Trunk grasping and manipulation of the African savannah elephants (Loxodonta africana) : behavioural and morpho-functional variability

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Trunk grasping and manipulation *of* the African savannah elephants (*Loxodonta africana*): behavioural and morpho-functional variability

Julie Soppelsa

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Tout observateur est un intrus dans le domaine d'un animal sauvage
et doit se rappeler que les droits de cet animal priment sur les intérêts humains.

Dian Fossey

Abstract

The trunk is a fundamental organ for the elephants that can perform both powerful and delicate functions. However, its evolution and precise adaptations remain an enigma. What are the parameters that may have played a role in the evolution of this organ? Although trunks do not fossilise, their adaptations can be addressed by studying extant proboscideans, whose populations vary in terms of behaviour and living environments. The challenge is therefore to understand the links between the environment, the morpho-functional variability and the behavioural variability in trunk use. The aim of this PhD work is to highlight these potential links during trunk grasping and manipulation behaviour in extant African savannah elephants (*Loxodonta africana*).

This work is divided into four parts. The first part contextualises the importance of the trunk by studying the behavioural variability of its uses. The second part focuses on the individual variability of trunk grasping and manipulation techniques, the third on the effects of the environment on these techniques. Finally, the last part addresses the effects of food properties on the distal shape of the trunk during grasping. The data were collected in two wild sites (one arid in Namibia and the other one wetter in South Africa) for the first three chapters, involving more than a hundred identified elephants, and in the Beauval Zoo Park (France) for the last chapter. The methodological approach is interdisciplinary, based on ethology and functional morphology. This "functional ethology" provides a better understanding of morphological adaptations linked to behaviour, and vice versa. Through these novels behavioural and morpho-functional quantification, we explore the variability of trunk use between individuals and populations.

Thus, this work provides a couple of important results. Several behaviours that involve the trunk vary according to the sex and age of the elephant. Similarly, trunk grasping and manipulation techniques vary greatly between individuals, depending on the morphology of their tusks, the object grasped and the task. Interestingly, these techniques also vary between the two studied populations, which live in very different environments. Finally, there is an influence of the size and shape of the food grasped on the preform of the trunk distal part. These results allow us to better understand how optimal grasps are performed with the trunk, and how it certainly improves the animal physical conditions. In this thesis, we also apprehend for the first time the effects of habitat and morphology on elephant grasping and manipulation.

Therefore, it brings new information on the questions of grasping and manipulation evolution in tetrapods. The perspectives of this work are numerous. Indeed, it is currently essential to understand how elephants adapt to rapid environmental changes, to help with the great challenge of their conservation. Furthermore, a better understanding of how elephant trunks work is a key issue in the design of new bio-inspired robotic arms, which need to be flexible, powerful and precise at the same time.

Résumé étendu

La trompe est un organe fondamental pour les éléphants : ils l'emploient pour connaître leur environnement, établir des liens sociaux, utiliser des outils, ou encore manipuler eau et nourriture. Ce proboscis étant très mobile et flexible, il peut se courber et s'enrouler dans toutes les directions, mais aussi s'étendre ou se condenser. Il est ainsi capable d'accomplir des fonctions à la fois puissantes et délicates, notamment en ce qui concerne la saisie et la manipulation. Or, l'évolution de la trompe chez les éléphants et ses adaptations précises restent une énigme. Quels sont les paramètres qui ont pu jouer un rôle dans l'évolution de cet organe ? Si les trompes ne se fossilisent pas, il est tout à fait possible d'aborder leurs adaptations en étudiant les Proboscidés actuels, dont les populations varient en termes de comportements et de milieux de vie.

L'enjeu est donc de comprendre quels sont les liens existants entre le milieu, la variabilité morpho-fonctionnelle et la variabilité comportementale associés à la trompe, pour appréhender ses adaptations et son évolution, et ainsi mieux comprendre comment les éléphants vivent et s'adaptent. Plus particulièrement, l'objectif de ce travail de thèse est de mettre en évidence les liens susceptibles d'exister entre écologie, forme et fonction lors des comportements de saisie et manipulation avec la trompe, et de comprendre quelles sont les techniques utilisées par les éléphants de savane d'Afrique actuels (*Loxodonta africana*) pour saisir et manipuler.

Ce travail de thèse se compose de quatre chapitres. Le premier permet de contextualiser l'importance de la trompe en caractérisant et quantifiant la variabilité comportementale de ses utilisations. Cette variabilité comportementale a été étudiée plus particulièrement sous le prisme des différences sexuelles et en prenant en compte l'âge des éléphants. L'éléphant de savane d'Afrique étant un animal avec un dimorphisme et une ségrégation sexuelle prononcés, ces différences comportementales entre mâles et femelles peuvent être d'autant plus marquées. En ce qui concerne les trois autres chapitres de la thèse, ils se focalisent plus directement sur les techniques de saisie et manipulations de la trompe. Ces techniques ont été caractérisées par un ensemble de critères de mouvements dans les chapitres deux et trois. Le deuxième chapitre porte plus particulièrement sur les variabilités individuelles des techniques de saisie et manipulation de la trompe, et la troisième sur

les effets du milieu sur ces techniques, en étudiant deux populations distinctes d'éléphants. Enfin, le dernier chapitre se concentre sur une technique de saisie précise avec la partie distale de la trompe, ainsi que les différences individuelles concernant cette partie distale. Plus précisément, ce dernier chapitre de la thèse aborde la préforme de la trompe, en regardant les effets des propriétés de la nourriture sur la conformation distale de celle-ci lors de saisies.

