels et aux aires de présence actuelles de l'éléphant. L'Inde est également le seul pays dont la population sauvage croît (Asian Elephant Range States Meeting 2017). Partout ailleurs, les populations sauvages déclinent fortement et sont menacées d'extinction selon l'IUCN. Parallèlement, le nombre d'éléphants captifs diminue et les interactions entre populations sauvages et captives s'amenuisent. Dans le cadre des cycles adaptatifs définis par Gunderson et Holling (2002), le système socio-écologique humain-éléphant semble avoir atteint dans de nombreux pays une phase K (chapitre 1.3.3) où les ressources sont de plus en plus contraintes et le système devient de moins en moins souple et réactif aux chocs externes, pouvant éventuellement conduire à une phase chaotique d'effondrement et de relâchement Ω .

5.2.2 Résilience du SSE au Laos

Le Laos a connu des changements majeurs au cours des dernières décennies aux niveaux économiques, démographiques et écologiques. Ces changements ont affecté la résilience du système socio-écologique homme-éléphant, sa capacité à s'adapter et à maintenir un équilibre durable.

5.2.2.1 D'un paysage multifonctionnel à la ségrégation des terres

Depuis la fin des années 1980, le gouvernement Lao a soutenu le développement d'une agriculture commerciale intensive face à l'agriculture de subsistance traditionnellement pratiquée dans le pays. Les politiques gouvernementales ont donc cherché à réorganiser l'utilisation des terres en délimitant les terres destinées à des usages agricoles et les terres dévolues à la conservation des écosystèmes. Ainsi un plan national d'allocation des terres et de zonage systématique des parcelles villageoises a été mis en place et des zones protégées (National Biodiversity Conservation Areas) ont été établies (chapitre 2). Cette politique de ségrégation territoriale fait écho au débat actuel entre une approche d'intégration territoriale (« Land sharing »), c'est-à-dire l'intégration des facteurs écologiques et économiques sur un même paysage multifonctionnel, versus la ségrégation territoriale (« Land sparing »), i.e. la séparation des terres dédiées à une agriculture intensive de celles destinées à la protection des écosystèmes (Castella et al. 2013). L'existence des zones protégées est alors justifiée en particulier par la valorisation économique de leurs services écosystémiques. L'Etat et les institutions internationales ont initié au Laos des programmes tels que Redd+ (Reducing emissions from deforestation and forest degradation), soit « la réduction des émissions liées à la déforestation et à la dégradation des forêts dans les pays en développement » en contrepartie de crédits carbone. Mais ces programmes ont obtenu des résultats très mitigés au Laos (Mustalahti et al. 2017) comme dans d'autres pays (Howson 2017; Marion Suiseeya 2017), du fait du décalage entre les objectifs des promoteurs (Etat, institutions internationales) et ceux des populations locales, des problèmes de gouvernance ou encore de l'absence de participation de la société civile au profit d'une approche du « haut vers le bas ». En conséquence, les populations locales indiquent ne pas comprendre ces programmes et enjeux et ne pas s'y intéresser (Mustalahti et al. 2017).

5.2.2.2 Dégradation de l'habitat des éléphants sauvages et de villages

L'intensification agricole et la politique d'allocation des terres ont mené à la disparition des forêts secondaires et des jachères. Or celles-ci constituaient les pâtures communes où les éléphants de villages étaient relâchés. Leur disparition oblige les cornacs à maintenir leurs éléphants à l'attache pour éviter qu'ils ne détruisent les cultures avoisinantes. Chaque jour,

le cornac doit alors déplacer l'éléphant vers une nouvelle attache et le faire boire. En l'absence de travail et de revenus, cette charge de travail est effectuée à perte et incite de nombreux propriétaires à vendre leurs éléphants. Par ailleurs, les forêts secondaires et les jachères constituaient également une part importante de l'alimentation des éléphants sauvages, d'autant que leur aire de distribution dépasse largement les zones de protection légale (Tableau 5).

Nom	Superficie hors du parc (km ²)	Superficie dans le parc (km ²)	Superficie totale (km ²)	% compris dans le parc	Estimation de la population d'éléphants
Nakai	587	703	1 290	54,50%	132 ([120 ; 149]) en 2006
NNT NPA	0	2 959	2 959	100,00%	<10
Nam Ha	904	663	1 567	42,30%	<20
Nam Pouy	275	1 398	1 673	83,50%	<100
Xe Sap	200	1 085	1 286	84,40%	<30

Tableau 5 : Proportion de l'aire de distribution des principales populations d'éléphants sauvages au Laos incluse dans des zones de protection

Extrait de Hedges, Fisher, and Rose (2008a).

Selon Fernando et Leimgruber (2011), l'une des principales raisons pour lesquelles la politique de conservation des éléphants a échoué est que la stratégie des ONG et des gouvernements se limite aux aires protégées. Or, l'habitat optimal pour les éléphants n'est pas une forêt non perturbée mais un habitat présentant un régime de perturbation intermédiaire. Ces habitats se trouvent surtout à l'extérieur des aires protégées, ce qu'a confirmé une étude récente menée à Bornéo (Evans et al. 2018b).

5.2.2.3 Dégradation de la relation humain-éléphant

La présence permanente ou temporaire d'éléphants sauvages hors des zones protégées provoque des conflits croissants avec les villageois. L'interdiction faite aux villageois d'accéder aux zones protégées pour récolter des produits forestiers alors que les éléphants sauvages pénètrent dans les zones villageoises provoquant des dégâts dans les cultures, est perçu comme une absence de réciprocité, au sens donné par Forbes (2009) ou Lescureux (2010;2006). Cela favorise l'intolérance des populations locales et le rejet des politiques de conservation (Münster et al. 2012). Ainsi, les cornacs de Paklay-Phieng ont une perception négative des éléphants sauvages. Ils considèrent qu'ils les empêchent de travailler et attaquent leurs éléphants de village. La responsabilité des attaques et les coûts engendrés par les destructions sont rejetés sur les autorités locales. Les mesures de protection sont

largement insatisfaisantes tant pour les éléphants sauvages que pour les communautés locales, ce qui conduit à un processus dans lequel l'Etat et les ONG internationales renforcent les lois, les décrets ou les patrouilles (Forbes 2009), tandis que les communautés locales sont en demande de mesures de protection de plus en plus technologiques telles que les clôtures électriques, les systèmes d'alerte, le paiement de compensations, etc. (Münster & Münster 2012). Par opposition, les cornacs de Thongmixay laissent parfois leurs femelles pâturer librement dans le parc national et tolèrent la présence d'un mâle sauvage qui vient saillir les femelles aux abords du village, illustrant le principe de réciprocité. La longue tradition de coexistence avec des éléphants sauvages a permis aux villageois d'acquérir des connaissances traditionnelles leur permettant d'anticiper le comportement des éléphants sauvages et de mettre en place des mesures d'évitement des conflits. La perte de ces connaissances traditionnelles fragilise la capacité d'adaptation des populations à la présence d'éléphants sauvages. Il en est de même pour les savoirs concernant l'élevage des éléphants de villages. Ceux-ci tendent également à disparaître, n'étant plus transmis de père en fils. La plupart des propriétaires d'éléphants interrogés indiquent que leurs enfants ne veulent plus faire ce métier. Le passage d'un mode d'élevage de type pastoral à un mode d'élevage plus intensif (au sens de Ingold 1980) a conduit les propriétaires d'éléphants à optimiser le nombre d'éléphants qu'ils élèvent en fonction du coût des ressources (pâturages disponibles, main d'œuvre constituée de jeunes cornacs inexpérimentés, coût de la saillie) et de la demande du marché (industrie du bois en déclin, tourisme, prix d'un éléphanteau, exports). Les critères économiques, en particulier le prix des éléphants et la disponibilité du travail (tourisme, débardage) sont devenus un facteur prépondérant dans la dynamique de la population à travers leur impact sur le taux de fécondité. Si l'augmentation du prix des éléphants favorise une reprise de la fécondité depuis 2012, l'équilibre reste menacé par les variations de la demande, les crises financières, la stochasticité économique ou encore les événements politiques en Thaïlande qui impactent la fréquentation touristique régionale (chapitre 3). Le cycle adaptatif du système est alors fortement dépendant des interactions entre plusieurs échelles (locales, régionales) sous forme de "panarchies" (Holling 2001; Walker et al. 2004).

5.2.2.4 Spécialisation fonctionnelle des acteurs socio-économiques

Le passage d'un écosystème multifonctionnel vers une spécialisation fonctionnelle des terres entre conservation et services écosystémiques d'une part, et agriculture-élevage productifs d'autre part, s'accompagne également d'une spécialisation fonctionnelle des acteurs socio-économiques. Alors que l'ensemble des fonctions liées à l'élevage de l'animal était effectué par la famille dans le système traditionnel, aujourd'hui le propriétaire de l'éléphant devient un gestionnaire, parfois même un investisseur sans lien avec le métier, comme certaines entreprises de tourisme. En termes d'activité, les propriétaires d'éléphants de Thongmixay se sont spécialisés dans la reproduction quand les propriétaires des autres districts cherchent des emplois dans le débardage ou le tourisme. Le gardiennage de l'éléphant n'est plus assuré par le propriétaire ou un de ses fils, mais par un employé, souvent un jeune inexpérimenté. Les soins sont prodigués par des vétérinaires et les médicaments remplacent la pharmacopée traditionnelle, tandis que la gestion des conflits avec les éléphants sauvages est déléguée aux fonctionnaires du département des Forêts.

5.2.2.5 Conséquences sur les dynamiques de populations d'éléphants

En fin de compte, les populations d'éléphants sauvages comme de villages sont toutes deux en fort déclin. Ainsi, la population sauvage du parc de Nam Pouy a connu une diminution annuelle de 8% au cours des vingt dernières années, soit une population estimée à 400-500 individus en 1992 pour une population de 60-80 en 2011. Parallèlement, la population d'éléphants de villages chutait de 1 000 à 540 individus sur la même période. La plupart des femelles de villages sont nullipares, leurs propriétaires ne trouvant pas d'arrangements pour organiser une saillie avec un mâle de village. L'isolement des populations d'éléphants sauvages et l'éloignement des éléphants de villages pourraient engendrer à terme un appauvrissement génétique et une dépression de consanguinité pour chacune des deux populations (chapitre 4).

5.2.2.6 Perte de résilience et changement d'état

La perte de la diversité fonctionnelle et de la diversité des réponses tant aux niveaux biologiques que socio-économiques a considérablement réduit la résilience du SSE et sa capacité à s'adapter à un changement de régime graduel ou brutal.

Les changements de régime dans les systèmes socio-écologiques ont été beaucoup étudiés et documentés, mais il est encore difficile de les anticiper (Filatova et al. 2016). La plupart des études concernent des SSE centrés sur des écosystèmes tels que des pâturages, zones forestières, lacs, etc., mais relativement peu de cas centrés sur des espèces animales ont été décrits car ils impliquent en général des échelles plus larges incluant potentiellement plusieurs écosystèmes. Bottom (2009) montre que la résilience des écosystèmes du saumon du Pacifique a été érodée par les pratiques humaines qui ont simplifié la structure complexe des populations de saumon et de leurs habitats. Cependant la résilience du SSE de Bristol Bay a pu être maintenue grâce à une culture et des institutions traditionnelles engagées dans la gestion de la ressource, qui ont permis de diversifier les espèces pêchées et les activités économiques des pêcheurs. La diversité fonctionnelle et la capacité de résilience du système ont pu être restaurées, alors que les seules mesures de gestion des stocks de saumons n'avaient pas suffi à restaurer la résilience du système de la Columbia River.

Forbes (2009) a montré également que le SSE de l'élevage du renne par les Nenets était fortement résilient et a su s'adapter en dépit de la fragmentation et de la transformation d'une large proportion de la toundra due aux activités humaines, au surpâturage, au développement industriel et au réchauffement climatique. Ainsi les Nenets ont pu adapter leurs pratiques pastorales, leurs routes migratoires et leur économie aux nouvelles conditions socio-écologiques. Mais l'arrivée massive de travailleurs et le développement d'infrastructures pétrochimiques menacent à terme la résilience du système.

Les changements majeurs des facteurs socio-écologiques survenus au Laos depuis deux décennies ont diminué la résilience du système socio-écologique humain-éléphant, le rendant vulnérable aux chocs et susceptible de s'effondrer. Les mêmes processus de ségrégation des terres et de spécialisation ont été décrits pour le système socio-écologique de collecte des produits forestiers non-ligneux (Non Timber Forest Products - NTPF) tels que la cardamome (*Elettaria cardamomum*) ou l'herbe à balais (*Thysanolaena latifolia*) au Nord du Laos, conduisant à une baisse de la diversité et de la résilience du système socio-écologique (Castella et al. 2013). Avec l'accès au marché et l'augmentation de la demande, les villageois se sont concentrés sur la récolte d'un petit nombre d'espèces ayant une forte valeur économique. L'intensité de leur collecte dépend alors des fluctuations de prix. Castella et collègues observent alors un processus de domestication de quelques espèces de

NTPF à forte valeur, exploitées de façon intensive par les villageois et leur désintérêt pour les autres espèces de moindre valeur. La diminution de la diversité fonctionnelle des NTPF due à leur exploitation intensive et la spécialisation économique des villageois a réduit la résilience du SSE et sa capacité à s'adapter à une perturbation. Cette situation est très similaire aux phénomènes que nous avons observés sur le SSE humain-éléphant au Laos.

Afin d'éviter la disparition de l'éléphant au Laos et l'effondrement du SSE, il convient de retrouver un état résilient du système par des politiques, modes de gestion ou innovations qui permettront, soit (i) d'adapter le système existant, c'est-à-dire de développer de nouvelles configurations socio-écologiques qui fonctionnent efficacement dans de nouvelles conditions, soit (ii) de le transformer, c'est-à-dire de créer un système fondamentalement nouveau lorsque les structures écologiques, économiques ou sociales rendent le système existant intenable (Walker 2004). La Figure 36 ci-après présente le cycle adaptatif du système socio-écologique avec les phases passée (*cohabitation*) et actuelle (*ségrégation*) détaillées dans le chapitre 2, ainsi que les voies possibles d'avenir que sont l'adaptation (*intégration*) ou la transformation du système (*protection & domestication*).

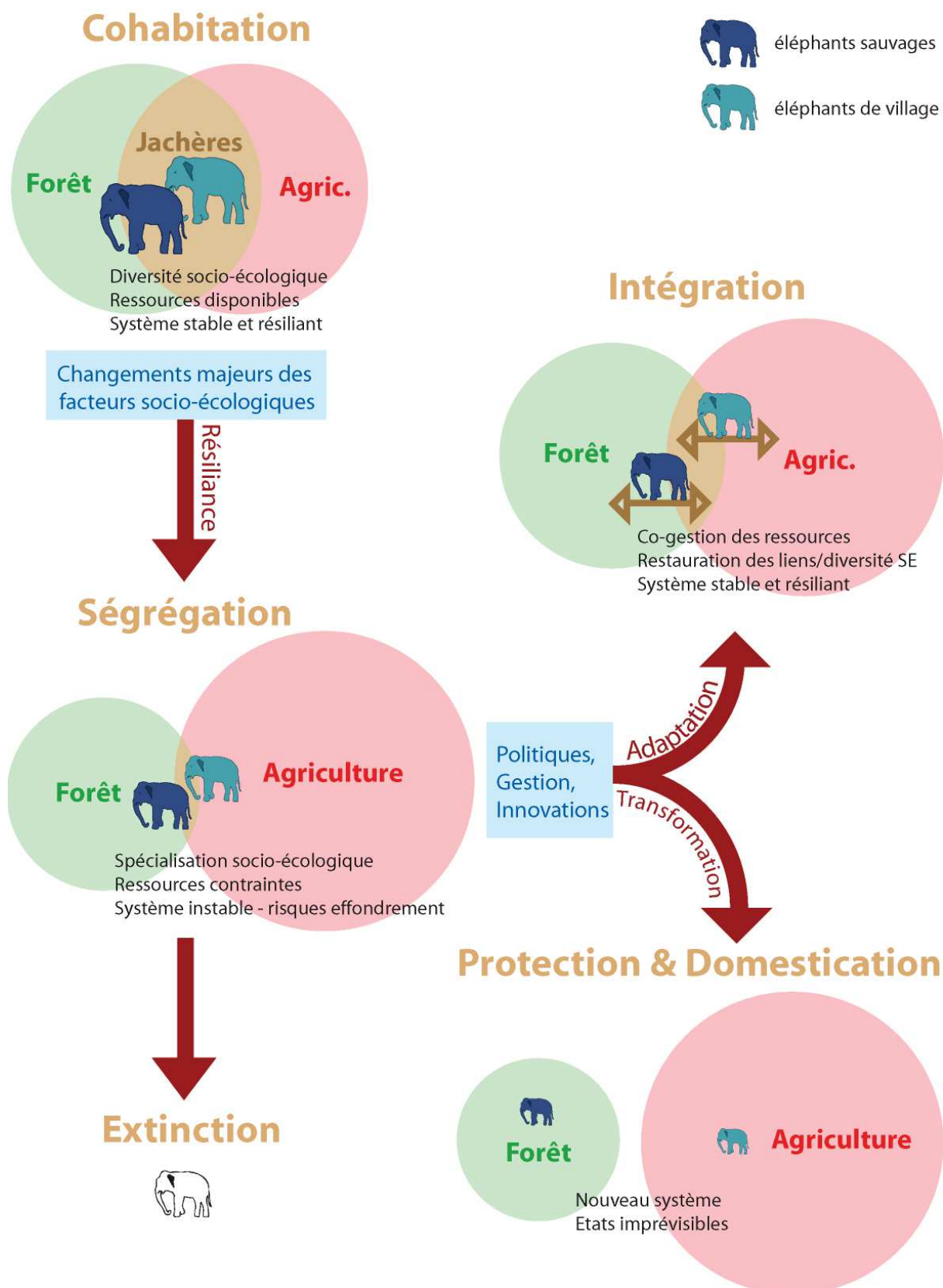


Figure 36 : Cycle adaptatif du système socio-écologique homme-éléphant au Laos

La résilience a permis l'adaptation d'un système traditionnel de *cohabitation* vers un le système actuel de *ségrégation* croissante. La perte de résilience due à la ségrégation, la spécialisation et la perte de diversité socio-écologique pourrait conduire à un changement de régime menant à l'*extinction* à terme de l'espèce et du SSE qui lui est associée. La mise en place de nouvelles pratiques, politiques et innovations devrait permettre au système de s'adapter (*intégration*) ou se transformer vers un nouveau système (*protection & domestication*).

5.3 Adaptation du système socio-écologique

Comme les actions humaines sont un facteur dominant de la dynamique des SSE, l'adaptabilité du système est principalement fonction de la composante sociale, c'est-à-dire des individus et des groupes qui agissent pour gérer le système et le cas échéant restaurer sa résilience (Walker et al. 2004). La gestion du système dépend à la fois des politiques gouvernementales, des programmes menés par les institutions internationales ou les organismes de conservation, des acteurs privés et des institutions communautaires. La capacité d'adaptation réside aussi dans les pratiques économiques, sociales et culturelles spécifiques des populations locales (Forbes et al. 2009). Nous avons montré que la réponse des cornacs au Laos était variable selon les individus et les régions (chapitre 2). Nous étudierons ici les possibilités d'adaptation du système exclusivement au regard des politiques et des programmes d'actions menés par les autorités et les ONG en prenant pour exemple le Plan d'Action de Conservation de l'Eléphant au Myanmar (MECAP – Myanmar Elephant Conservation Action Plan, Hedges et al. 2018) fixant les objectifs et le cadre de la conservation de l'éléphant au Myanmar pour les 100 ans à venir.

5.3.1 Programme d'Action de conservation de l'éléphant au Myanmar, une approche novatrice ?

Entériné en janvier 2018 par le Ministère de l'Environnement et des Ressources Naturelles, appuyé par un consortium d'organisations internationales de conservation, le plan MECAP vise à assurer la sauvegarde de l'éléphant pour les 100 ans à venir. Cet objectif est décliné dans un cadre opérationnel pour la prochaine décennie. Une lecture critique de ce plan permet de mettre en lumière les objectifs et les approches soutenues par les acteurs gouvernementaux et institutionnels dans la prise en compte, ou non, des dynamiques du système socio-écologique et des interactions entre éléphants sauvages et captifs. Ainsi le premier paragraphe du document précise l'importance et la spécificité du Myanmar pour la conservation de l'éléphant d'Asie :

While Myanmar's wild elephant population is relatively small at maybe 2000 individuals, a great deal of elephant habitat remains in the country. There is, therefore, a great opportunity for the country's wild elephant population to grow very significantly and become perhaps the largest in Southeast Asia — provided

Myanmar's elephants and elephant habitat are well protected and managed wisely. Myanmar also has a long and proud history of managing elephants in captivity as working animals and has therefore a vast repository of knowledge about captive elephant husbandry. Finally, Myanmar is in the unique position of having many more captive elephants (some 5000) than wild elephants and this brings both challenges and opportunities. For example, some of Myanmar's captive elephants are thought to be suitable for experimental reintroduction back into the wild and Myanmar could become a world leader in such 're-wilding' (MECAP, p6).

Il convient avant tout de préciser ce que l'on entend conserver. S'agit-il de l'espèce, de populations, d'individus, de gènes, d'un écosystème, d'un patrimoine culturel ou encore d'un système bio-culturel ? La réponse dépend bien entendu des types d'acteurs et des individus. Selon ses auteurs, « *MECAP was developed to guide Government of Myanmar planners (including politicians and civil servants), NGO staff as well as other wildlife biologists and conservationists, and civil society in their efforts to create the social, economic, and biological conditions that allow elephants to co-exist with humans in the same landscapes* » (MECAP, p7). Ainsi la conservation de l'éléphant semble s'inscrire dans le cadre d'un système socio-écologique humain-éléphant. Cette approche est reprise dans la vision à long terme (100 ans) de la conservation de l'éléphant dans le pays : « *Wild elephants thrive across their current and recoverable range in Myanmar while co-existing harmoniously with people in ecologically functional landscapes* » (MECAP, p9). Cependant cette vision ne concerne plus l'espèce dans son ensemble mais ses représentants sauvages uniquement.

Au-delà des recommandations classiques liées à la protection de l'habitat, la lutte contre le braconnage et le commerce illégal ou la réduction des conflits humains-éléphants, ce programme reprend le concept d'Aires Gérées de présence de l'Eléphant ou Managed Elephant Ranges – MER (Santiapillai & Jackson 1978). Le concept de MER fournit une approche à l'échelle du paysage dans laquelle les gestionnaires évaluent les besoins d'habitat des éléphants sur de grandes superficies et permettent des activités humaines compatibles, telles que la foresterie à impact réduit, les cultures itinérantes à rotation lente et le pâturage contrôlé du bétail. Les MER sont habituellement établies en tant qu'extensions aux aires protégées existantes et comprennent souvent des corridors d'habitat reliant les aires protégées. Cependant, le plein potentiel des MER pour promouvoir

une utilisation des terres compatible avec les éléphants n'a pas encore été correctement évalué (Hedges et al. 2008b). Il s'agit ici de la reconnaissance explicite que les seules zones protégées ne suffisent ou ne suffiront pas à assurer le maintien (et, le cas échéant, la restauration) de densités de populations d'éléphants. Le concept de MER implique aussi que ces mêmes populations sauvages ne restent pas confinées aux seules zones protégées mais partagent un habitat utilisé par l'homme. De fait, le développement de MER remet en cause le paradigme de ségrégation territoriale (land sparing) largement soutenu par les gouvernements de la région et les institutions internationales telles que la Banque Mondiale, la Banque Asiatique pour le Développement ou l'IUCN (Lestrelin 2010; Evrard 2004; Goldman 2001) et de façon plus ambivalente par les ONG de conservation (Castella et al. 2013; Aubertin 2003). Même si le concept de MER est ancien (Santiapillai & Jackson 1978), il peine à s'imposer dans les programmes de conservation (Fernando & Pastorini 2011). Les activités humaines compatibles avec la présence des éléphants sauvages soutenues dans l'objectif général du MECAP et le concept de MER sont également citées comme les principaux facteurs de la dégradation de l'habitat menaçant les éléphants : « dégradation de l'habitat due à la présence d'animaux d'élevage (compétition, surpâturage et compétition sur les ressources), de plantes envahissantes, d'incendies trop fréquents et/ou extensifs, de collecte de fourrage et de bois de chauffage ». A la lecture de ce document, l'intérêt d'un système agroforestier plurifonctionnel permettant aux populations d'éléphants sauvages de coexister avec l'homme reste donc un sujet équivoque pour les ONG et le gouvernement.

MECAP revient largement dans son introduction sur le rôle des populations captives dans la symbolique et la relation humain-nature au Myanmar, justifiant ainsi l'importance de sauvegarder cette espèce.

Asian Elephants are the largest living land animals in Asia and are an icon of the wild and of humans' interactions with nature (e.g. they are both worshipped as Gods and tamed and used as working animals). It has been said that one can start from Ganesha (the Hindu elephant-headed deity) and work from there in an unbroken line to almost any aspect of Indian culture; similar observations could be made about the role of elephants in the cultures of many other countries in Asia; e.g., the white elephant which is a state symbol and revered as a blessing in Myanmar. In addition, Asian Elephants are obvious channels for people to express their love for and

fascination with nature. [...] Captive elephants are often referred to as domestic elephants but this is a misnomer. [...] Domestic elephants should therefore be thought of as captive wild animals and treated as such (MECAP, p 23).

L'importance du lien homme-éléphant, son rôle culturel et la place prépondérante occupée par les éléphants captifs sont érigés en justification de la sauvegarde de l'espèce dans le pays. Cependant la question de sauvegarder ou non les populations captives est éludée. Seul le défi que constitue la présence d'une population de 5000 éléphants captifs plus nombreuse que la population sauvage est soulevé. Ainsi, le septième et dernier objectif à long-terme indique :

Myanmar's captive elephant population is well-managed, not a threat to wild elephants, and contributing to wild elephant conservation. This goal recognizes that the successful conservation of a species with captive relatives – including Asian Elephants – requires the captive population to be managed in such a manner that it does not constitute a threat to the wild population (MECAP, p 29).

Cet objectif est décliné en recommandations d'actions sous le titre « Gestion des éléphants captifs et des interactions captifs-sauvages au Myanmar ». Les recommandations consistent à améliorer le contrôle et la gestion des individus captifs [c'est-à-dire dans le but de limiter les risques de capture et de commerce illégal], d'évaluer la pertinence d'emplois alternatifs [à l'extraction du bois] et d'évaluer s'il est nécessaire de maintenir le nombre actuel d'éléphants captifs au Myanmar ou s'il faut réduire leur nombre par l'intermédiaire d'un contrôle de la reproduction (contraception), des réintroductions et d'autres moyens appropriés. Les interactions sauvages-captifs sont envisagées principalement dans le sens de la réduction des menaces sur les populations sauvages et non pas dans le cadre d'un système socio-écologique complexe et dynamique prenant en compte le rôle économique, social, culturel et écologique que les éléphants captifs pourraient jouer en faveur de la conservation des sauvages. Les ONG partenaires suggèrent de mettre en place un programme de contraception mais notent le manque de volonté politique du gouvernement pour contrôler la reproduction (reproduction systématique des animaux en cas de besoin ou manipulation des processus de reproduction) (MECAP, p 77). Toutefois le potentiel de réintroduction des éléphants captifs est suggéré mais n'est pas considéré comme une

priorité, et ne fait donc pas l'objet de recommandations d'actions. Enfin le rôle des éléphants captifs dans la gestion des conflits humain-éléphant se limite à l'utilisation de patrouilles montées à dos d'éléphant. L'ensemble des mesures de réduction des conflits est basé sur le déploiement d'un cadre légal et de moyens sous l'égide de l'Etat ou des organisations environnementales. Le rôle des connaissances traditionnelles ou plus généralement l'implication des populations locales dans la définition et la mise en place de mesures de réduction des conflits n'est pas évoquée, alors qu'elles contribuent fortement à la réussite des actions engagées et sont un facteur fondamental de la résilience du SSE.

Le plan MECAP représente une avancée en faveur de politiques et de programmes d'action destinés à adapter le système et assurer sa résilience à travers la reconnaissance d'un système socio-écologique multifonctionnel et des interactions entre populations d'éléphants sauvages et captifs. Mais en pratique, les recommandations restent limitées à une approche dualiste éléphants sauvages-captifs où les éléphants captifs constituent une menace pour la conservation de l'espèce. L'intégration territoriale et le concept de MER constituent plus une option par défaut face à l'impossibilité d'étendre largement les zones protégées, qu'une politique pro-active en faveur du maintien de paysages multifonctionnels et de la diversité des moyens de subsistance qui permettraient d'améliorer la résilience du système (Wilson 2010). La participation des populations locales à travers un processus de co-construction semble également écartée dans MECAP.

5.3.2 Restaurer les liens humains-éléphants

L'étude que nous avons menée au Laos montre l'importance de maintenir/restaurer les liens entre l'humain et l'éléphant, entre les populations sauvages et de villages, dans le cadre d'un système agroforestier multifonctionnel. En d'autres termes, il convient d'étendre la conservation au système bio-culturel plutôt qu'aux seules populations sauvages et à leur habitat. Le retour à un système résilient et durable nécessite de développer de nouvelles configurations socio-écologiques. Nous pouvons ici suggérer plusieurs pistes complémentaires aux recommandations contenues dans MECAP qui pourraient également être adaptées à la situation du Laos. Outre les actions déjà envisagées dans le plan MECAP, il conviendrait de favoriser :

- **Le maintien de populations d'éléphants de villages viables** (chapitre 2,3). Il est important de rappeler qu'en raison de la faible fécondité de la population captive thaïlandaise, le marché du tourisme à dos d'éléphants est suspecté d'alimenter la capture d'éléphants sauvages au Myanmar et leur trafic illégal vers la Thaïlande (Nijman 2014) ;
- **Le maintien de la diversité génétique de la population de village** (chapitre 4). La valeur potentielle d'une importante population captive pour la conservation de l'espèce a été reconnue (Dublin et al. 2006). Si les populations captives doivent former des réservoirs ou assurances pour la survie de populations sauvages isolées, il est important que leur diversité génétique soit représentative de la diversité existant dans la nature (Sato et al. 2017) ;
- **Le maintien et la réhabilitation des « éléphants de villages » élevés en semi-captivité** plutôt que leur maintien dans des camps de tourisme en zone péri-urbaine (chapitre 2), en développant des zones de cultures en rotation, collectes de produits forestiers compatibles avec la pâture des éléphants, ou bien des politiques de tourisme écoresponsables, etc. ;
- **La mise en place de zones de reproduction croisées entre populations sauvages et éléphant de villages** (chapitre 2, 3) dans le cadre de MER ou de parcs naturels. Les conditions d'accès à ces zones de reproduction (délimitation spatiale et périodes d'accès, conditions sanitaires des éléphants de villages, etc.) doivent faire l'objet d'une concertation et une coordination entre les communautés de cornacs /propriétaires d'éléphants et les autorités/ONG. Les cornacs pourraient, le cas échéant, assister les patrouilles dans leurs missions de surveillance et de suivi ;
- **La mise en place de systèmes de « congés maternités » pour contrebalancer les effets de la variation de la demande et du prix des éléphants sur la fécondité** (chapitre 3) ;
- **Le maintien et la valorisation des connaissances traditionnelles liées à l'élevage des éléphants et / ou la gestion des conflits ;**
- **La mise en place de processus de gestion des ressources naturelles et de gouvernance adaptatives afin de garantir l'adaptabilité et la résilience du système** (Walker et al. 2004). La participation des communautés à l'élaboration des politiques foncières et de conservation, à la gestion et la réduction des conflits peut garantir

que les compromis existants entre la conservation et le développement sont négociés au niveau local. La participation des communautés devrait permettre d'éviter de reproduire ou d'accroître les inégalités socio-économiques par des interventions qui ne tiennent pas compte des conditions locales et des moyens d'existence. Elle peut aussi permettre une exploration collective des impacts des changements de paysage et des pratiques économiques sur les services écosystémiques et les moyens de subsistance locaux (Castella et al. 2013).

L'adaptation du SSE nécessite donc la mise en place de plans d'action et de politiques concertées, de pratiques innovantes qui favoriseront le retour du système à une phase de croissance.

5.4 Transformation du système socio-écologique

Lorsque les structures écologiques, économiques ou sociales rendent le système existant intenable, une alternative est de créer un système fondamentalement nouveau (Walker 2004). Si les tendances observées se confirment, voire se renforcent, on peut imaginer que le système socio-écologique se transformera selon un processus conjoint de « protection-domestication ».