Les données analysées sont issues du milieu naturel pour les trois premiers chapitres, avec des données récoltées en milieu aride en Namibie et des données récoltées en milieu plus humide en Afrique du Sud. Ces données observationnelles impliquent plus d'une centaine d'éléphants sauvages identifiés, fait rare pour une étude comportementale de mammifères. Concernant le dernier chapitre, ce sont des données expérimentales qui ont été récoltées auprès de six éléphantes du ZooParc de Beauval (France) et sur lesquelles des analyses de morphométrie géométrique ont été appliquées. L'utilisation de ces analyses pour quantifier la préforme d'une structure souple, ici la partie distale de la trompe, est une approche totalement inédite. L'approche méthodologique de la thèse est alors pluridisciplinaire, articulée autour de l'éthologie et de la morphologie fonctionnelle. Cette « éthologie fonctionnelle » permet de mieux comprendre les adaptations morphologiques liées aux comportements, et inversement. Nous explorons ainsi, par des quantifications comportementales et morpho-fonctionnelles inédites, les variabilités d'utilisation de la trompe entre individus et entre populations.

Ce travail apporte de nombreux résultats majeurs. Tout d'abord, certaines activités de l'éléphant qui impliquent la trompe varient en fonction de son sexe et de son âge. Néanmoins, le temps passé à utiliser la trompe dans ces activités ne varie pas entre les mâles et femelles. Les techniques principales de saisie et de manipulation de la trompe ont également été caractérisées, ainsi que leurs variations individuelles et populationnelles. Ces techniques varient grandement en fonction de l'objet saisi, de la tâche de saisie ou de manipulation, des individus, de leur environnement social et de la morphologie de leurs défenses. De manière très intéressante, ces techniques varient aussi fortement entre les deux populations étudiées, qui vivent dans des milieux très différents et possèdent des morphologies différentes. Enfin, il existe une influence de la taille et de la forme de la nourriture saisie sur la préforme de la partie distale de la trompe. Cette préforme varie selon les individus, qui ont chacun une forme de partie distale unique.

Ces résultats permettent d'en apprendre davantage sur l'utilisation et les adaptations de la trompe des éléphants, mais aussi d'explorer les capacités de préhension et manipulation d'un hydrostat musculaire. Ce travail de thèse est le

premier à explorer et quantifier les utilisations de la trompe chez des éléphants sauvages. Il permet de mieux comprendre comment les saisies optimales sont effectuées avec la trompe, et comment cela améliore très probablement les conditions physiques de l'animal. La mise en avant de techniques de saisie et manipulation différentes en fonction des individus et populations a également permis d'aborder pour la première fois les questions d'effets de l'habitat et de la morphologie sur la saisie et la manipulation chez les éléphants. Comprendre ces fonctionnements en milieu naturel apporte alors des connaissances sur l'évolution de la préhension et la manipulation chez les éléphants, mais aussi plus généralement chez les tétrapodes.

Les perspectives de ces travaux sont nombreuses. Ce travail de thèse pourra avoir des applications directes notamment en ce qui concerne le domaine de la robotique souple bio-inspirée, mais aussi en ce qui concerne la conservation des éléphants sauvages, actuellement en danger d'extinction. En effet, mieux comprendre le fonctionnement des trompes d'éléphant constitue un enjeu essentiel dans la conception de nouveaux bras robotiques bio-inspirés, flexibles, puissants et précis. De plus, il est actuellement essentiel de comprendre comment les éléphants s'adaptent aux changements rapides d'environnement, pour aider au grand défi qu'est leur conservation.

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Table of contents

Tables list

Figures list

General introduction

General introduction

The Last Giants

The elephants are part of the taxonomic order Proboscidea (Illiger, 1811), literally "trunk" in Greek (*proboskis*) and Latin (*proboscis*). Indeed, most Proboscidea species are easily identifiable by the presence of a trunk. The others distinctive features present in several proboscideans are their evolved incisors, the tusks, their massive heights and their specialised dentition for browse and graze (Göhlich, 1999; Osborn, 1936; see Shoshani, 1998 for a review). However, in the early proboscideans' taxa such as *Eritherium azzouzorum*, the oldest known Proboscidea (60 million years, Gheerbrant, 2009), it was determined, with the skull, that the trunk was certainly absent. Proboscidea order is composed of a profusion of species, mostly fossils, with different types of trunks, tusks, and body masses in different habitats (Göhlich, 1999; Haynes, 1993; Osborn, 1936). Currently, it remains only one living family, the Elephantidae, which appeared during the Miocene (Kalb, 1996). These giants are represented by only three extant species: the Asian elephant (*Elephas maximus*), the African forest elephant (*Loxodonta cyclotis*) and the African savannah elephant (*Loxodonta africana*, Hart et al., 2021; Roca et al., 2001). Besides the tusks, long trunks and large bodies, these mammals are also easily identifiable by their wrinkled grey skin with few hairs and their big flapping ears.

The elephants are well known to the general public because of their imposing stature. Children are taught to recognise them from an early age through a large variety of stories, with great representation of their trumpeting, high memory, tool use, tusks sparring and great migration abilities (Hart et al., 2008; Poole & Granli 2011; Purdon et al., 2018, **Figure 0.1**). These animals have always had a special place in human history, whether with divine representation or when escorting humans in war conquests. Indeed, Asian elephant exploitation has been going on for at least 3,000 years for war, tiger hunting, carrying burdens, logging and tourism (Cheeran & Poole, 1996). For African elephants, the practice was relinquished but the animal still remains an important resource for tourism, as part of the Big Five (the five large animals to see in Africa).

Figure 0.1 – Tusks sparring between two male adult elephants during social play. Picture © J. Soppelsa.

As their names suggest, African savannah elephants and African forest elephants inhabit the African continent. *Loxodonta africana* are found in a diverse range of environments throughout the continent, except, today, in the north (Gobush et al., 2021a). *Loxodonta cyclotis* are restricted to the central and western African rainforests and their outskirts (Bonnald et al., 2021; Grubb et al., 2000). Forest elephants are smaller than savannah elephants (Grubb et al., 2000). They have rounder and smaller ears, thinner and uncurved tusks, and darker and hairier skin. The number of toenails also differs between the two species: *Loxodonta africana* has four toenails on its forelegs and three on its hind legs, while it is five and four for *Loxodonta cyclotis* (Sikes, 1971). In these two species, the trunk tip ends in two digital expansions. This is different for the Asian elephant, which has only one digital expansion on the upper part of its trunk tip (Hoffmann et al., 2004, **Figure 0.2**).