Ainsi les populations sauvages seraient strictement protégées dans des parcs suffisamment grands pour assurer leur viabilité. L'Etat, assisté par les organisations de protection de la faune, serait alors garant de la survie de l'espèce à travers des politiques de protection-conservation. Il ne semble pas envisageable d'étendre largement les zones protégées en raison de la croissance démographique humaine et de l'intensification agricole, mais une stratégie de sélection de populations et d'habitats viables permettrait de concentrer les moyens sur ces quelques zones. Des moyens humains, financiers et techniques, dont de nouvelles technologies, peuvent être mobilisés pour restaurer des habitats, lutter contre le braconnage et réduire les conflits. Par exemple, le braconnage pourra être réduit par la professionnalisation ou la militarisation des patrouilles. L'utilisation de portiques de détection des éléphants sauvages couplés à des alertes par SMS des villageois est actuellement testée comme méthode de réduction des conflits. Le transfert d'individus agressifs ou de hardes sauvages occupant des zones de présence humaine serait appelé à se développer (Anon 2017a; Chakraborty et al. 2014). Le transfert d'individus ou de petits

groupes pourrait également permettre de réduire les risques de consanguinité et de baisse de la diversité génétique. Ainsi la population sauvage du Parc de Cat Tien au Vietnam, estimée à 11 individus, pourrait être renforcée par le transfert d'autres groupes isolés dans des habitats défavorables du pays (Vidya et al. 2007). Cependant, il convient d'améliorer les techniques de transfert qui à ce jour restent problématiques. La réintroduction ou la translocation, la constitution de territoires spécifiques, les techniques de capture et de transfert, la sélection d'individus et leurs croisements en fonction de leur patrimoine génétique, le nourrissage, l'acclimatation, le radio-tracking, la télémesure, sont autant de moyens permettant de créer ce que certains considèrent comme un sauvage artificiel (Micoud 1993; Larrère 1994) et créent des conditions similaires à celles de la gestion cynégétique ayant précédé la domestication des ongulés sauvages (Larson & Fuller 2014).

La ségrégation des éléphants captifs s'apparenterait également à un processus de domestication dans son sens biologique, c'est-à-dire le contrôle de la reproduction et la sélection, ou bien dans son acception sociale, i.e. la sécurisation de l'accès à une ressource d'intérêt (Zeder 2015). L'élevage d'éléphants dans des camps nécessitera de passer d'un système extensif à un système de contrôle et de domination permanente de l'humain sur l'animal, à la fois en termes de conduite de l'animal, d'alimentation ou de reproduction aboutissant à la perte d'autonomie de l'animal. La reproduction en captivité reste à ce jour difficile. Le nouveau système devra donc mettre en place des procédures et des modes de gestion qui assureront la viabilité de la population tels que les systèmes de pédigrées utilisés pour d'autres espèces domestiques. L'insémination artificielle, aujourd'hui encore mal maîtrisée chez l'éléphant, pourra le cas échéant pallier le déficit en mâles reproducteurs. Le contrôle de la reproduction et la recherche de certains traits, en particulier la docilité, pourrait engendrer un processus de sélection qui à long terme mènerait à une divergence entre populations sauvages et captives, ainsi qu'une modification biologique et comportementale de l'éléphant domestiqué. Il a d'ailleurs déjà été montré que l'isolement et le confinement des éléphants de temple en Inde, en l'absence de congénères, affecte leur physiologie et leur comportement et conduit souvent au développement de comportements stéréotypés (Clubb & Mason 2002; Kurt & Mar 2003).

La plupart des mesures suggérées ci-dessus, qu'elles concernent la protection des éléphants sauvages ou la domestication des éléphants de villages, nécessitent de développer des

pratiques, des techniques innovantes et des connaissances qui sont amenées à remplacer les savoirs traditionnels mais ne sont pas pleinement maîtrisées aujourd’hui. Ce processus conduit à scinder le SSE actuel en deux systèmes prétendument indépendants, chacun de ces systèmes devant assurer sa propre résilience. La création d’entités véritablement séparées et imperméables reste cependant une gageure si l’on considère par exemple les risques de capture illégale ou l’empiètement de l’habitat favorable aux éléphants sauvages pour entretenir les éléphants captifs. Cette approche s’inscrit dans le paradigme dominant de création d’ontologies dichotomiques telles que nature vs culture, humain vs non-humain, domestique vs sauvage, moderne vs traditionnel (Latour 1991). Il est intéressant de noter que les nombreuses organisations ou personnes militant contre la captivité des éléphants et en faveur de la purification de l’espèce (au sens de Latour 1999 et Ghosal et al. 2013) de la mise sous cloche de l’éléphant sauvage, favorisent par la même le processus de domestication des éléphants de villages.

Les espèces à longue durée de vie, comme l’éléphant d’Asie, sont très sensibles aux phénomènes d’inertie démographique. Il faut beaucoup de temps avant que la population puisse se rétablir de tout changement dans un taux vital (chapitre 3), ce que Lebreton (2006) appelle la malédiction des espèces longévives. Ainsi, les pratiques socio-économiques, les politiques et les programmes de conservation actuels impactent fortement la dynamique de l’espèce pour plusieurs décennies. Les choix qui seront faits par les acteurs joueront un rôle primordial dans l’orientation du cycle adaptatif vers la restauration de la résilience du système actuel, son adaptation vers un système intégré, sa transformation vers un système protection-domestication ou son extinction.

6 CONCLUSION ET PERSPECTIVES

Cette étude a présenté une analyse des interactions et des facteurs déterminant le système socio-écologique humain - éléphant de village - éléphant sauvage et sa résilience au Laos en particulier.

Le premier apport de ce travail réside dans la description et l'analyse de la structure et du fonctionnement de ce système (chapitre 2). L'émergence depuis les années 2000 de la marchandisation de la nature et la division de l'accès aux ressources naturelles a conduit d'une part à la ségrégation entre éléphants sauvages et éléphants de villages, et d'autre part à l'intensification de l'élevage de ces derniers. Ainsi les forêts sont protégées par la loi, valorisées pour leurs services écosystémiques tandis que leur accès est interdit aux villageois comme aux éléphants de villages. La présence d'éléphants sauvages hors de ces zones protégées provoque des conflits croissants avec les communautés humaines locales. Parallèlement, la ségrégation territoriale entre les zones dédiées à la conservation et les zones destinées à la production agricole a fait disparaître les pâtures communes. Les éléphants de villages sont désormais à l'attache, leur reproduction est contrôlée et conditionnée au paiement pour la saillie. L'intensification du travail dans le débardage du bois puis dans le tourisme s'apparente à une forme d'élevage intensif proche du ranching (au sens de Ingold 1980) qui impacte la dynamique de la population comme la perception de l'espèce par les cornacs et propriétaires d'éléphants. Cette étude se différencie d'une monographie de la relation humain-éléphant pour une communauté spécifique (village ou district par exemple), en privilégiant l'analyse de la dynamique et des interactions entre les constituants du système humain-éléphant à l'échelle d'un pays. Il serait intéressant néanmoins de la compléter par une étude plus approfondie de la symbolique et des spécificités liées à l'appartenance ethnique des cornacs et propriétaires d'éléphants. Nous les avons considérés ici comme une communauté relativement homogène présentant des variations régionales dans sa réponse aux perturbations et aux changements du système. De plus, l'étude s'est concentrée sur les propriétaires d'éléphants et les cornacs sans considérer les habitants qui n'étaient pas directement impliqués dans cette activité d'élevage. Il conviendrait donc d'élargir cette étude aux autres catégories socio-professionnelles.

Le deuxième apport de cette étude réside dans l'analyse détaillée de deux aspects, la démographie et la génétique, déterminant le fonctionnement du système et contribuant à sa résilience globale. Nous avons montré qu'au Laos la fécondité des éléphants de villages était conditionnée à court terme par l'incitation financière des propriétaires à faire de la reproduction, tandis que la dynamique de la population sauvage impactait la démographie des éléphants de villages sur le long terme à travers la reproduction entre femelles de villages et mâles sauvages (chapitre 3). Ainsi la viabilité de la population est fortement dépendante des variations économiques et de l'accès aux mâles reproducteurs sauvages. La diversité des stratégies d'élevage, en particulier la spécialisation des propriétaires de Thongmixay dans la reproduction des femelles avec des mâles sauvages, a permis toutefois de maintenir la résilience du système (chapitre 2). L'étude de génétique des populations a montré que la diversité génétique des populations sauvages et de villages était élevée et que ces populations constituaient un ensemble homogène (chapitre 4). L'isolement des populations sauvages et la ségrégation croissante des populations de villages engendreront un appauvrissement génétique sur le long terme qu'il est possible de limiter par des mesures de gestion favorisant le flux de gènes au niveau régional et entre les deux populations. Ces deux études illustrent que la résilience d'un système est la résultante de multiples facteurs agissant à différents niveaux ou échelles, dont les effets sont parfois opposés et qui sont appelés « révolte » et « mémoire » dans le cadre de la panarchie (chapitre 1.3.4). Ainsi l'incitation économique des propriétaires d'éléphants à faire de la reproduction agit comme révolte à court terme sur la démographie des éléphants tandis que la dynamique de la population sauvage stabilise et conserve la mémoire accumulée de la dynamique du système (Gunderson & Holling 2002). De la même façon, les individus ou les petites populations isolées sont menacés de consanguinité ou d'appauvrissement génétique mais le niveau élevé de diversité génétique à l'échelle de la métapopulation stabilise et conserve la mémoire du système. Nous avons abordé brièvement les interactions entre échelles, en particulier l'échelle locale et l'échelle globale. La mobilisation d'autres disciplines telles que l'écologie spatiale, ou la géographie permettrait (i) d'approfondir la compréhension du système, l'usage des différents écosystèmes dans le paysage par les humains, les éléphants de villages et sauvages, ainsi que leurs interactions dans l'espace et le temps et (ii) d'identifier le cas échéant des facteurs critiques de la résilience du système et de décrire plus en détail les effets inter-échelles.

L'étude explore également des scénarios d'adaptation ou de transformation du système socio-écologique en évoquant le processus conjoint de domestication et d'artificialisation du sauvage. Ce dernier est fortement lié à la vision du monde des organisations internationales engagées dans la conservation des éléphants sauvages, vision ancrée dans la dichotomie nature / culture propre aux sociétés occidentales. Ces organisations tentent d'obtenir un soutien local des communautés aux programmes de conservation définis selon des objectifs de conservation, sans tenir compte de la façon dont les communautés locales se représentent leur environnement, phénomène décrit également par Infield (2017). Le problème n'est pas tellement que les quelques organisations internationales engagées dans la conservation de l'éléphant sauvage au Laos ou au Myanmar fondent leurs actions sur une certaine vision du monde et de la conservation, mais plutôt l'absence d'interlocuteurs, d'organisations locales de la société civile porteurs de perceptions ou de visions différentes. En effet, au Laos, les organisations de la société civile sont interdites. Ailleurs en Asie, lorsque les organisations locales sont autorisées, leur faible capacité d'organisation et leur manque de moyens humains et financiers limitent généralement leur participation à l'élaboration des politiques nationales. Or, comme nous l'indiquons dans le chapitre 1, les diverses valeurs économiques, culturelles et spirituelles peuvent fournir la diversité de la réponse sociale dont les communautés humaines ont besoin pour s'adapter avec succès aux environnements changeants (Senos et al. 2006; Turner et al. 2003).

De plus en plus de travaux académiques promeuvent une approche bioculturelle de la conservation. Ces approches s'appuient de façon explicite sur les perspectives culturelles locales - qui englobent les valeurs, les savoirs et les besoins locaux - et reconnaissent les rétroactions entre les écosystèmes et le bien-être humain (Sterling et al. 2017; Caillon et al. 2017; Maffi 2005). Elles défendent l'intégration des acteurs locaux, des membres de la communauté et des organisations locales dans la recherche et l'action par le biais d'études de résilience des systèmes socio-écologiques, la co-construction et la gestion communautaire des programmes. Les organisations internationales engagées dans la conservation de l'éléphant en Asie se doivent d'encourager les échanges avec les acteurs locaux et les communautés, de remettre au centre des programmes les perceptions, les savoirs et les besoins locaux afin de faciliter l'identification des problèmes et des solutions qui font souvent défaut dans les cadres nationaux ou internationaux (Sterling et al. 2017). La

voie de l'adaptation du SSE intégrant, sans exclure, les trois pôles humain, éléphant de village, éléphant sauvage me semble une approche plus ambitieuse et plus durable de la conservation de l'éléphant d'Asie, bien que certainement plus complexe à mettre en œuvre que la protection légale de populations d'éléphants et de forêts primaires relictuelles qui se révèlent peu adaptées à l'écologie de l'espèce. Cette approche nécessite non seulement de confronter des perceptions parfois divergentes entre communautés locales et organisations de conservation, mais aussi entre objectifs écologiques et objectifs socio-économiques variables selon le niveau local, national ou régional.

Forbes (2009) rappelle que les liens sont aussi importants que les objets ou les lieux :

Relationships are as fundamental as places and things. Conservationists made a strategic error in assuming that our work is more a legal act than a cultural act, in assuming that we can protect land from people through laws, as opposed to with people through relationships. Laws codify values; they do not create them.

Les acteurs locaux, gouvernementaux, institutionnels, privés devraient s'attacher à préserver les liens existant au sein du système socio-écologique plutôt que de se concentrer uniquement sur deux éléments considérés comme des biens, c'est-à-dire l'éléphant et son habitat. Cela passe par le maintien des liens entre éléphants de villages et éléphants sauvages mais également entre les communautés humaines et leur environnement, en tenant compte de leur mémoire et leur expérience physique et spirituelle de ce dernier.

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8 ANNEXES

8.1 Supplementary information Article 1

From cohabitation to segregation: evolving human–elephant relationships in a changing socio-ecological system in Laos

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8.1.1 Interview guide: Elephant owners handling practices and interactions

N°: Date: Village: District: Province:

Elephant ID form

Name:					
Sex:					
Age:					
DOB:					
Reg nb					
Relat°					

KNOWLEDGE & PERCEPTIONS

General questions about elephants:

1. Are elephants a special species?
2. How different are elephants from other species?
3. What are the similarities between human and elephants?
4. Are there different types of elephants?
5. How do you recognize the different types of elephants?
6. Do you know traditional classifications used by elders or mahouts? If yes, explain.
7. Are there good and bad elephants? Explain.
8. What is a wild elephant?
9. What is a captive/domesticated elephant?
10. Are wild elephants different from captive ones? What differences?
In terms of physical characteristics? In terms of behaviors?
11. Could a wild elephant become captive/domesticated? How?
12. When a captive/domesticated cow gives birth, is the new-born considered as wild or captive/domesticated?
13. What does the taming change in an elephant?

14. Could a captive/domesticated elephant become wild? How? Do you know examples of captive elephants escaping with their wild congeners?
15. How were elephants captured in the past / now?
16. What differences you see between a wild-caught elephant and a captive born?
17. Does a wild-caught elephant work better than a domestic-born elephant?
18. Speaking about domestic-born elephants, if the father is wild or captive does it make a difference? In terms of physical characteristics? In terms of behaviors? In terms of work?

YOUR ELEPHANT

1. Tell me the story about your elephant?
2. When and where did you get it?
3. Explain your elephant genealogy (ancestors)
4. Tell me about your elephant breeding history?

Number of gestations, partner origin, mating conditions

5. Could you recognize a good breeder? What signs?
6. Are all elephant good breeders – males / females?
7. Is it difficult to breed an elephant? Why?
8. Do wild elephant breed better than captive ones? Explain (about males, about females).
9. Is it easier to breed a captive female with wild male?
10. Would you like your elephant to breed in the future?
11. How much does an elephant cost (calf/juvenile/adult – male/female)?
12. Are prices changing? What are the reasons for such changes according to you?

HANDLING PRACTICES AND INTERACTIONS WITH WILD ELEPHANTS

We will now discuss about how you take care about your elephant

1. What is the work done by your elephant?
2. How many mahouts are working with this elephant? How old are they?
3. What tasks do you have to perform every day to care your elephant?
4. What other tasks should be done on a weekly / monthly / yearly basis?
5. How long the elephant is resting? (daily/weekly/yearly)
6. Where is the elephant resting (after working hours)?

7. Do you release the elephant completely?
8. How do you choose the location?
9. When resting, your elephant is isolate or in contact with others (captive/wild – male/females)?
10. Could you estimate the frequency and length of these resting periods?
11. Could you draw a map of pasture areas?
12. Have you ever seen wild elephants?
13. Where, when, how often, at what period of the year?
14. Does your elephant ever meet with wild ones? When, at what occasions?
15. This year, how many times has your elephant met with wild ones?
16. What happens when your elephant meets wild ones?
17. Could captive elephant live together with wild ones?
18. Do the wild elephants make troubles?
19. Do they provoke damages or conflicts? What sort?
20. Does it cost a lot of money?
21. Is it a good thing if wild elephants are living near the place where you keep your own elephant?
22. Have you ever heard of elephant hunted or poached?
23. Was it wild elephants? Captive/domesticated elephants?

PERCEPTION OF THE FUTURE

We will speak now about your work

1. Who owns this elephant?
2. Are you employed as mahout? How long has it been?
3. Number of elephants you own or you work with?
4. Where and when did you learn to be a mahout?
5. Do you like to be a mahout, to work with elephants? Why?
6. Do you think that there will be always people working with elephants in the future?
7. What will be the work of elephants in the future?
8. [if owner] Do you want to sell your elephant?
9. Do you want your children to be a mahout/work with elephants in the future?
10. Do you think there will still be elephants in the future? Wild elephants? Captive elephants?
11. Is the number of elephants changing compared to the past? Why?

12. If the elephant population is decreasing, do you think it is a problem? What if the elephants disappeared?
13. Do you think that the captive elephant population could survive if there were no more wild elephants?
14. Anything else you would like to add?

RESPONDENT IDENTIFICATION FORM

Family name:

First name:

Age:

Sex:

Village:

District:

Province:

8.1.2 Multiple Correspondance Analysis

Categorical variables (eta2)

	Dim.1	Dim.2	Dim.3	Dim.4
Family_owners	0.329	0.001	0.000	0.046
Nulliparous	0.573	0.215	0.078	0.010
At_least_1_calf	0.452	0.283	0.071	0.003
Pregnant	0.501	0.002	0.012	0.002
success_breed_10y	0.464	0.295	0.007	0.020
No_breed_10y	0.581	0.165	0.025	0.003
wild_captive_coex_Only_female	0.132	0.000	0.000	0.173
wild_captive_coex_Possible	0.100	0.015	0.258	0.116
wild_captive_coex_Not_possible	0.009	0.078	0.456	0.021
wild_percept_Future_generation_admire	0.002	0.005	0.033	0.135
wild_percept_No_problem	0.021	0.272	0.068	0.088
wild_percept_Good_for_capture	0.001	0.090	0.077	0.008
wild_percept_Good_for_breeding	0.014	0.015	0.009	0.381
wild_percept_Destroy_crops	0.025	0.042	0.129	0.429
wild_percept_Dangerous_attack_people	0.129	0.000	0.103	0.093
wild_percept_Attack_captive_elephants	0.138	0.002	0.206	0.004
wild_percept_Dont_know_No_wild	0.106	0.043	0.014	0.135
wild_captive_Fighting	0.004	0.049	0.309	0.038
wild_captive_Only_males_fight	0.006	0.051	0.002	0.285
wild_captive_No_fight	0.014	0.063	0.331	0.039
Pasture_Always_chained	0.556	0.231	0.033	0.004
Pasture_Release_not_possible	0.146	0.515	0.000	0.005
Pasture_Limited_released	0.524	0.254	0.040	0.002
Pasture_Too_many_fields	0.127	0.242	0.108	0.035

Supplementary categorical variables (eta2)

	Dim.1	Dim.2	Dim.3	Dim.4
Bought	0.229	0.020	0.118	0.011
Female	0.147	0.021	0.032	0.000
Region	0.509	0.288	0.065	0.143

Table 6 : Contribution of each variable to the construction of dimensions 1 to 5

[illegible]

Table 7 : data used in the MCA. Each column corresponds to one respondent.

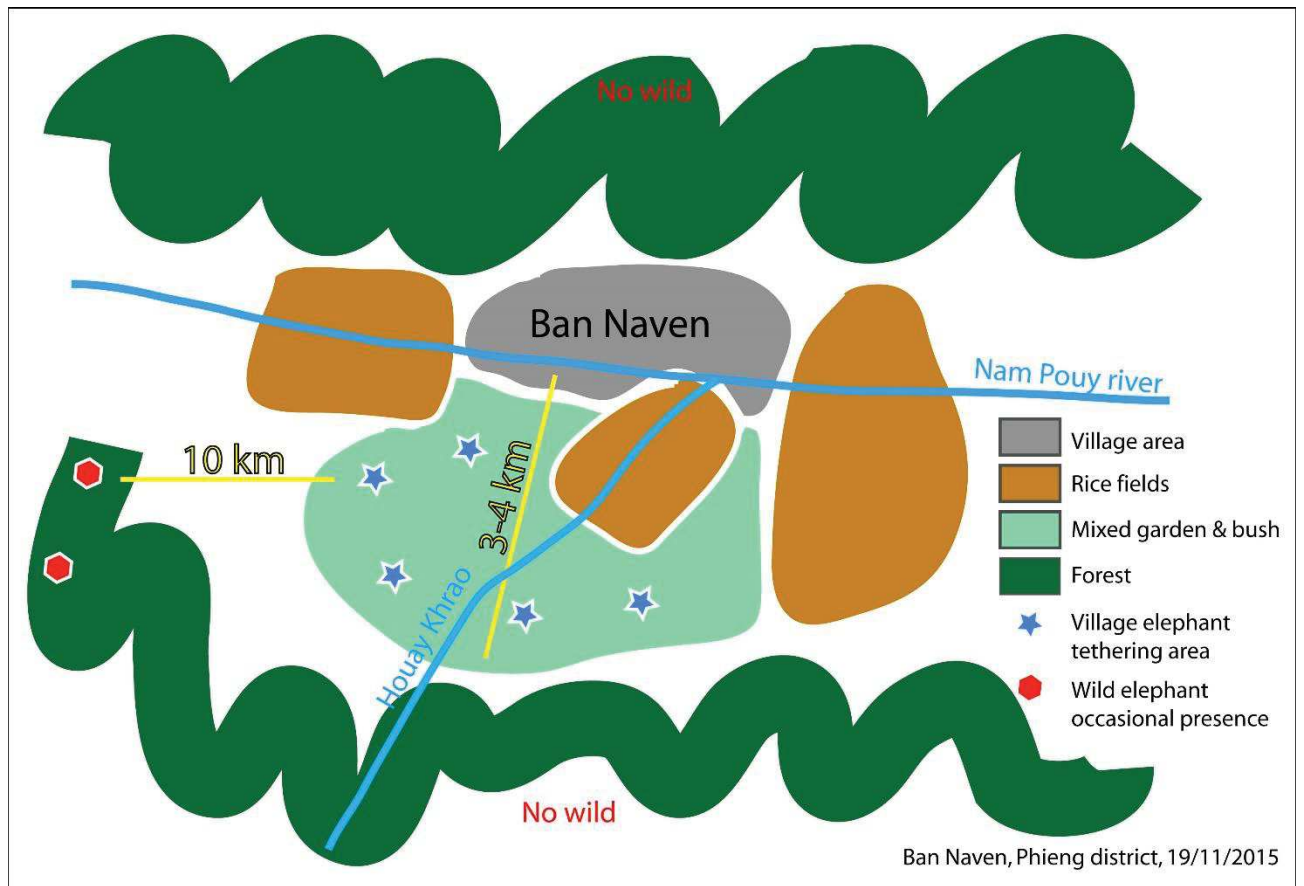


Figure 37 : Map of elephant keeping areas in Ban Naven, Phieng district
Village elephants are kept attached next to the village fields

8.2 Supplementary information Article 2

Wild-captive interactions and economy drive Asian elephant dynamics in Laos

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8.2.1 Breeding practices in Lao PDR

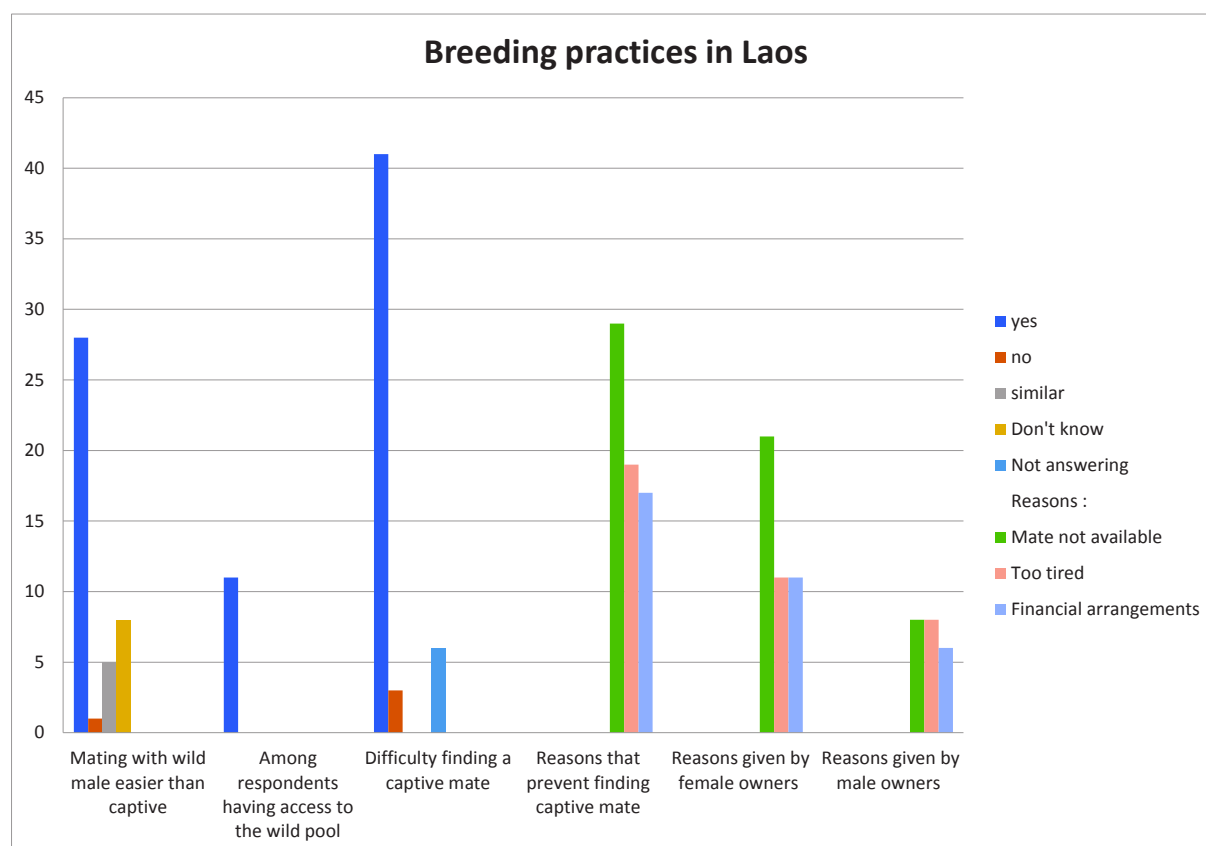


Figure 38 : Results from an anthropological study among elephant owners and keepers in Laos
Extracts from semi-structured interviews undertook in 2015 about elephant owners and keepers handling practices and their impact on the wild-captive interactions.

8.2.2 Modelling the owner decision-making process

To obtain projections from our bio-economic model, we developed a model to capture the owner decision-making process. Consistent with economic theory, we assume elephant owners maximize expected utility, where expected utility is wholly determined by expected profits (i.e., profits are the only argument in the owners' utility function, which is a standard in agricultural decision models) and where the only uncertainty stems from future prices and logging income. We also assume that owners make discrete time decisions in each period, but consider the future income stream in making each periods decision. So, an owner decides whether to breed or not by comparing the expected net-present value of profit from breeding to the expected net-present value of profit from not breeding. Considering these two states of the world for each individual female elephant in any decision period, the owner compares:

$$(1) E[NPV \text{ of profit from breeding}] = surv_3 * \frac{E[Price_{t+3}]}{(1+r)^4} + \sum_{t=4}^T \frac{E[Income_t]}{(1+r)^t}$$

with

$$(2) E[NPV \text{ of profit from not breeding}] = \sum_{t=1}^T \frac{E[Income_t]}{(1+r)^t}.$$

This expected utility(profit) maximization problem can be explicitly expressed as:

$$Max E[\pi] = \delta \left(surv_3 * \frac{E[Price_{t+3}]}{(1+r)^4} + \sum_{t=4}^T \frac{E[Income_t]}{(1+r)^t} \right) + (1 - \delta) \sum_{t=1}^T \frac{E[Income_t]}{(1+r)^t},$$

where $\delta = 1$ if the owner chooses to breed and zero if not. Solving this optimization problem results in an interior equilibrium where: $surv_3 * \frac{E[Price_{t+3}]}{(1+r)^4} = \sum_{t=1}^3 \frac{E[Income_t]}{(1+r)^t}$, or where the expected net present value of breeding exactly equals the opportunity cost of breeding (i.e., foregone timber income). Thus, owners will optimally choose to breed their elephants (or not) until this condition is met, which is equivalent to choosing to breed (or not) until the profit ratio is equal to 1.

Equation (2) gives the profit ratio P of the elephant price over the net-present value of logging income adjusted by the survival at 3 years:

$$P = surv_3 * \left[\frac{Price_{t+3}}{(1+r)^4} \right] / \left[\frac{Inc_t}{1+r} + \frac{Inc_{t+1}}{(1+r)^2} + \frac{Inc_{t+2}}{(1+r)^3} \right] \quad (2)$$

However, when the owner should make a decision, he does not know the future price of the elephant or his income at time $t + 3$; the different situations that may arise are summarized in the table below:

Time (in years)	t-1 DECISION	t	t+1	t+2	t+3 PROFIT
Reproduction	mating & 1st year gestation	2 nd year gestation	Birth, 1st year nursing	2 nd year nursing	3rd year nursing, taming
Income from breeding	Working Income (t-1)	0	0	0	Working Income (t+3) + Calf Price (t+3)
Income from working	Working Income (t-1)	Working Income (t)	Working Income (t+1)	Working Income (t+2)	Working Income (t+3)
Matrix parameters	Elephant price (t-1) & Income (t-1)	Fecundity (t), Price(t), Income(t)	Population Pop (t+1)	-	-

Table 8: Captive breeding timeframe

The mahout relies on the information at his disposal to motivate his choice, i.e. on prices in previous years, using the same approach described for European livestock farmers (Bonnays & Latouche 1989). Once his decision is made, he depends on the market price at time $t + 3$. Therefore, to estimate future prices, the mahout applies the average growth rate of the last two years over the coming years:

(i) the annual price increase of an elephant:
$$\Delta P = \left[\frac{Price_{t-2}}{Price_{t-3}} + \frac{Price_{t-1}}{Price_{t-2}} \right] / 2 \quad (S1)$$

(ii) the annual income increase:
$$\Delta I = \left[\frac{Income_{t-2}}{Income_{t-3}} + \frac{Income_{t-1}}{Income_{t-2}} \right] / 2 \quad (S2)$$

From equations (S1) and (S2), the mahout can estimate the future prices and incomes as follows:

Price_{t+3} = ΔP^4 * Price_{t-1}; Income_t = ΔI * Income_{t-1}; Income_{t+1} = ΔI^2 * Income_{t-1} and so on.