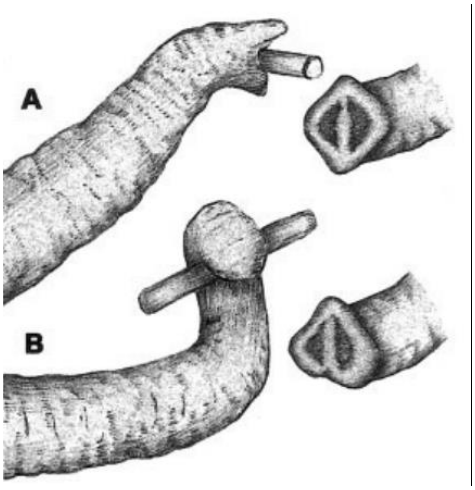

Figure 0.2 – (A) Trunk tip morphology of the African savannah elephant (*Loxodonta africana*) with two digital expansions that permits the precise pinch grip. (B) Trunk tip morphology of the Asian elephants (*Elephas maximus*) with one digital expansion; the grip usually involves curling of the trunk around an object. In Hoffman et al., 2004.

Living across Southern Asia in a forest environment, *Elephas maximus* never overlapped with the range of the two other species (Olivier, 1978; Williams et al., 2020). These habitat variations for the three species lead to differences in diets. Although these exclusive vegetarians eat a wide variety of plants, the type and parts of plants eaten differ with the species (Koirala et al., 2016; Owen-Smith & Chafota, 2012; Pretorius et al., 2012). Their diet consist mainly of grasses, leaves, branchs, lianas, bark, and sometimes termite mounds, soil deposits and salt-rich waterholes for mineral supplements (Mwangi et al., 2004; Weir, 1969). African elephants and Asian elephants also differ in their general morphology: Asian elephant backs and heads are bulging (twin-domed head), their ears are smaller and more rectangular, their skin smoother and their teeth differ in shapes (Haynes, 1993; Todd, 2010, **Figure 0.3**). The tusks differ too, as in modern Asian elephant females and some males have rudimentary tusks, while both sexes in African elephants generally exhibit tusks. *Elephas maximus* also possess different number of toenails (Csuti et al., 2001). Although clear marked differences between the three species in morphology, behaviour and genetics (Debruyne, 2004; Grubb et al., 2000; Hart et al., 2021; Hedwig et al., 2021; Payne, 2013; Roca et al., 2001), they remain together the last largest extant animals on earth, particularly the African savannah elephants.

Figure 0.3 – Males Asian elephants (*Elephas maximus*), African forest elephant (*Loxodonta cyclotis*) and African savannah elephant (*Loxodonta africana*). Pictures © Dr Isura Wijayalath, © Richard Ruggiero/USFWS and © J. Soppelsa.

With their complex social and communication systems (Hedwig et al., 2021; Payne, 2013) and their high thinking, altruism and learning skills, elephants have been studied for decades and are used as models in a large variety of fields. In cognitive sciences, elephant abilities such as auto medication, problem solving, numerical skills, cooperation, coordination, tool use and tool modification are well documented (Barrett & Benson-Amram, 2021; Bates et al., 2008; Irie-Sugimoto et al., 2008; Jacobson & Plotnik, 2020a; Plotnik et al., 2011, 2019). They use tools extensively, in the wild or in captivity, and mainly for grooming (80%, Chevalier-Skolnikoff & Liska, 1993). Many other aspects of Asian and African elephant's life have also been studied. We know henceforth more about their reproduction and childcare (Hufenus et al., 2018; Lahdenperä et al., 2016; Lee, 1987; Rasmussen & Schulte, 1998), diseases

(Lindeque & Turnbull, 1994; Zachariah et al., 2013), lifespan (60 years), sexual dimorphism (Baotic & Stoeger, 2017; Owen-Smith, 1988; Poole et al., 2011), olfaction (Plotnik et al., 2014; Schmitt et al., 2018) and thermoregulation abilities (with ears and skin, Mole et al., 2016). Nevertheless, for the African forest elephants, due to the low number of individuals, their dense habitat that hides them, their absence in zoos and their recent official distinction with the African savannah elephant, distinct data on this species are scarce.

Especially for their social and communication systems, the African savannah elephant systems are more diverse than the Asian elephant ones. Their hierarchical structure is intricate, their gathering more fluctuant, and therefore they require a more substantial communication system. Douglas-Hamilton (1972), Moss and Poole (1983) and Martin (1978) highlighted that African savannah elephants live in family herds led by matriarchs and composed of related adult females and their offspring, whereas adult males live in bachelor groups or solitary. As elephants have a highly territorial flexibility, merging regularly occur with the herds and males (for a limited period, Wittemyer et al., 2005). The synchronisation of the herd, and the status of musth in adult males (iterative state of nervousness and sexual excitement, with avoidance between musth males, Poole, 1987) requires a well-coded hierarchical system on both large and small scales. Elephant communication is therefore abundant, with numerous tactile, visual, sound, chemical and infrasound signals (infrasound for remote communication, detected in the ground with the trunk and feet, Kahl & Armstrong, 2000; Payne & Langbauer, 1992; Payne et al., 1986; Poole & Granli, 2011, 2021; Purkart et al., 2022; Schulte et al., 2005; see Meyer, 2015 for a review).

African savannah elephants are also especially interesting for their great diversity of habitats. While *Loxodonta cyclotis* and *Elephas maximus* are now only present in forest habitats, *Loxodonta africana* are present from arid habitats to forests. They can be found in deserts and semi-deserts, savannah steppes and bushes and large gallery forests (Gobush et al., 2021a). This variety of habitat create a diversity of diets, depending on the elephant population environments.

The diets of these gravigrades are also greatly studied as it impacts the landscape directly (Abraham et al., 2021; Dudley, 2017; Edkins, 2008; see Guldemond et al., 2017 for a review). Indeed, with approximately 150 kg of food and 100 L of water per day, African savannah elephants modify profoundly the environment (Owen-Smith & Chafota, 2012). Besides its great seed dispersion support, with its poorly digested level of excrement (Gonthier, 2009), Stevens and collaborators (2016) demonstrated that *Loxodonta africana* enables the maintenance of bushes and savannah plains. They play an extremely important role in today's ecosystems and are regarded as an umbrella species (Guldemond et al., 2017; Pringle, 2008), i.e. a species

that lives on an extensive territory rich in biodiversity, and whose habitat must be safeguarded to preserve other species. The stakes for their conservation are therefore major. Nevertheless, there are many threats to these animals, beginning with their habitat fragmentation (great migrations hobble, less gene dispersal, limitation in resources, Gobush, 2021a). This undoubtedly leads to major conflicts with humans, with the elephants crossing roads and villages, and feeding from crops (O'Connell-Rodwell et al., 2000; Pozo et al., 2018; Scrizzi et al.; 2018). The current climate crisis exacerbates these problematic, with modification of their habitat and an increase of drought frequency and severity (Boult et al., 2019). Furthermore, the elephants can be threatened by political troubles and have to cope with poaching (trophy, meat, hairs, skin and tusks, Maisels et al., 2013; Schlossberg et al., 2020). Their tusks are highly popular for ivory figurines; elephants are therefore targeted by large-scale ivory traffic. Ivory hunts represent 30,000 dead African elephants per year, approximately 8% of the population (82 per day). The African savannah elephant is also listed as Endangered in the IUCN (International Union for Conservation of Nature) Red List of Threatened Species (Gobush et al., 2021a, Critically Endangered for the African forest elephant and Endangered for the Asian elephant). They are strictly protected by the CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora, Appendix I, Lemieux & Clarke, 2009). An exception is stated for the populations of Botswana, Namibia, South Africa and Zimbabwe included in Appendix II, as their counts are high. However, the overall African savannah elephant census and range are declining, in similar proportions as for the two other elephant species (Gobush et al., 2021b; Williams et al., 2020). Both African elephants (no clear distinction for the census) were estimated at 415,000 individuals in 2016 (mostly *Loxodonta africana*), while they were estimated at 1,000,000 in the 1970's with a much larger range (Chase et al., 2016; Douglas-Hamilton, 1987; Thouless, 2016, **Figure 0.4**). Yet, the African savannah elephants remain the elephant species that is the most profuse in the wild.

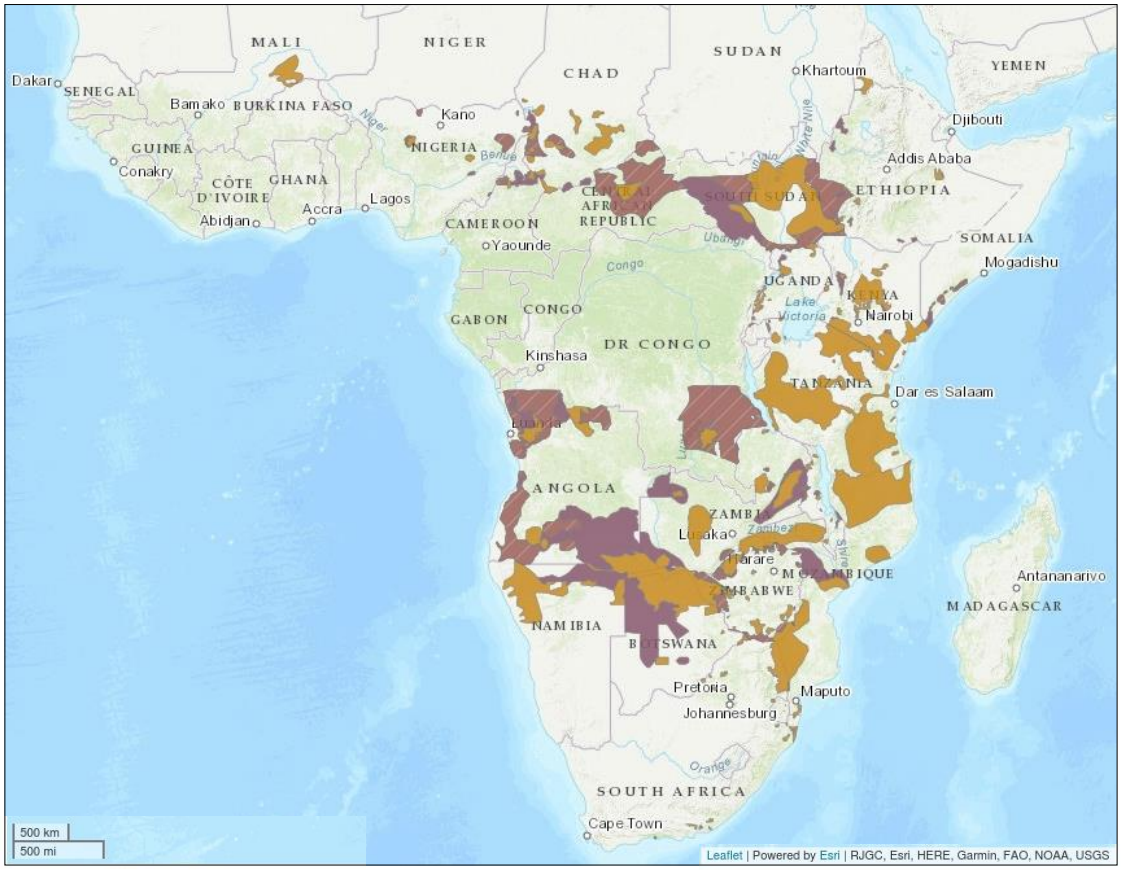

Figure 0.4 – Distribution map of the African savannah elephant. © IUCN SSC African Elephant Specialist Group 2021, https://dx.doi.org/10.2305/IUCN.UK.2021–2.RLTS.T181008073A204401095.en

Elephants and especially African savannah elephants are emblematic species, with a strong value as a scientific model and essential to the ecosystems, facing many threats to their survival. The stakes are high to maintain the populations in the context of increasing poaching, habitat fragmentation, conflicts with human and climate change. However, although one of the most representative characteristics of the Proboscidea order is the presence of the trunk, and although the trunk is deeply involved in the elephant lives, little is known about trunk evolution and precise functions and usage.