We obtain a revised version of the profit ratio (Eqn 2) based on price and income at time $t - 1$ when the mahout makes his decision:

$$profit = surv_3 * \left[\frac{\Delta P^4 * Price_{t-1}}{(1+r)^4} \right] - \left[\frac{\Delta I * Income_{t-1}}{1+r} \right] * \left[1 + \frac{\Delta I}{1+r} + \left(\frac{\Delta I}{1+r} \right)^2 \right] \quad (S3)$$

References

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8.2.3 Elasticity analysis

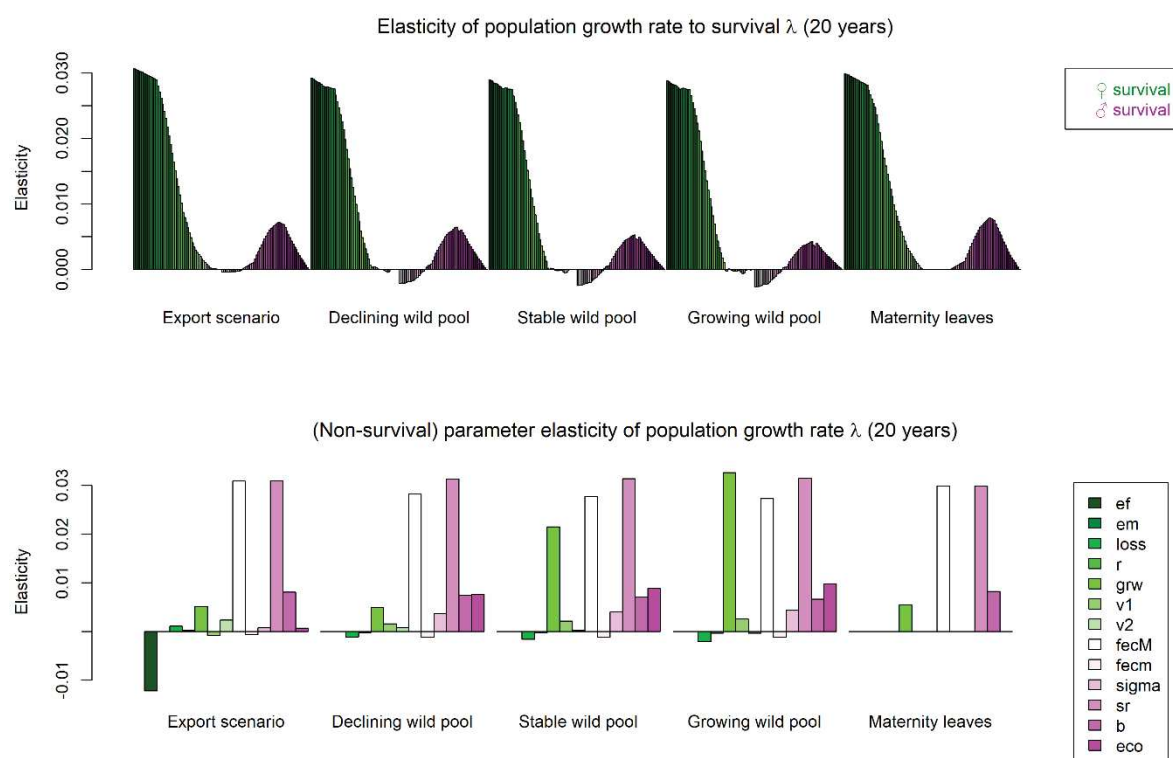


Figure 39 : Elasticity of population growth rate (λ) to model parameters (20-year projection)
Elasticity is given for survival from year 1 to 55 (upper chart) Parameters description (non survival parameters)

ef	Export rate – females
em	Export rate – males
loss	Maternity leave (Income=0)
r	Discount rate
grw	Wild pool growth
v1	Price regression intersect
v2	Price regression slope
fecM	Maximum fecundity
fecm	Minimum fecundity
sigma	Steepness of the fecundity function
sr	Sex ratio
b	Stretching exponent (Density Dep. reprod. Function).
eco	Economic growth rate projections

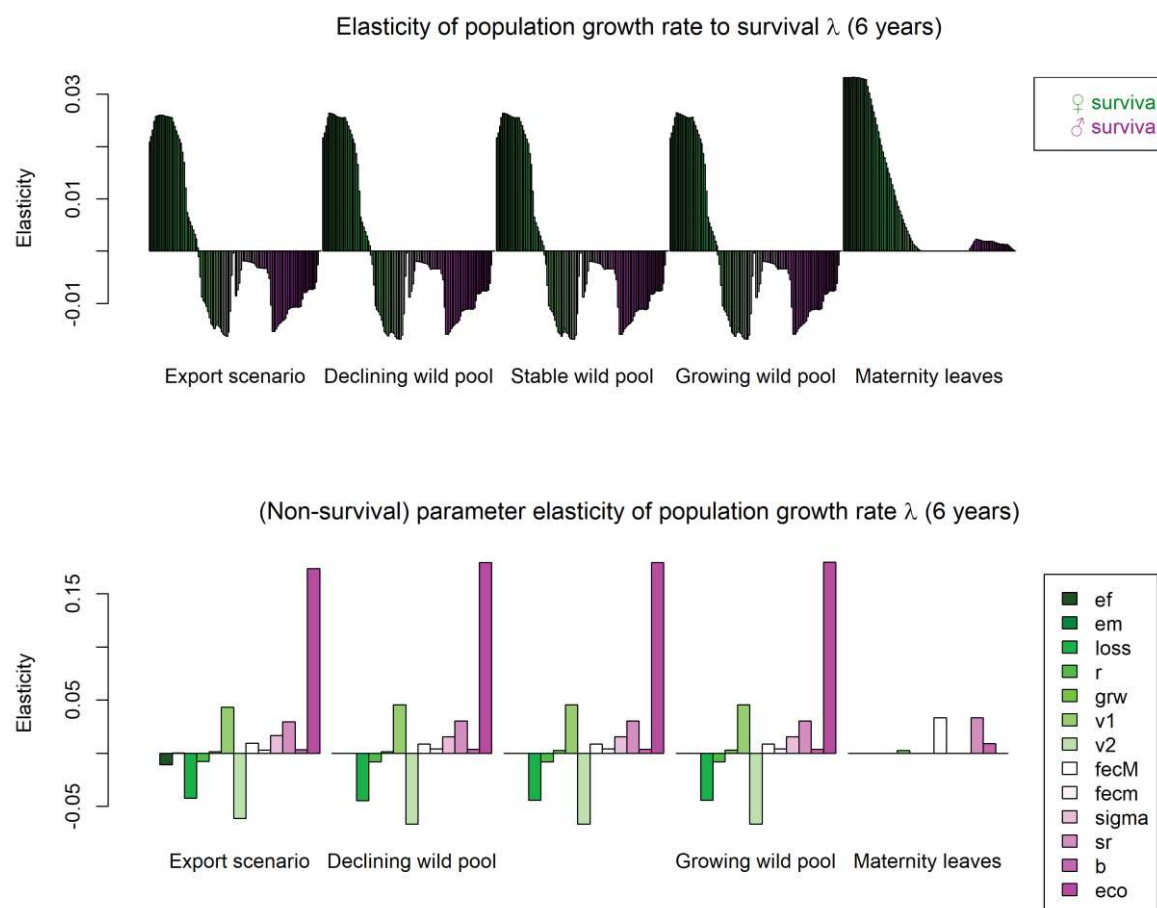


Figure 40 : Elasticity of population growth rate (λ) to model parameters (6-year projection)

On the short term (6 years) the population growth is highly sensitive to variation in economic growth (eco) with an elasticity of 0.18 and other economic-related parameters (v1 and v2 prices, loss of income during gestation) showing elasticities around 0.05. On a mid-term basis (20 years), the highest values of elasticities are for fecundity parameters [maximum fecundity (fecM) and sex ratio (sr) – 0.03], the wild pool growing rate [0.033 (growing wild pool) – 0.021 (stable wild pool) – 0.05 (declining wild pool)] and female export rate (0.05). Comparing the relative contribution of the model parameters on two different time scales confirms that socio-economic parameters are strongly impacting the population dynamics on the short term, while demographic rates (export, wild pool, fecundity, survival) are driving the dynamics on the long term.

8.2.4 Data and model parameters

Selected scenarios

	Female export (ef)	Male export (em)	Wild pool growth (grw)	Maternity leave (Income=0)
i) Reference scenario <i>No export scenarios below:</i>	0.04	0.01	0.92	1
ii) Declining wild pool	0	0	0.92	1
iii) Stable wild pool	0	0	1	1
iv) Growing wild pool	0	0	1.03	1
v) Maternity leave	0	0	0.92	0

Table 9 : parameters for the selected scenarios

Note 1: Calculation and sources for the Reference scenario (i) are given below.

Note 2: Other scenarios have been tested but not reported here. All scenarios with exports at the given reference rate lead to extinction, whatever the dynamics of the wild pool or maternity-leaves scheme.

Other parameters

	Description	Value	Source/comments
fecM	Maximum fecundity	0.155	From Sukumar, 1997 (Sukumar et al. 1997)
fecm	Minimum fecundity	0.02	From Suter, 2011 (Suter et al. 2013)
sigma	Steepness of the fecundity function	3	Fecundity is maximum when the profit ratio equals 2, i.e. stud fees equal income
sr	Sex ratio	0.5	
b	Stretching exponent (Density dependent reprod. Function).	2	From DD in manuscript
wm0	Wild pool at time 0	68	See wild pool estimate below
r	Discount rate	0.1	From Fisher, 2011; Markandya 1991; Tomish, 2001 (Fisher et al. 2011; Tomish et al. 2001; Markandya & Pearce 1991)
v1	Price regression intersect	119200	See prices below
v2	Price regression slope	-0.003633	
Inc	Income at time 0	4213	In constant USD from Suter, 2013 (Suter et al. 2013)
eco	Economic growth rate projections	1.051 (2012) 1.04 (+10 years) 1.035 (+10 years) 1.03 (+10 years) 1.025 (+10 years) 1,020	From ADB GDP long term projections (Asian Development Bank 2011)
N	Stochastic economic var.	Eco * N (1,0.01)	mean 1; variance 0.01

Table 10 : Other parameters used in the model

Survival rates

Year	Female	Male	Year	Female	Male	Year	Female	Male
0	0.918	0.908	19	0.991	0.991	38	0.973	0.958
1	0.951	0.925	20	0.996	0.981	39	0.959	0.957
2	0.976	0.964	21	0.996	0.99	40	1	0.985
3	0.984	0.975	22	0.988	0.98	41	0.978	0.954
4	0.952	0.918	23	0.992	0.99	42	1	0.968
5	0.946	0.945	24	0.991	0.99	43	0.98	0.983
6	0.976	0.956	25	0.98	0.98	44	0.931	0.966
7	0.99	0.962	26	0.986	0.99	45	0.986	0.947
8	0.992	0.984	27	0.995	0.979	46	0.926	0.981
9	0.995	0.984	28	0.989	0.989	47	1	0.962
10	0.994	0.967	29	0.989	0.978	48	0.972	0.941
11	0.999	0.992	30	0.985	0.978	49	0.962	0.958
12	0.994	0.991	31	0.985	0.977	50	0.962	0.891
13	0.992	0.983	32	0.993	0.977	51	0.962	0.985
14	0.996	0.982	33	0.993	0.976	52	0.962	0.99
15	0.987	0.991	34	0.992	0.976	53	0.962	0.95
16	0.997	0.991	35	0.97	0.963	54	0.962	0.895
17	0.99	0.982	36	0.981	0.974	55	0	0
18	0.996	0.981	37	0.98	0.96			

Table 11 : Survival rates by sex and age

Source : From Mar, 2007 (Mar 2007)

Female component of the matrix

$$\begin{bmatrix}
 0 & 0 & \dots & \dots & 0 & sf^0.sr.d.F & sf^0.sr.d.F & \dots & sf^0.sr.d.F & 0 & \dots & 0 & 0 \\
 sf^1 & 0 & & & & & & & & & & 0 & 0 \\
 0 & sf^2 & \dots & & & & & \dots & & \dots & & 0 & 0 \\
 \vdots & \ddots & & & & & & & & & & \vdots & \vdots \\
 & & sf^6 * (1 - ef) & & & & & & & & & & \\
 & & & \ddots & sf^{14} * (1 - ef) & & & & & & & & \\
 \vdots & & & & & sf^{15} * (1 - ef) & & & & & & \vdots & \\
 & & & & & & sf^{16} & & & & & & \\
 \vdots & & & & & & & \ddots & sf^{50} & & & & \\
 0 & 0 & & & & & & & & sf^{51} & & 0 & 0 \\
 0 & 0 & & \dots & & & \dots & & & & \ddots & sf^{54} & sf^{55}
 \end{bmatrix}$$

Eq. S4: Matrix – female component

The diagram above represents the first 55 columns corresponding to the 55 age classes of females only. The survival of females (sf^n) is expressed by age from 0 to 55 years. Fecundity (F) is applied to the age classes of females between 15 and 50 years with a sex ratio (sr) equal to 0.5 and corrected for survival before the first birthday (sf^0). Female export rate (ef) is applied between 5 to 15 years old. The matrix is supplemented by its equivalent for males. Export rate for males is applied to the same age classes (5-15 years) with a rate (em).

Data at origin (year 2012)

Captive population in 2012 by sex and age-class

Age class	Female	Male
[1:10]	23	11
[11:20]	20	16
[21:30]	64	73
[31:40]	97	64
[41:50]	86	47
[51:55]	20	7
Total	311	217

Table 12 : Captive population numbers by sex and age-class in 2012

Sources : Lao Elephant Care and Management Program (Lao Department of Livestock and Fisheries), data published in Suter, 2014 (Suter et al. 2014)

Wild pool growth rate estimate for the reference scenario

We modeled the dynamics of the wild pool using geometric growth calculated from

published data. The population growth from time t to time t' equals: $\left(\frac{N_{t'}}{N_t}\right)^{\frac{1}{t'-t}}$.

Year	Mean	range	Source
1990	450	400-500	From Phanthavong, 1992 (Phanthavong & Santiapillai 1992)
2000	350		From Duckworth, 1999 (Duckworth et al. 1999)
2009	100	100	From Khounboline, 2011 (Khounboline 2011)
2011	70	60-80	From Maurer, 2011 (Maurer & Bouchard 2011)

Table 13 : Estimates of the Nam Pouy wild population across time

We calculated the average geometric growth (grw) over the period 1990-2012 and modeled the population such as $w_m(t+1) = grw \times w_m(t)$, with $w_m(t)$ the total population at time t , $w_m(0) = 68$ the population at time 0, and $grw = 0.92$ the average growth rate of the population. This annual decrease of 8% illustrates the sharp decline of this population over the last 20 years.

Elephant prices

Year	1994	1997	1999	2006	2007	2008	2009	2010	2011	2012	2013
USD	7830	6690	5010	9330	9960	18300	15800	11500	15400	17000	19000
			9740		8900			9420	16800	17900	
					12200			13700		19300	
					8770			13300		25000	
								14100			
								14300			
								14900			
								11900			

Table 14 : Elephant prices in constant USD

Source : Ethno-ecological study, prices have been converted in constant USD in the year 2000 using the methodology of Williamson (Williamson & Officer 2010).

8.2.5 List of references Appendixes article 2

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8.3 Published version of Article 2

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Wild-captive interactions and economics drive dynamics of Asian elephants in Laos

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The interactions between wild and captive populations of Asian elephants (*Elephas maximus*) persist in most countries of the species distribution, notably through the reproduction between captive females and wild males. However, these complex interactions have been poorly studied, despite their relevance for conservation of this endangered species. Laos has a centuries-long tradition of raising Asian elephants. Besides being cultural icons, captive elephants are inextricably linked to economics through their work in forestry. Using an ecological-economic model, we investigated the effect of socio-economic strategies on fecundity of the Lao population whose dynamics is shaped by human practices. We demonstrated that fecundity is impacted by: i) the dynamics of the wild elephant pool through mating of captive females by wild males, and ii) the financial incentive of elephant owners to breed their animals. As a result, we expect fecundity to rise in response to increases in elephant prices. The captive population will tend towards an asymptotic limit determined by the wild pool growth rate. However, the population will tend to extinction if exports continue. Our ecological-economic approach, by accounting for economic incentives, allows us to predict new equilibria that can serve as a baseline for designing sustainable management strategies for the species.

The population of Asian elephants, *Elephas maximus*, is in overall decline and classified as endangered by the International Union for Conservation of Nature. Total population abundance ranges from 30,000 to 50,000 individuals; however, these figures are probably overestimates^{1–3}. One-quarter to one-third of the population consists of captive elephants^{4,5}. Captive elephants were traditionally sourced from wild populations though bans on wild capture have been in place since the 1970s^{6–8}. These so-called “domestic” elephants are, however, not a domesticated species and are similar to their wild counterparts in terms of genetics and behaviour⁹.

The interactions between wild and captive populations persist in most countries of the species distribution, mainly through reproduction between captive females and wild males. In Laos, India and Myanmar, captive females are released in the forest and pair with wild males^{9–12}. Nearly 80% of calves born in captivity in Laos during the past decade are from wild genitors from the Nam Pouy Protected Area (V. Chanthavong, pers. comm.). In Myanmar, live capture of wild elephants has been used to sustain the captive pool. This practice may, however, pose a serious threat to the survival of the country’s wild population⁴. Elephant calves also have great appeal to tourists and, hence, are highly valued¹³. With corruption, a lack of law enforcement, and deficient registration systems of captive individuals in many Asian countries, the incentive is high to illegally capture and smuggle calves to supply the tourism sector¹⁴. As a result, the captive population partially relies on wild males for breeding, while the wild pool is threatened by illegal captures to supplement the captive pool. Both captive and wild pools also share common threats and conservation challenges, such as habitat destruction, poaching, increased conflicts with local human populations, and risks of inbreeding depression¹². Despite their relevance for the conservation of the species, the complex interactions between wild and captive pools have been poorly studied.

The understanding of Asian elephant demography and ecology has recently improved thanks to a longitudinal study of a large semi-captive population in Myanmar. For example, it has been shown how life histories could

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impact reproductive success, survival or senescence^{15–18}. Climate variations also impact age-specific survival of Asian elephants^{19,20}. Besides survival, large variations in average fecundity rates have been observed in different populations across the region and over time, with a fecundity rate of 0.023 (2.3% of breeding females) in Laos²¹, 0.083 in Myanmar¹¹, and varying from 0.095 to 0.155 for a captive elephant population in India over the past century¹⁰. No systematic assessment explains why the captive birth rates are highly variable and lower than birth rates observed in wild populations. It has been hypothesized to be the consequence of management and husbandry practices, which in effect place breeding secondary to work⁴.