The trunk, a formidable grasping and manipulative tool

As previously state, the African elephant's trunk tip end with two digit expansions, whereas there is only one digit expansion on the Asian elephant trunk tip. With the two digits, the African elephants can perform precise grasp with a pinch. Due to this interesting ability, the African savannah elephant trunks are more studied than the Asian elephant trunks. The scarce and elusive African forest elephants were not studied regarding their trunk. Thereby, the following information on trunk anatomy and abilities directly concerns the African savannah elephants.

The elephant trunk is a muscular hydrostat, similar to tongues or octopus tentacles (Kier & Smith, 1985), i.e. it is compose only on muscles that, for any change in shape, retain its volume. However, the elephant proboscis differs from the other muscular hydrostat structures by its large size, the presence of nasal cavities and its muscle structure (Fowler & Mikota, 2006). This elongate coalescence of the nose and the upper lip (Rasmussen & Munger, 1996) does not have any cartilage and consists of 100,000 to 150,000 muscles and tendons. Its muscles are split in four groups: longitudinal near the skin, radial in depth, and two obliques in helical form along the axis (Wilson et al., 1991, **Figure 0.5**).

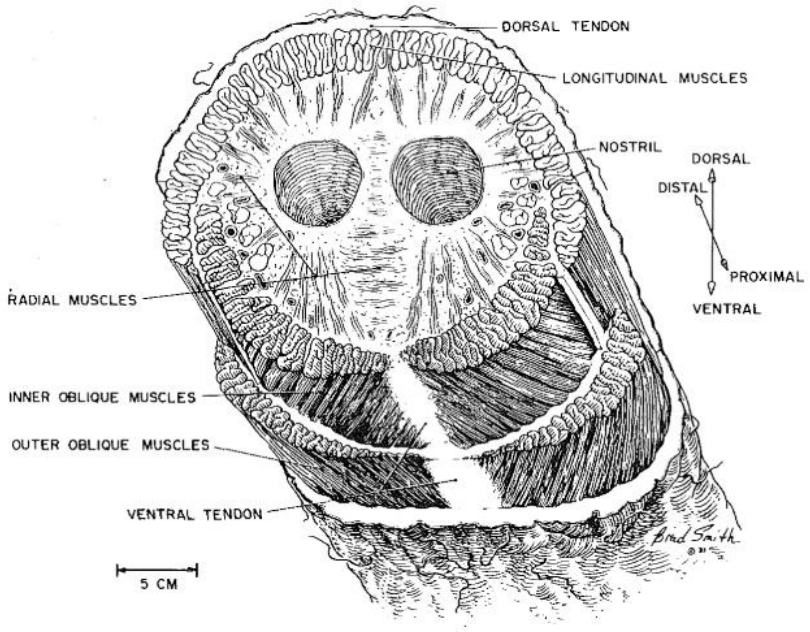

Figure 0.5 – Elephant's trunk cross section showing the muscles distribution. In Wilson et al., 1991.

The nerve fibre network is substantial too, with three subgroups of nerves in the front, back and sides of the proboscis (Fowler & Mikota, 2006; Purkart et al., 2022; Rasmussen & Munger, 1996). The trunk tip especially contains numerous nerves, but also Pacinian corpuscles and whiskers (Rasmussen & Munger, 1996; Witter et al., 2007). Smaller whiskers can be found all over the trunk (Rasmussen & Munger, 1996). Moreover, nasal cavities contain a large number of mucous glandes for the transport of volatile molecules (Fowler & Mikota, 2006).

With the proboscideans evolution toward gigantism and their neck and snout shorten, their neck also shortens, probably to support the heavy head, and the trunk may have compensated these short neck length by connecting the mouth and the ground where the food is. However, with the lack of trunk fossils due to the absence of cartilage, the proboscideans trunk evolution and adaptations remain to be explored. Various trunk evolutionary convergences occurred in mammals, but not with as many abilities and uses as the elephant proboscis (Buskell & Currie, 2021; Milewski & Dierenfeld, 2013). Indeed, the trunk is involved in many crucial functions in the elephant day-to-day life. With their trunk, the elephants feed themselves, drink, groom their bodies, detect water and congeners, explore their environment, defend themselves and their relatives and can breathe in the water (trunk as snorkel, West, 2001). The trunk is also widely use during social interactions, with visual, olfactory, sound and tactile signals (Allen et al., 2021; Poole & Granli, 2011; Purkart et al., 2022; Smet & Byrne, 2020; Stoeger et al., 2021; Yasui & Idani, 2017).

This diversity of behaviour is possible by the many abilities of the trunk. Indeed, the elephant proboscis has great sensory skills with developed olfactory, tactile and low vibration detection senses, especially on the trunk tip (Jacobson & Plotnik, 2020b; O'Connell-Rodwell et al., 2007; Purkart et al., 2022; Rasmussen & Munger, 1996). Moreover, the trunk is highly flexible and mobile. It can extend uniformly through the skin wrinkles and folds, bend and twist in any direction and grasp items (Kier & Smith, 1985; Rasmussen & Munger, 1996; Schulz et al., 2022; Shoshani, 1998; Wilson et al., 1991; Wu et al., 2018). The grasping capacities are particularly interesting as the trunk can lift heavy masses with a wrap (4.5% of its mass), perform precise grasp with a pinch (**Figure 0.6**) and vacuum up an item (Schulz et al., 2021). Recently, several studied have shed light on biomechanics and techniques in elephant trunk manipulation: although the trunk movements large degree of freedom, its use is reduced to a sequence of elementary movements, that usually go along with rigid joint formation and an inward curvature from the trunk tip (Dagenais et al., 2021; Wu et al., 2018). The manipulation techniques also seem to depend on the individual and the manipulate item characteristics (Lefeuvre, 2020).

Figure 0.6 – Precise grasp of a small branch with a pinch of the trunk tip. Picture © J. Soppelsa.

Regarding especially the grasping and manipulative skills, they are widespread in tetrapods (Pouydebat et al., 2022; Sustaita et al., 2013). They are involved in many crucial functions (Pouydebat et al., 2022; Sustaita et al., 2013) and can be performed with hands, feet, mouths, tongue, tentacles and trunks (Christel, 1993; Pouydebat & Bardo, 2019; Sustaita et al., 2013). Research that focuses on these abilities and their evolution are prolific, but focus generally on the primate hands with their individualised fingers (Christel, 1993). Human hand grasping and manipulative abilities are well described (Elliot & Connolly, 1984; Lemelin & Schmitt, 2016; Napier, 1993; Santello et al., 1998), as well as other primates' dynamic manual abilities and static grip postures (Ansuini et al., 2008; Bardo et al., 2016, 2017; Crast et al., 2009, Marzke et al., 2015; see Pouydebat & Bardo, 2019 and Pouydebat et al., 2014a for reviews), including precision grip (Christel, 1993; Jones-Engels & Bard, 1996; Marzke & Wullstein, 1996; Pouydebat et al., 2011). However, knowledge in this field is scarce for grasping and manipulative appendages other than the hand. Yet, we can see with the elephant trunks that the primate hand is not unique in terms of grasping abilities. These aptitudes were indeed firstly hypothesising as correlated with features inherent to the hand, such as the presence of opposable thumbs (Napier, 1960; Marzke, 1997), but the elephants do not display this feature. Their highly use muscular hydrostat, by its shape and many abilities, especially grasping and manipulative skills, is a unique organ within the mammals. Such skills seem to predispose the pachyderms to complex behaviour like tool use, similar as primates in which tool use and manual abilities may have coevolved (Wilson, 1998). These highly studied behaviour in elephants thus directly involve the trunk and its grasping and manipulation aptitudes. Similar as for other muscular hydrostat (Grasso, 2008), elephant trunk abilities just beginning to be studied, especially African savannah elephants as sources of bio inspiration for the

robotic and in medicine (trunk-shape robots and aorta prosthesis, Cianchetti & Menciassi, 2017; Dagenais et al., 2021; Hannan & Walker, 2003; Lefeuvre et al., 2020, 2021; Schulz et al., 2021, 2022; Wu et al., 2018) but many questions are still unresolved.

Aims of the thesis

The elephants are species with strong scientific, symbolic, ecological and economic values. Their most representative characteristic, the trunk, is involved in a large variety of behaviour, but its evolution is an enigma. Therefore, this great variability remains to be explored regarding the trunk morphology, social structures and living environments that are likely to explain it. Particularly, little is known about the actual grasping and manipulative abilities of the two-fingered trunk of the African savannah elephant, its evolution and adaptations. By investigating the grasping and manipulative abilities of the African savannah elephant trunk and its behavioural and morphological characteristics, we can apprehend the adaptation of its use and better understand how elephants live and adapt.

Thus, in this context, the thesis dissertation is developed on three main research questions:

When grasping and manipulating with the trunk, what are the main techniques used?

Do these techniques vary according to the individual and its sex, age and morphology?

Are these techniques linked to habitat?

We defined precisely the techniques in the Chapters 2 and 3 by a set of movement criteria. As Dagenais and collaborators (2021) highlight that trunk movements are usually reduced to a sequence of elementary movements, we hypothesised that there are a few main techniques used by the elephants for grasping and manipulate, in regard to the technique criteria we defined. We also hypothesised that, similar as other grasping appendages (Bardo et al., 2016, 2017; Lonsdorf & Hopkins, 2005), these techniques vary with the individual, but also with the habitat.

To answer these questions, an interdisciplinary approach combining ethology and functional morphology was used. We studied the functional morphology and behavioural features of the African savannah elephant trunk during grasping and manipulation. To do so, first, we characterised and quantified the use of the trunk in the elephant lives, i.e. every time that the trunk was moved to be involved in a behaviour. We also highlighted how this use of the trunk can change with two inherent individual variables, the sex and age of the elephant. Chapter 1 display these results. On the other chapters, we focused directly on the grasping and manipulation techniques. In Chapter 2, we characterised the main techniques in several grasping and manipulation tasks and we highlighted individual variations, especially with tusks profiles. In Chapter 3, we concentrated on the grasping and manipulation technique differences between two elephant populations. We therefore indicated how distinct habitats may induce different grasping and manipulation techniques within a species. In the last chapter, the Chapter 4, we focused on a specific grasping technique with the trunk tip, exploring if elephants have individual trunk tip shape, and if they may display a preshaping of the distal part of their trunk when performing a precise grip.

This dissertation is thus composed of four chapters written as scientific articles, with the first one submitted, the second and the third ones both in preparation, and the last one published (PeerJ 10:e13108. DOI: 10.7717/peerj.13108). The first chapter also contains a preliminary section with additional data of the submitted article. The general discussion that will follow the chapters will connect the different results to answer the three main research questions. The four chapters are identified as follows.

Chapter 1. Variations in trunk use in wild African savannah elephants near water in Kruger National Park: effect of sex.

Chapter 2. Trunk grasping and manipulation techniques in Kruger elephants: effects of tusk profiles.

Chapter 3. Effect of the habitat (Etosha vs Kruger) on trunk grasping and manipulation techniques in African savannah elephants.

Chapter 4. The relationship between distal trunk morphology and object grasping in the African savannah elephant.

Material and methods

Material and methods

A multidisciplinary approach

To characterise elephant trunk grasping and manipulation techniques, several methodological approaches had to be used. Firstly, these techniques are directly related to the behaviour of the elephants. To understand how and why the elephants performe the techniques, we had to study the related natural behavioural patterns as evolutionarily adaptive traits. An ethology approach was therefore necessary (Lorenz, 1981). This non-invasive method (based on behavioural observations) provides a reliable characterisation and quantification of the behaviour, and can highlight the ecological and evolutionary factors that may affect these behaviour (Lorenz, 1981; Tinbergen, 1963).