The alteration of vital rates in the dynamics of wild-captive Asian elephant populations illustrates the intricacies of mixing natural and human-induced mechanisms²². Our objective was to assess the effect of these interactions on the viability of Asian elephant populations using an ecological-economic modelling approach with Lao populations as a case study.

Lao captive elephants are traditionally used as draught animals in the logging industry and share the same habitat as their wild conspecifics. In the last twenty years, the intensification of elephants' workload has affected the fecundity of the population, leading to a sharp decline from 1,000 to 540 individuals²¹. The long gestation and lactation period for female elephants is not compatible with work⁴. Owners consider breeding to represent a loss of income for nearly three years and therefore avoid breeding their elephants, preferring the high incomes generated by the logging industry⁴. Meanwhile, the contiguous Nam Pouy wild population has experienced a sharp decrease from 400–500 individuals in 1990 to 60–80 in 2010^{23–25}, further hindering the reproductive potential between wild males and captive females. Finally, the Lao captive population has also been affected by the withdrawal of individuals through the export of captive juveniles to third countries. These exports violate the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) despite its ratification by the Lao government in 2014. While exports are highly regulated, the trade of captive elephants is unregulated on the domestic market²⁶.

To develop a demographic model incorporating economic constraints, we considered the processes impacting the dynamics of captive elephants with a focus on the determinants of fecundity. Therefore, we developed a model including three components: (i) a demographic component structured by sex and age, including the exports of living captive elephants, to estimate the captive population abundance at a given time; (ii) a wild elephant component to account for the wild male breeding potential; (iii) and an economic component to model the elephant owner's decision-making process. Finally, we defined several demographic and socioeconomic scenarios to investigate new ecological-economic equilibria that can serve as a basis to design sustainable management strategy for the species.

Results

Changes in breeding practices. Breeding practices radically changed since Laos transitioned to an open market economy in 1989. Traditionally, captive elephants were used for occasional village work while spending most of their time in small herds, grazing freely in the village surroundings. Mating of captive females with either captive or wild males was uncontrolled.

In 2015, we conducted 52 semi-structured interviews among elephant owners, keepers, and officials throughout the distribution of captive elephants in Laos – 41 out of 50 respondents indicated difficulties finding a captive mate. Among owners of females, the main reason given for the difficulty in finding a captive male was the absence of captive breeding males (21 out of 43) because “there is no male nearby”, “males are kept far away”, “they (males) are engaged in logging and therefore not available for mating”, or “the few males living nearby” are “too young” or “sterile”. Two other reasons were given equally (11): stud fees being too expensive, and their elephant being too tired for breeding. Owners of males indicated having difficulties finding a captive female for mating because “females are not available” (8), “their male is too tired for mating” (8), and “females owners do not want to pay stud fees” (6).

Meanwhile 28 out of 42 respondents considered that mating with a wild male is easier than with a captive one, including all respondents (11) living at the edge of Nam Pouy park and having access to the wild pool. Such a mating system was easier because wild males are “available”, “free of their movements”, “in good health”, “not exhausted unlike the working captive males”, and “do not ask for stud fee payment”.

As a consequence, the reproduction of captive females depends mainly on the presence of wild males in Nam Pouy, and to a lesser extent, on the availability of a captive mate. Unlike in wild populations, the reproduction of captive females is density-dependent towards males.

How much does an elephant cost? The captive population dynamics are also driven by the willingness of owners to breed their female. According to economic theory, owners maximize profits, and therefore have to make an economic choice between breeding their female or having them work in the logging industry. The owner estimates how much he can earn by selling a calf after weaning and compares these earnings with the foregone alternative income from logging during the three-year gestation and weaning period.

Our model incorporated the price of an elephant following supply and demand theory – that is, a product (i.e., elephant) is a function of its quantity (i.e., the population). Thus, the price of an elephant can be expressed in terms of the population size given by the demographic component of the model. We associated the sale price given by 26 owners who sold their elephants between 1994 and 2012, to the population size produced by the model at the time of sale. Elephant prices in constant USD were exponentially related to total population (all parameters being different from 0 with p -value < 0.035).

The price of an elephant in constant USD increased with the decrease in population (Fig. 1). From 1990 to 2012, the increasing scarcity of elephants was accompanied by a rapid increase in sale prices exceeding 20,000 constant USD²⁷. This result illustrates that the relationship between quantity and price is consistent with economic

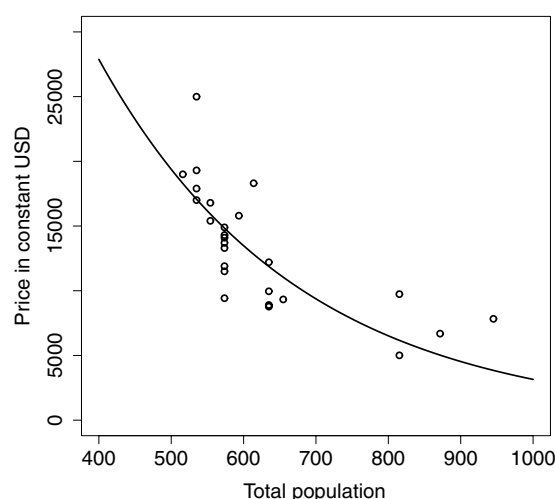


Figure 1. Elephant price is a function of total population abundance. Prices are given in constant USD, base year 2000.

theory. Lower populations (quantity available to the market) lead to higher prices, which lead more owners to conclude it is profitable to breed their elephants rather than using them for logging.

Population projections depending on ecological-economic scenarios. Using our ecological-economic model, we investigated the impacts of economic and government policies on future trends in the captive population. The government may impact the population dynamics by revising its policy on the controversial export of elephants to third countries and by fighting illegal trade. The government could also reinforce its wild elephant conservation policy by enforcing the law and effectively protecting the Nam Pouy park wild pool. Finally, the government and private stakeholders could promote pro-birth policies for captive elephants (e.g., by compensating owners for foregone logging returns).

Based on the 2012 population census of captive elephants and on estimates of the Nam Pouy wild population, we selected five scenarios that are representative of the different dynamics of the wild pool and levels of exports. All scenarios are based on a price-dependent domestic market. The reference scenario (i) showed the current level of exports of juveniles and a decreasing wild pool at a rate of 8%. The four other scenarios were based on an effective prevention of exports with (ii) a decreasing wild pool, (iii) a stabilized wild pool to investigate the effect of a conservation policy, (iv) a growing wild pool, and (v) a maternity-leave scheme that financially compensates owners for the loss of income during the breeding period. We ran all scenarios for a period of 100 years with stochasticity in the economic growth rate.

Whatever the scenario, the population decreases during the first 35 years until it recovers from the transient and unstable structure observed in 2012 (Fig. 2a). If current export practices continue (i), the population decline slows, but tends to extinction over the long term with an estimated population of 10 individuals after 480 years. If exports are prevented, the population reaches an asymptotic equilibrium that depends on the dynamics of the wild pool. After 100 years, the captive population reaches an abundance of 355, 371 and 408 individuals for a decreasing (ii), stabilized (iii), or growing (iv) wild pool. Maternity leaves (v) are the only scenario allowing the population to exceed 2012 abundance with 554 individuals. In this case, compensating the owners' loss of income counteracts the prevailing effect of economic incentives on elephant fecundity.

The population decrease due to exports (i) tends to sharply pull prices upward (Fig. 2c), reaching prices over 800,000 constant USD. The population increases for the other scenarios equalize prices from USD 206,000 [s.d. 20,000] (scenario v) to USD 428,000 [s.d. 39,000] (scenario ii). Consequently, the profit ratio (Fig. 2d) stabilizes respectively at 1.36 [s.d. 0.02] (iv), 1.56 [s.d. 0.02] (iii) and 1.65 [s.d. 0.03] (ii). The rising prices in the export scenario (i) brings the profit ratio to 3.35 [s.d. 0.05] after 100 years. As maternity leaves cover the loss of income, profit ratio of scenario (v) tends to infinity.

Fecundity rates (Fig. 2b) follow the same growing trend as the profit ratio, but are constrained by density dependence in reproduction (see Methods). Export scenario (i) displays the higher fecundity rate of 0.117 followed by the maternity leave (v) fecundity rate 0.105. The fecundity rates in the three other scenarios (ii to iv) are approximately 0.095.

Changes in demand for elephants. Because we study elephant population dynamics, we built an economic model centered on supply. Variations in supply, the total population, explain price fluctuations given that demand for elephants is proportional to supply. We investigated the effect of a change in demand by applying a 25% decrease and increase in elephant prices. If demand fluctuates over time, using fixed rates allowed us to define a maximum interval bounding the total population estimates under supply and demand equilibrium (Fig. 3).

In the export scenario (i), population estimates range from 141 to 172 for a 25% decrease and a 25% increase in demand for elephants. The declining (ii) and growing (iv) wild pool scenarios have respective population

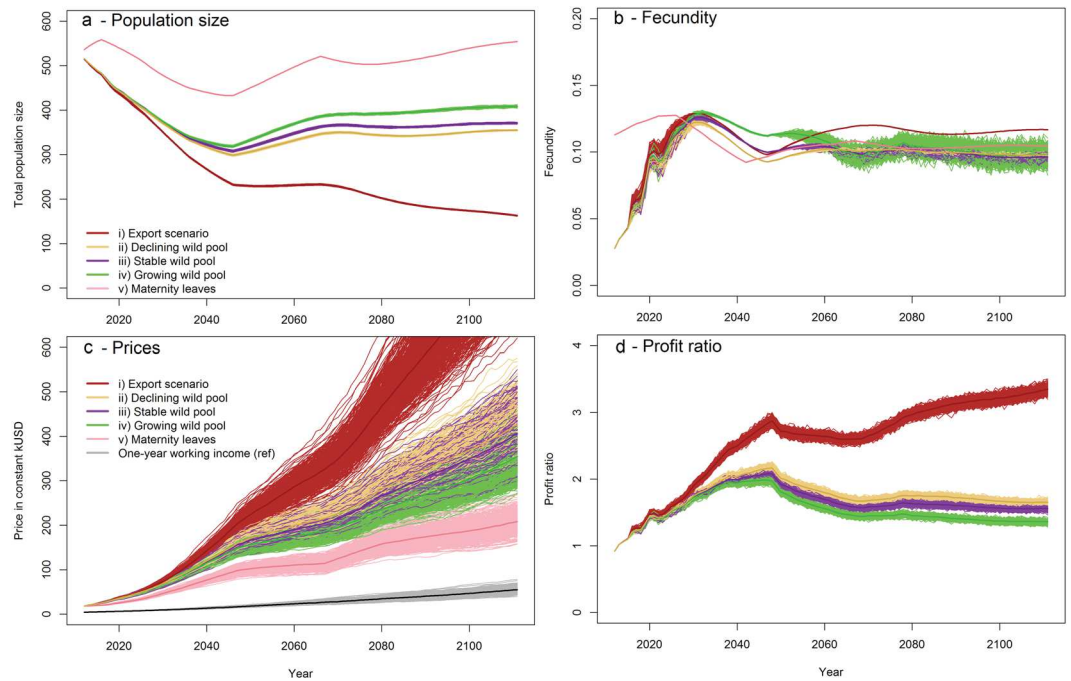


Figure 2. Model projections depending on ecological-economic scenarios (a) Population estimates; (b) Fecundity; (c) Elephant prices in constant thousand USD; (d) Profit ratio. The different scenarios within each figure are: (i) Current level of exports and declining wild pool; (ii) No export and declining wild pool at a growth rate of 0.92; (iii) No export and stable wild pool; (iv) No export and growing wild pool at a growth rate of 1.03; (v) Maternity-leave compensation scheme with no export and declining wild pool. The median value of the 500 simulations is shown in contrasted color. The gray line in (d) shows one-year working income as a reference. (d) does not show the profit ratio for the maternity-leave scenario (v) as it tends to infinity.

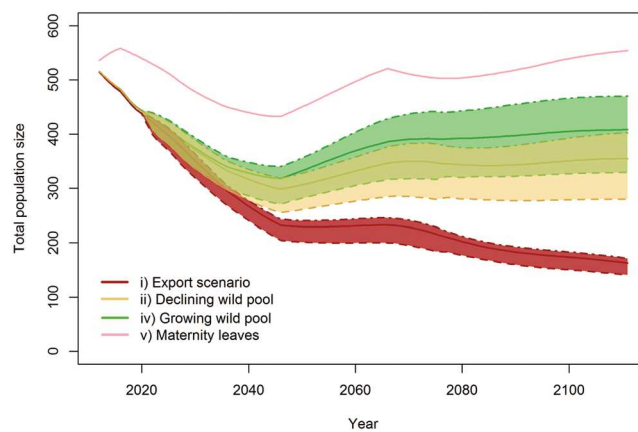


Figure 3. Population size projections under various scenarios of demand variation. (i) Current level of exports and declining wild pool. (ii) No export and declining wild pool at 8% per year. (iv) No export and growing wild pool at 3% per year. (v) Maternity-leave compensation scheme with no export and declining wild pool. Dot-dashed lines give the total population size for demand increase (upper estimate), dashed lines the total population size for demand decrease (lower estimate) and plain lines the total population size with constant demand (as shown in Fig. 2a). Demand variations do not affect maternity-leave scenario (v).

estimates of 280 to 402 and 330 to 470. Once again, population size in the maternity-leave scenario (vi) is not affected by the variation in demand.

Elasticity analysis. We projected the population out 20 years in each scenario and calculated the elasticity of the resulting population growth rate to model parameters (see Supp. Note 3). The parameter showing the highest elasticity (0.033) is the wild pool growth rate (grw) for the growing wild pool scenario (iv). It decreases to 0.021 for the stable wild pool scenario (iii) and 0.005 for the declining wild pool (ii), export (i) and maternity-leaves

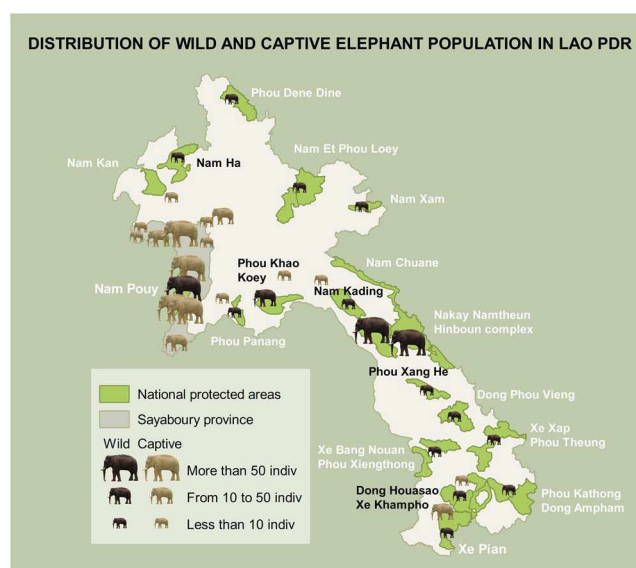


Figure 4. Map of captive and wild elephant populations in Lao PDR. Map has been designed with QGIS version 2.14.0-Essen (www.qgis.org) and Photoshop version 9.0 (www.adobe.com). Protected areas shape files are downloaded from The World Database on Protected Areas (WDPA), IUCN and UNEP-WCMC (2017), available at: www.protectedplanet.net.

(v). The female export rate shows a medium-range elasticity (0.012) for the export scenario (i) while it is null for all other scenarios. All other parameters show similar elasticities whatever the scenario with maximum fecundity and sex ratio at a rate of approximately 0.03. Elasticity to female survival rates decline continuously from 0.03 to zero. Elasticity to male survival shows much lower values with a maximum of 0.007 for the 35 years age class. Other model parameters have an elasticity rate lower than 0.001, including all economic parameters.

Discussion

No study has investigated the effects of socio-economic strategies on the fecundity of an animal population whose dynamics are shaped by human economic practices. We demonstrate that fecundity of captive elephants is impacted by: i) the dynamics of the wild elephant pool through mating of captive females by wild males, and ii) the economic incentives of elephant owners to breed their animals. As a result, we expect fecundity to rise again gradually in response to the rapid increase in the price of elephants. The captive population will tend towards an asymptotic limit determined by the dynamics of the wild pool. In any case, the population will tend to extinction if the government does not stop export practices at current rates. Elephant exports, mostly to Chinese zoos and tourism enterprises, threaten the survival of the Laotian population.