Nevertheless, this field alone do not let us apprehend the elephant trunk grasping and manipulation techniques in its wholeness. These techniques are also directly dependent on the functional morphology capacities of the trunk (Dagenais, 2021; Lefeuvre et al., 2020; Racine, 1980). Studying in detail the functioning of the trunk is therefore fundamental for the characterisation of the techniques. With functional morphology, the relation between a structure and its function can be explored (Lauder, 1990; Wainwright, 1994), and be linked to evolutionary and ecological contexts. Thus, using this discipline in our research questions context is also essential.

Thereby, to characterise as a whole trunk grasping and manipulation techniques, both ethology and functional morphology disciplines were required. Through their broad-spectrum natures and similar applications, the two disciplines complement each other greatly. We called a simultaneous use of both fields' functional ethology. With this innovative approach, we can highlight with accuracy the diverse ways that behavioural, biological and physical factors interact during the use of the trunk. Moreover, we can rely on well-establish and recent methodologies and discoveries of both fields.

Consequently, in the first chapter of the dissertation thesis, we use specifically ethology. In the last chapter (Chapter 4), we use functional morphology, and in the second and third chapters, we use the functional ethology.

Specimens

In this thesis, we choose to focus on one species of the three extant elephants, *Loxodonta africana*. Every time the "elephant" word will be used in the next parts of this dissertation, it will refer only to the African savannah elephant, except when specified. The African savannah elephant was selected for several of its characteristics:

- its large range that covers a great diversity of habitats (see **Figure 0.4**),
- its trunk tip with two digits that enable pinch grasp,
- the new discoveries on its trunk biomechanic, primarily Dagenais et al., 2021; Lefeuvre et al., 2021; Schulz et al., 2021, 2022; Wu et al., 2018,
- the accessibility of the specimens in wild and zoo conditions.

The first three chapters of this thesis were carried out under natural conditions and are on observational data only. We identified and collected data on 100 wild African savannah elephants from the Kruger National Park in South Africa. Through the large elephant density (17,000 individuals in 2015 and 39 elephant per km^2, Ferreira et al., 2017; Louw et al., 2021) and numerous observational spots in the park, the Kruger enable to collect a large number of elephant data in a short period. We used a different number of individuals from these 100 elephants depending on the chapter and the question asked. In Chapter 1, 91 specimens with a similar water environment context were used. Chapter 2 focuses on 32 individuals that performed grasping and manipulation. Chapter 3 included 30 of the 32 elephants from the previous chapter, but also 13 elephants from data collected in the Etosha National Park in Namibia, where the elephant population was estimated at 2,900 individuals and 0.153 elephant per km^2 (Craig et al., 2021). The environment of the study site in this park greatly differs with the Kruger Park study site environment as it is located in a more arid region. In the Kruger, the environment of the study site displays mostly Mopane and Bushwillow woodlands and Mopane scrub grasslands (Venter & Gertenbach, 1986, Venter et al., 2003) and consistent water presence (Abraham et al., 2021, **Figure 0.7**).

Figure 0.7 – Typical habitats of the study sites in Etosha National Park (picture above) and Kruger National Park (picture below) where the data were collected. Pictures © J. Soppelsa.

Finally, the Chapter 4 experiments were performed on the six female African savannah elephants of the Beauval Zoo Park in France. Every studied elephant in this thesis was identified, sex and age classed. The age and sex repartition, as well as the characteristics used to determine them, are details in the Material and Methods sections of each chapter.

Methods

For Chapters 1 to 3, we collected data last week of January 2020 in Etosha National Park and the first week of February 2020 in Kruger National Park, during the late wet season, with the vegetation in sheets. To optimise the observation period, to study as much of the elephants as possible, and to obtain accuracy on brief movements, we used a film observational method. Thanks to a new elephant behavioural repertoire on trunk use during feeding (Lefeuvre et al. 2020) and a comprehensive ethogram of wild African savannah elephants (Poole & Granli, 2021), we were able to rapidly identified the behaviour displayed by the recorded elephants. For the fine scale video data analyses, we employed classical behavioural quantification methods (Tinbergen, 1963), with the software Boris assistance in Chapter 1 (Friard & Gamba, 2016). In every chapter, we applied several statistical analyses to the observational data to test our hypothesis (Fisher-Pitman permutation tests, Pearson's Chi-square tests, Multiple Correspondence Analysis, Berry et al., 2002; Kassambara, 2017; McHugh, 2013).

For Chapter 4, the experiments were conducted in spring 2019 over six weeks, during the elephants' weekly training sessions. We presented elephants with several types of food to grasp in order to record the shape of their trunk tips during grasping. To obtained and compared trunk tip shapes, we used a Geometric Morphometric (GM) technique. Thus, a two-dimensional approach generally applied to bony shapes was used on a soft object: the trunk tip (Adams et al., 2004; Gunz & Mitteroecker, 2013; Rohlf & Slice, 1990). Finally, we performed multivariate analyses (Principal Components Analysis (PCA), Canonical Variable Analysis (CVA), Schlager, 2017) and MANOVA statistical tests.

Full details of data collection and analysis can be found in the Material and Methods sections of the corresponding chapters.

Thesis context, aim and methods – summary

Context: the trunk evolution is still an enigma, but there is a high variability of trunk uses and abilities, in diverse ecological and social contexts, and with a high elephant morphology variability.

Issues: Lack of knowledge on elephant trunk evolution and adaptations, on its accurate uses and especially grasping and manipulation abilities, no data on the links between the morpho-functional, behavioural and ecological variability in trunk use.

Aims: to investigate trunk grasping and manipulation abilities and associated behavioural and morphological features to apprehend its adaptations. Focus on use techniques and their individual and environmental variations.

Material and methods: conjoint use of ethology and functional morphology on *Loxodonta africana*, with observational data in the wild (Namibia, N = 13; Kruger, N = 100) and experimental data at Beauval ZooPark (N = 6).