Our model illustrates the strong interactions between the wild and captive pools. The value of captive elephants for conservation have been recognized, not only because of their numbers and the threat that their capture could pose to wild pools, but also for their potential roles in reintroduction, patrolling, human-elephant conflict mitigation, and scientific research^{9,28}. Beyond the risks of extinction of wild populations, we showed that wild pool dynamics directly impact the survival of the captive population through crossbreeding. The elasticity analysis confirms the influential contribution of a stable or growing wild pool to the growth of the captive population. The Nam Pouy wild pool was modelled using a geometric growth rate, based on published data^{23–25}; however, these data are scarce and approximate. A better estimate and monitoring of the abundance of this population would reinforce the recognition of how dynamics of the wild pool affect the demography of the captive pool. For the time being, it seems urgent to strictly protect the wild populations and consider organizing new wild-captive breeding areas in Laos. Policy-makers should also consider the side-benefits of a strict conservation strategy for wild elephants in regards to the cultural and economic role played by captive elephants.

Our ecological-economic approach also emphasizes the impacts of human practices on the dynamics of the captive elephant pool. Several models have been developed to search for potential balance between ecological and economic dynamics. Most of these models favored a macroeconomic approach – searching for a global equilibrium between total profit maximization and population survival^{29–31}. In our case, we directly linked fecundity with owner profit maximization. In the absence of reliable macroeconomic data, this microeconomic approach allowed us to model the owner's decision-making process and study its impact on species' demography. However, our elephant price dataset was derived from data for a population between 530 and 900 individuals. Therefore, the estimated price of elephants in a population of less than 200 individuals remains questionable, being far from the original data range. This was one reason we limited our projections to 100 years.

As shown by our model, changes in handling practices have long-term effects on population structure and dynamics. In 2012, the population was already transient and unstable, with a strong bias in favour of adults over 20 years old (see the age pyramid in Methods – Model calibration). As a result, the model indicates it will take 35 years before the population grows again. Long-lived species, such as the Asian elephant, are highly sensitive to

population inertia³², with long periods before the population may recover from any change in a vital rate. Further investigation of such transient status and its consequences on elephant population dynamics are needed. But our model demonstrates that the commodification of captive elephants and its accompanying changes in handling practices have probably dominated the ecological dynamics of this population, as shown by the short-term elasticity analysis (Supp. Note 3).

Our maternity-leave compensation scheme provides additional insights into the conservation questions surrounding captive and semi-captive populations. If owners are compensated for their loss of income during breeding, the steep economic trade-off between using an elephant for breeding versus work is removed, the elasticity of all economic parameters being null under this scenario. By covering the opportunity cost of breeding, the maternity-leave scheme we analysed allows the population to exceed its 2012 abundance. Such a policy could be funded either by a tax on elephant incomes or directly by the tourism industry, for which calves are highly prized. Because the tourism industry is also a buyer of elephants, supporting such population growth would also put downward pressure on elephant prices (Fig. 2c).

Overall, our ecological-economic model does not explicitly predict the size of the elephant population in a century. It rather provides a framework for policy-makers, conservationists and managers to anticipate the impacts of socio-economic determinants and their policies —such as exports, or wild elephant conservation— on the fate of the population. Moreover, the interactions between captive and wild pools should be further investigated as they set in motion poorly understood demographic, genetic, epidemiological, economic and socio-cultural processes that strongly influence the species' population viability.

Methods

Study Species and Area. Laos has a centuries-long tradition of raising Asian elephants²³. Most captive elephants live in remote areas and are used to extract logs in the forestry industry^{27,33}. After their daily working hours, they are tied to trees where they can forage by themselves and are moved twice a day by their keepers. Keepers also often release their elephants in the forest for a few months while the keepers are engaged in rice farming³⁴. Most of the country's captive elephants live in Sayaboury province (Fig. 4), which also hosts the Nam Pouy National Park (Lat: 18°12'–18°58'N, Long: 101°04'–101°32'E) – home of the second largest wild population in the country^{23,27,34}.

Population data. Since 2006, the Lao Care and Management Program (LECMP) of the Department of Livestock and Fisheries of Lao PDR has implemented a national campaign to register all captive elephants. Captive elephants are microchipped by the LECMP. Their records, including name, microchip number, sex, age, physical description, medical history, ownership details and location, are saved in a database. Data are updated twice-yearly during LECMP veterinary care visits. We used the data on captive populations structured by sex and age extracted from the database with the year 2012 as a reference²¹. Data on the Nam Pouy wild elephant population from 1990 to 2012 were extracted from the literature^{23–25}. More details on the data used throughout are provided in Supplementary Note 4.

Trade in captive elephants. Captive elephants are privately owned in Laos. Domestic trade is allowed after the payment of a tax to local authorities²⁶. Elephant prices are driven by demand on the domestic market. Domestic sales or re-sales do not change the size of the population unlike exports. CITES Convention does not allow international trade in elephants. Despite its ratification by the Lao government in 2004, the export of living elephants continues. Juvenile females illegally cross the border into Thailand and China⁹. National authorities also export young elephants in the form of “rentals” or diplomatic gifts²¹. Being either legal or illegal, exports are considered as permanent, individuals are permanently removed from the captive population.

Breeding practices in Lao PDR. We studied mahout (elephant handler) practices and their impacts on wild-captive interactions using ethno-ecological methods. The topics covered in this study included the perception of the species and its wild-captive status, the description of husbandry practices, including working, temporary releasing, breeding and interacting with the wild pool, and the respondent perception of the future. In particular, this study described the free-grazing and husbandry practices in Laos that are potentially interfering with the wild elephant pool, and described the mating systems between captive mates. The breeding practices observed during the ethno-ecological study served as a basis to model the drivers of captive population fecundity. Another article is in preparation that will present the global results of the ethno-ecological study.

In 2015, we conducted 52 semi-structured interviews among elephant owners, handlers, and officials throughout the distribution of captive elephants in Laos. Interviews were conducted in Lao language by the first author, recorded on a Zoom H1 handy recorder, and fully translated into French and English. All methods were carried out in accordance with the guidelines for anthropological surveys³⁵, and in accordance with the legal requirements of France and the National Center for Scientific Research (CNRS) institutional protocols for research. Research protocol has been approved by Montpellier University. All participants provided informed verbal consent before participation. Sampling was done using a stratified method based on the district of residence and ownership status of the respondent. We coded answers using MaxQDA Analytics Pro 12 software for qualitative data analysis.

Demographic model for the captive population. We developed a population model composed of a two-sex and 55-age-class matrix to account for the sexual dimorphism in vital rates and sex-specific animal handling practices (Fig. 5).

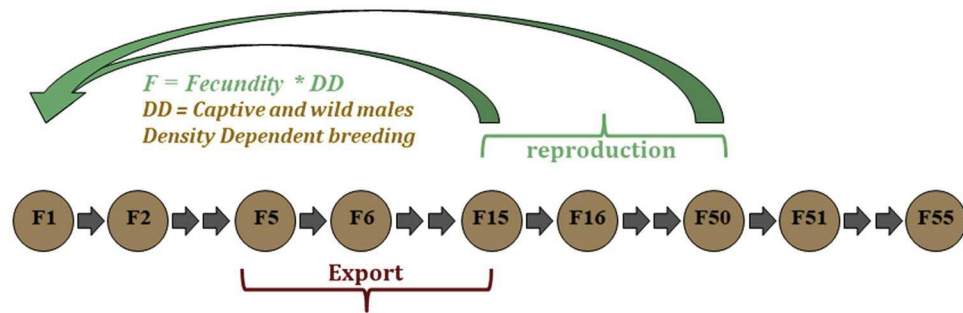


Figure 5. Life cycle of captive females.

Survival. Demographic data from Laos did not allow estimation of survival rates. We used sex- and age-specific survival rates for a semi-captive elephant population in neighboring Myanmar that shares similar working practices³⁶. Survival is given per year from age 0 to 55 with sf^n the female survival at age n and sm^n the male survival (see data in Supp. Note 4).

Exports. From a population perspective, exports to foreign countries are considered permanent migration. We apply an export function to survival for individuals aged 5 to 15 years with $sf^n(1-ef)$ for females and $sm^n(1-em)$ for males. We defined 2 scenarios: a ban on exports (ef and em equal 0) and the reference scenario showing the current level of exports. Since females are preferred to males due to their docility and reproductive potential, the respective rates for ef and em are set to 0.04 and 0.01 for the reference scenario.

Birth. Yearly recruitment is given by the product ($sf^0 sr d F$) for females aged from 15 to 50, with sf^0 the female survival before their first year, sr a balanced sex ratio at birth, d the density dependence function and F the fecundity function, described hereafter. The same formula is used for males with sm^0 as the male survival rate.

Density-dependent reproduction. As captive males are engaged in logging activities, many owners of females do not find male mates. Working males are chained to a tree during their resting time and are therefore not available for mating. A prior breeding agreement between female and male owners is therefore required. But female owners found the costs of stud fees too expensive and male owners are reluctant to engage their males in mating because mating is time-consuming and believed to reduce a male's working strength. Most births therefore result from mating between a captive female and a wild male from Nam Pouy Park. When the breeding process depends on external factors, such as the availability of captive males or the presence of a wild mating pool, the fecundity function is weighted by a coefficient d ³⁷. We introduced a density-dependent reproductive function in relation to the proportion of the mating pool³⁸ where the probability for a captive female to reproduce is dependent on the ratio of the number of breeding males from the captive and wild pools to the number of captive breeding females:

$$d = \frac{1}{1 + e^{-\frac{bNm}{Nf}}} \quad (1)$$

with Nf the number of captive females of breeding age (15 to 50 years), Nm the number of captive breeding males from 30 to 55 years plus the estimated number of wild males living in Nam Pouy Park, and b the stretching exponent of the function. The parameter b allows the growth of the function to be adjusted. In the case of this long-lived polygynous species, we set the stretching exponent to 2. Thus, for a given population of 200 reproductive females and 20, 60 or 100 breeding males respectively, fecundity will be affected by a coefficient d equal to 0.57, 0.71 or 0.92, illustrating a steep decrease in the reproductive potential due to the unavailability of males (Fig. 6).

Population dynamics of the wild pool. The reproduction of captive females depends partially on the Nam Pouy wild pool, as explained above. Given the limited information available on this population, we model the change in Nam Pouy wild population using a population growth rate $wm(t+1) = grw \times wm(t)$, with $wm(t)$ the total population at time t ($wm(0) = 68$ the population at time 0) and grw the yearly average growth rate of Nam Pouy population. We select three different growth rates to explore how wild elephant conservation policies could impact the captive dynamics: an increasing wild pool at a rate of 3% per year, a stable wild pool, and a declining wild pool at a rate of 8% per year. This annual decrease of 8% reflects the sharp decline of this population over the last 20 years (see data in Supplementary Note 4).

Economic decision-making. According to microeconomic theory, owners tend to maximize profit. Because breeding is not compatible with female elephants working, elephant owners make an economic choice between having their female elephants breed or work. Thus, our economic model assumes owners maximize expected profits by choosing whether or not to breed their females, where the expectation arises because owners do not know future elephant prices or logging income with certainty. This decision framework implies a decision rule where owners will choose to breed up until the expected net present value of breeding exactly equals the

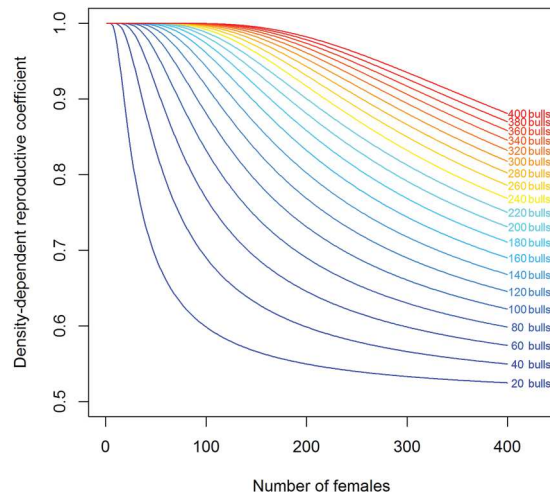


Figure 6. Density-dependent reproductive coefficient depending on the number of females. The density-dependent reproductive function is plotted for several male breeding stock levels: from 20 males (blue line) up to 400 (red line), at 20-male intervals. For a given male stock (one line in the chart), the density-dependent coefficient decreases when the number of females increases, meaning that fecundity is negatively impacted by the excess of females relative to breeding males.

opportunity cost of breeding (i.e., foregone timber income). This is equivalent to choosing to breed until the profit ratio (2) is equal to or greater than 1.

At any point in time, the owner compares how much they could receive in net present value by selling a calf after weaning ($Price_{t+3}$), knowing that the survival at 3 years ($surv_3$) is 0.75, with the alternative income from logging during the 3 years. The profit ratio P is therefore:

$$P = \left[surv_3 * \frac{Price_{t+3}}{(1+r)^4} \right] \left/ \left[\frac{Inc_t}{1+r} + \frac{Inc_{t+1}}{(1+r)^2} + \frac{Inc_{t+2}}{(1+r)^3} \right] \right. \quad (2)$$

with $r = 10\%$, the discount rate that takes into account the time value of money or the risk aversion for agricultural projects in Asian developing countries^{39–41}. Thus, a profit ratio greater than 1 implies there is an economic incentive to breed females, whereas a profit ratio less than 1 implies that the opportunity cost of foregone logging profits is too large to justify breeding. More information on owners' price estimation methods are given in Supplementary Note 2. Finally, the costs related to each activity do not appear in the calculation of the profit because they are limited – elephants are foraging freely in Laos, and the cost of guarding is identical with or without a calf. As a result, feeding and labor costs of the two alternatives do not influence the marginal decision to breed or not.

All monetary values, including incomes and profit, have been converted to constant US dollars (USD) in the year 2000 using the methods of Williamson⁴² in order to correct prices for the high inflation in Laos.

Price and Income. According to supply and demand theory, the price of an elephant can be expressed in terms of the population size given by the demographic components of the model. From the ethno-ecological study conducted among 26 owners who sold elephants between 1994 and 2012, we assigned each reported price to the population estimate given by the model at the time of sale. Elephant price in constant USD follows an exponential relationship:

$$Price = v_1 e^{v_2 \text{ population}} \quad (3)$$

with v_1 (Est. = 119200, $t = 2.234$, $p = 0.035$) and v_2 (Est. = -0.003633 , $t = -4.697$, $p \ll 0.01$).

Working incomes are estimated from IC Suter's 2011 survey²⁷ among 133 elephant owners and keepers, which indicated that average income was equivalent to 4,070 constant USD (i.e., 6.11 times the constant per capita Gross Domestic Product (GDP)). Economists generally use GDP per capita as an indicator of changes in household incomes⁴³.

To estimate prices and incomes after 2012, we applied an average economic growth rate (eco_t) to the owner income and price of an elephant according to the long-term GDP projections from the Asian Development Bank⁴⁴. Moreover, we added stochastic variation to the projected economic growth rate following a normal distribution with mean 1 and a variance of 0.01. Thus, from 2012 and forward, prices at time t equal: $Future\ prices_t = Reg(price_t) \prod_{j=1}^t eco_j * \mathcal{N}(1, 0.01)$, with $Reg(Price)$ the price function (Equation 3). Income at time $t + 1$ is given by $Income_{t+1} = Income_t * eco_t * \mathcal{N}(1, 0.01)$.

Linking fecundity with elephant owners' profit. Fecundity is driven by the financial incentive of owners to breed their elephants instead of having them work. When working income exceeds that of breeding (profit ratio $P < 1$), the incentive to breed is low and fecundity is minimal or opportunistic (f_{min}). Fecundity increases as

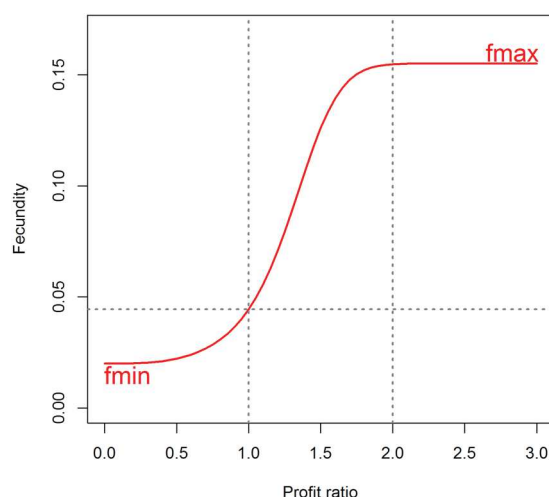


Figure 7. Fecundity as a function of the owner's profit. Profit is the ratio of the calf's selling price to the income generated by the foregone work. Fecundity is maximum when breeding generates twice as much as working.

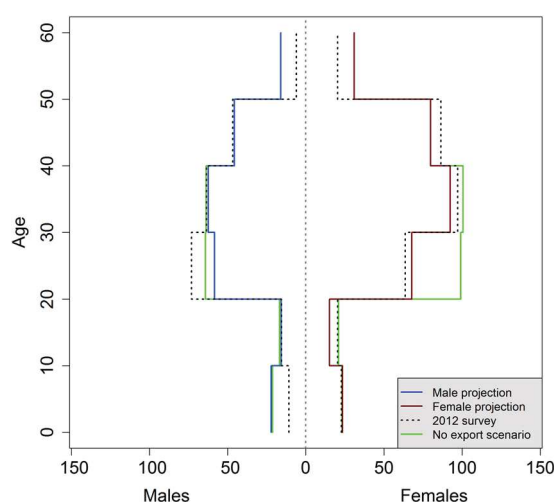


Figure 8. Age pyramid of captive elephants in 2012. Dotted lines show the number of males and females given by the 2012 census. Solid lines indicate the results of the model projection for year 2012. The green line shows the structure of the population in absence of export, confirming the effect of this practice on the number of females aged from 20 to 30 years.

profit increases up to a maximum (f_{max}) set by the biological constraints of the species (Fig. 7). Thus, we model fecundity (F) as a logistic function:

$$F = f_{max} \frac{1}{1 + \left(\frac{f_{max}}{f_{min}} - 1 \right) e^{-P^\sigma}} \quad (4)$$

where P is the profit ratio (2). The function is bounded respectively by f_{max} the maximal fecundity and f_{min} the opportunistic fecundity. The parameter σ is used to fit the steepness of the function⁴⁵ so that fecundity is maximized when the profit ratio equals 2. We retained a profit ratio of 2 for f_{max} to account for the most extreme case in breeding arrangements (i.e., where all owners consider it profitable to breed their females). Such a rate is a strong incentive for any owner able to pair his female with a wild male. However, the owner of a captive sire usually claims a maximum of one third of the calf value or calf ownership as stud fee, leaving 2/3 of the calf price to the female's owner (Netvalue = 2/3). In this case the profit for the female's owner should be positive if: $Price * surv_3 * Netvalue \geq \sum_{t=1}^3 Inc_t$ (derived from Equation 2), or profit ratio $P \geq 2$. As a result, parameter values used in our model are $f_{max} = 0.155$ ¹⁰, $f_{min} = 0.02$ ²¹, and $\sigma = 3$.

Sensitivity and elasticity analyses. The sensitivity analysis allows studying the effect of variation in the model parameters on the population dynamics as measured by their asymptotic growth rate (λ). The asymptotic population growth rate, calculated as the dominant eigenvalue of the matrix, is calculated using the R popbio package⁴⁶. We used elasticities instead of sensitivities because these metrics take into account the unit in which the demographic parameters are measured and thus make comparisons possible between these parameters. The elasticity (EL) of parameter α is given by:

$$EL(\alpha) = \frac{(\lambda' - \lambda)}{\lambda(1 + \Delta\alpha)}$$

where λ' is the new value of λ after applying a variation Δ to the parameter α .

Model calibration. To calibrate our model, we projected the population over 20 years starting from a stable structured population of one thousand individuals in 1992 and compared its demographic structure with the observed structure in 2012. Population abundance reached 530 individuals, consistent with 2012 estimate of 527 individuals. Moreover, the population structure is highly transient and unstable. A strong bias is observed in favor of elephants over 20 years old and a deficit of females in the 20–29 years age class resulting from our hypotheses (sharp drop in fecundity and export of juvenile females during the last twenty years). The population structure derived in the model (Fig. 8) cannot be distinguished from the structure inferred from the 2012 census data (Chisq = 13.6, df = 11, p = 0.25). All analyses were performed with R version 3.2.3⁴⁷.

Data Availability. All data generated or analysed during this study are included in this published article (and its Supplementary Information files).

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Author Contributions

G.M. and O.G. designed the study. V.C. and G.M. collected the data. G.M. built the model and analysed the data with O.G. and B.R. G.M. wrote the paper with contributions from O.G. and B.R. All authors reviewed the manuscript.

Additional Information

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8.4 Supplementary information Article 3

Genetic structure of wild and captive elephants across Laos and Myanmar with implications for management

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8.4.1 Analysis of Molecular Variance and pairwise FST

Source of variation	d.f.	Sum of squares	Variance components	Percentage of variation
Among groups	1	11.085	0.08663 Va	2.36
Among populations within groups	4	17.384	0.01862 Vb	0.51
Among individuals within populations	116	417.764	0.03636 Vc	0.99
Within individuals	122	430.500	3.52869 Vd	96.14
Total	243	876.734	3.67030	

Fixation Indices

FIS : 0.01020

FSC : 0.00520

FCT : 0.02360

FIT : 0.03858

Population pairwise FSTs	South Laos	Central Laos	Breeding Laos	North Laos	Myanmar East	Myanmar West
South Laos	0.00000					
Central Laos	0.00515	0.00000				
Breeding Laos	0.00991	0.00971*	0.00000			
North Laos	0.00344	0.00261	0.00338	0.00000		
Myanmar East	0.06775*	0.02942*	0.06342*	0.04077*	0.00000	
Myanmar West	0.01744	0.00270	0.02535*	0.01708	0.00511	0.00000

	South Laos	Central Laos	Breeding Laos	North Laos	Myanmar Captive born	Myanmar Wild caught
South Laos	0.00000					
Central Laos	0.00515	0.00000				
Breeding Laos	0.00991	0.00971*	0.00000			
North Laos	0.00344	0.00261	0.00338	0.00000		
Myanmar Captive born	0.04276*	0.01521*	0.04245*	0.02676*	0.00000	
Myanmar Wild caught	0.02987	0.00593	0.04063*	0.02483	-0.00824	0.00000

Table 15 : Analysis of Molecular Variance and pairwise FST

8.4.2 Estimate of the number of clusters K in the population structure

8.4.2.1 Model assuming admixture, ignoring population affiliation and allowing for correlation of allele frequencies between clusters.

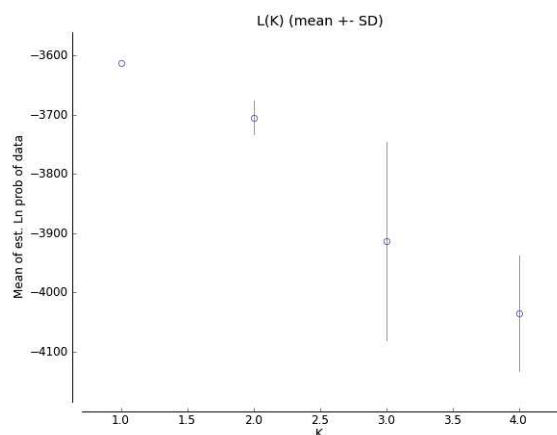


Figure 41 : Mean and Standard deviation of estimate of the posterior probability of the data for a given K without population affiliation

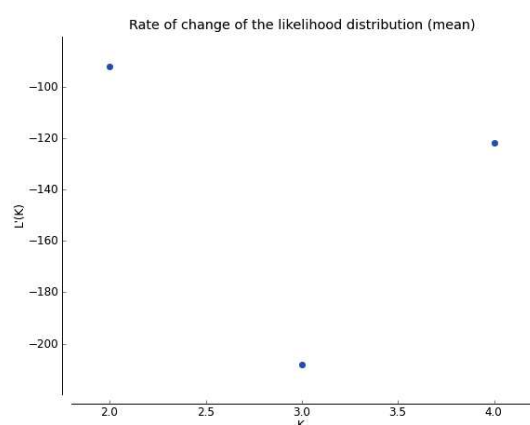


Figure 42 : Rate of change of the likelihood distribution for a given K without population affiliation

K	Reps	Mean LnP(K)	St dev LnP(K)	Ln'(K)	Ln''(K)	Delta K
1	5	-3612.9000	0.3674	NA	NA	NA
2	5	-3705.0200	28.7666	-92.120000	116.000000	4.032455
3	5	-3913.1400	167.6622	-208.120000	86.360000	0.515083
4	5	-4034.9000	97.6808	-121.760000	NA	NA

Table 16 : Data for a given K without population affiliation (Evanno et al. 2005 method)

Reps : Number of replicates;

Mean LnP(K): Mean and Standard deviation of estimate of the posterior probability of the data for a given K;

St dev LnP(K): Standard deviation of estimate of the posterior probability of the data for a given K;

Ln'(K) : Rate of change of the likelihood distribution;

|Ln''(K)| : Absolute values of the second order rate of change of the likelihood distribution;

Delta K : modal value of the distribution of ΔK .

8.4.2.2 Model assuming admixture, including population affiliation and allowing for correlation of allele frequencies between clusters.

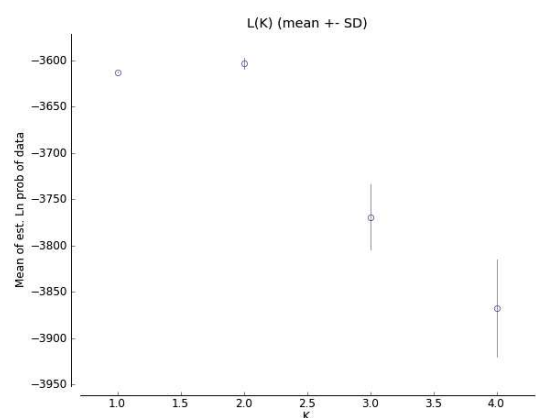


Figure 43 : Mean and Standard deviation of estimate of the posterior probability of the data for a given K with population affiliation

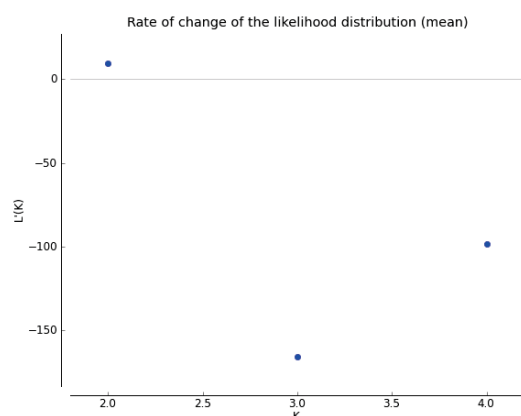


Figure 44 : Rate of change of the likelihood distribution for a given K with population affiliation

K	Reps	Mean LnP(K)	Stdev LnP(K)	Ln'(K)	Ln''(K)	Delta K
1	15	-3612.98000	0.290812	—	—	—
2	15	-3603.42000	6.262268	9.560000	175.260000	27.986666
3	15	-3769.12000	34.827128	-165.700000	67.253333	1.931062
4	15	-3867.56667	52.369384	-98.446667	—	—

Table 17 : Data for a given K without population affiliation (Evanno et al. 2005 method)

From Earl, Dent A. and vonHoldt, Bridgett M. (2012)

Reps : Number of replicates;

Mean LnP(K): Mean and Standard deviation of estimate of the posterior probability of the data for a given K;

St dev LnP(K): Standard deviation of estimate of the posterior probability of the data for a given K;

Ln'(K) : Rate of change of the likelihood distribution;

|Ln''(K)| : Absolute values of the second order rate of change of the likelihood distribution;

Delta K : modal value of the distribution of ΔK .

STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method.

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10 Thesis Abstract

Title : Asian elephant (*Elephas maximus*) conservation through the study of interactions between human, captive and wild elephant populations: an integrated approach

For thousands of years, the Asian elephant has played an important role in the culture, economy and construction of Asian nations. Almost a quarter of the population of this emblematic and threatened species consists of so-called captive elephants. However, both national legislation and conservation programmes tend to treat captive and wild populations separately. In Laos and Myanmar, the tradition of elephant handling by villagers and the interactions between wild and village elephants still persist.

The objective of this thesis is to qualify and quantify these interactions to better understand their dynamics and roles in the survival of the species. I described the factors driving the socio-ecological system between humans, village and wild elephants and its resilience through an interdisciplinary and integrative approach.

Based on an ethnoecological study, I analyzed the recent evolution of the human-elephant socio-ecological system in Laos and its consequences on human-elephant relations, husbandry practices and the perception of the species among elephant owners. The emergence since 2000 of the commodification of nature and the restriction of access to forests has led, on the one hand, to the segregation between wild and village elephants and, on the other hand, to the transition from a traditional to an intensive keeping system of village elephants. Community perception and tolerance towards wild elephants is linked to the principle of reciprocity. Owners having access to wild males to sire their females accept the presence of wild elephants contrary to mahouts engaged in logging activities.

I then built a bio-economic model to quantify the effects of socio-economic strategies on the long-term viability of village elephant population in Laos. I demonstrated that fecundity is impacted primarily by the dynamics of the wild population through reproduction between village females and wild males. Second, the fecundity is impacted by the financial incentive of elephant owners to

breed their animals instead of working. Thus population viability is highly dependent on socio-economic conditions in the short term and the efficiency of wild elephant conservation in the long term.

A population genetics study showed that the genetic diversity of wild and village elephant was high and differentiation was weak between Laos and Myanmar. The isolation of wild populations and the increasing segregation of village elephants will lead to genetic loss and inbreeding that can be managed by promoting gene flows at the regional level and between the two populations. The study suggests considering both populations from the two countries as a unique management unit. These two studies illustrate that resilience of the socio-ecological system is the result of multiple factors acting at different levels or scales, sometimes in opposite ways.

Finally, this thesis allows to discuss the conditions of resilience and long-term viability of the human-elephant socio-ecological system and to explore potential scenarios including the on-going domestication process of the species.

Keywords : *elephas maximus*, socio-ecological system, domestication, conservation, interactions, Laos

11 Résumé de la thèse

Depuis des millénaires, l'éléphant d'Asie joue un rôle important dans la culture, l'économie et la construction des pays asiatiques. Près d'un quart de la population de cette espèce emblématique et menacée est constituée d'éléphants dits captifs. Toutefois, les législations nationales comme les programmes de conservation ont tendance à traiter séparément les populations captives et sauvages. Au Laos et au Myanmar, la tradition d'élevage par les villageois et les interactions entre éléphants sauvages et éléphants de villages perdurent.

L'objectif de cette thèse est de qualifier et quantifier ces interactions afin de mieux comprendre leurs dynamiques et leurs rôles dans la survie de l'espèce. Je me suis attaché à décrire les facteurs déterminant le système socio-écologique humain - éléphant de village - éléphant sauvage et sa résilience à travers une approche interdisciplinaire et intégrative.

Une étude ethnoécologique a permis d'analyser l'évolution récente du système socio-écologique homme-éléphant au Laos et ses conséquences sur les relations humain-éléphant, les pratiques d'élevage et la perception de l'espèce chez les propriétaires d'éléphants. L'émergence depuis les années 2000 de la marchandisation de la nature et de la restriction de l'accès aux forêts a conduit, d'une part, à la ségrégation entre éléphants sauvages et éléphants de villages, et d'autre part, à l'intensification de l'élevage de ces derniers. Or, la tolérance des communautés à la présence des éléphants sauvages semble liée au principe de réciprocité. Ainsi, les propriétaires ayant accès aux mâles sauvages pour féconder leurs femelles acceptent leur présence contrairement aux cornacs engagés dans le débardage du bois.

J'ai ensuite construit un modèle bio-économique pour quantifier les effets des stratégies socio-économiques sur la viabilité à long terme de la population d'éléphants de villages du Laos. J'ai montré que la fécondité est impactée en premier lieu par la dynamique de la population sauvage à travers la reproduction entre femelles de villages et mâles sauvages. En second lieu, le taux de fécondité dépend de l'intérêt financier des propriétaires à faire de la reproduction. Ainsi la viabilité de la population est fortement dépendante des conditions socio-économiques sur le court terme et de l'efficacité de la conservation des populations sauvages sur le long terme.

Une étude de génétique des populations a montré que la diversité génétique des populations sauvages et de villages était élevée et que ces populations constituaient un ensemble homogène au Laos et au Myanmar. L'isolement des populations sauvages et la ségrégation croissante des populations de villages engendreront un appauvrissement génétique sur le long terme qu'il est possible de limiter par des mesures de gestion favorisant le flux de gènes au niveau régional et entre les deux populations, notamment en les considérant comme une unité de gestion commune.

Ces deux études illustrent que la résilience du système socio-écologique est la résultante de multiples facteurs agissant à différents niveaux ou échelles, dont les effets sont parfois opposés.

Cette thèse permet enfin de discuter des conditions de la résilience et de la viabilité à long terme du système socio-écologique humain-éléphant et d'explorer différents scénarios futurs en s'interrogeant également sur le possible processus de domestication de l'espèce.

Mots clefs : *elephas maximus*, système socio-écologique, domestication, conservation, interactions, Laos