Unfolding:

1. Behavioural characterisation and quantification of trunk use (Kruger, South Africa).
2. Characterisation of the main trunk grasping and manipulation functional techniques (Kruger, South Africa).
3. Highlighting the effect of the habitats (Kruger, South Africa vs Etosha, Namibia) on trunk grasping and manipulation techniques.
4. Focus on a specific morpho-functional grasping technique with the trunk tip.

Chapter 1

Variations in trunk use in wild African savannah elephants near water in Kruger National Park: effect of sex

Chapter 1

Variations in trunk use in wild African savannah elephants near water in Kruger National Park: effect of sex

Manuscript submitted

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Key words: Behaviour, trunk, sex differences, African savannah elephant, wild, variability, age, prehensile, *Loxodonta africana*

Initial information

In this chapter, we choose to quantify the use of the trunk through the lens of the variation between the sexes. As all the observational data in this chapter were collected near rivers and waterholes, this chapter is included within a water environment context.

In addition to this study, we define the activities that may involve the trunk and the time budget of these activities in the water environment context. We also highlighted the time spent using the trunk in each of these activities. Although these data do not go along with the sexual variation scope of this article's chapter, they are essential for the thesis setting. Therefore, we incorporate them in this dissertation chapter as initial results and discussion.

Introduction

The prehensile appendages such as hands, feet and trunks have a fundamental role in tetrapod day-to-day life. They are particularly involved in locomotion, social interactions, foraging and feeding movements (Pouydebat et al., 2022; Sustaita et al., 2013). With these appendages, the animal can move, grasp, manipulate, communicate with gestures and feel (tactile sense mostly, Purkart et al., 2022). However, the use of these prehensile appendages is intricately linked to intrinsic factors such as age and sex (Hopkins et al., 2009; Koops et al., 2015). The influence of animal sex on its grasping and manipulation techniques and performances was studied, especially in primates. For example, chimpanzee males and females have different hand preferences (Hopkins et al., 2009) and different performances in object manipulation (Hopkins et al., 2009; Koops et al., 2015). In humans, the hand use lateralisation is also sex-related (Tan et al., 1991) and the optimal pinch differs between women and men (Dempsey & Ayoub, 1996). Diverse sex differences were also demonstrated in animal foraging behaviour, where the prehensile appendage is heavily involved. Female and male rats show different patterns for reaching food (Field & Whishaw, 2005). Foraging activity budgets also differ between the sexes in white-faced capuchin monkeys (Rose, 1994), green monkeys (Harrison, 1983), squirrel monkeys (Boinski, 1988) and ungulates (Ruckstuhl & Neuhaus, 2002). Finally, locomotor, play and groom behaviour that may involve the prehensile appendage can also be different between males and females in various species of primates (Doran, 1993; Lonsdorf, 2017). All

these differences are particularly striking in species with strong sexual dimorphism (Doran, 1993; Rose, 1994) and sexual segregation (Ruckstuhl & Neuhaus, 2002).

The elephant is an emblematic species known for its strong sexual dimorphism, particularly regarding body size (Owen-Smith, 1988) and head and body shape (Moss, 1996). This highly social species (Wittemyer et al., 2005) also lives under sexual segregation: related females and their offspring composed family groups (Buss & Smith, 1966; de Silva & Wittemyer, 2012; Poole, 1994) that regularly associate themselves with fission and fusion structure (Fishlock et al., 2008; Wittemyer et al., 2005). The males have a more swaying structure, as they leave the family group at their sexual maturity to live alone, with other males, or to associate in mating season with female groups (de Silva & Wittemyer, 2012; Poole, 1994; Stoeger & Baotic, 2016).

Moreover, the elephants benefit from an incredible prehensile appendage, the trunk, involved in a huge variety of types of behaviour (Lefeuvre et al., 2020). While elephant grasping abilities have often been discussed as similar (both in function and techniques involved) to those related to the primate hand (Hoffmann et al., 2004; Onodera & Hicks, 1999), the trunk has not been studied as much. To date, we know that the elephant trunk is a muscular hydrostat that can move in all directions, shorten or elongate (Kier & Smith, 1985; Schulz et al., 2022; Wilson et al., 1991). The trunk has high sensory capabilities through unique sensory innervation, especially at the trunk tip (Hoffmann et al., 2004; Rasmussen & Munger, 1996). Moreover, this muscular hydrostat can lift large and heavy items by coiling around it, and pinch or vacuum up tiny items (with the trunk tip, Schulz et al., 2021; Wu et al., 2018). Specifically, the two fingers on the African elephant trunk tip, unlike Asian elephants that have only one, let them perform grasping with high precision (Hoffmann et al., 2004).

In links with these capacities, the trunk is involved in many crucial functions, such as communication for mating, for the play or especially to reinforce their social bond (Kahl & Armstrong, 2000; Lee & Moss, 2014; Poole & Granli, 2011). They communicate mostly with a large spectre of acoustic sounds, produced by blowing air through the trunk (Leighty et al., 2008; Poole, 1994; Poole & Granli, 2011; Stoeger et al., 2021). Seismic sounds, detected by feet and trunk on the ground (O'Connell-Rodwell, 2007), and chemical signals, captured by trunk receptors (Rasmussen, 1999; Jacobson & Plotnik, 2020b) are also widely use in elephant communication. Elephant body posture and especially trunk position, such as periscope sniff sometimes used as pointing gesture, are also considerable in elephant communication (Poole & Granli, 2011; Smet & Byrne, 2020; Yasui & Idani, 2017). Finally, tactile behaviour is an essential part of elephant communication (Jacobson & Plotnik, 2020b; Poole & Granli, 2011; Purkart et al., 2022). Moreover, all these trunk-related senses are extensively used to explore the environment and detect preferred food (McArthur et al., 2019;

Plotnik et al., 2014), water (Wood et al., 2021), other elephants (Jacobson & Plotnik, 2020b) or predators. The trunk is also involved in other day-to-day elephant's life types of behaviour such as drinking, eating, grooming (throwing water, dirt, sand or mud on the body; Nair, 1989) and touching its own body (scratching, calf trunk sucking for comfort, Kahl and Armstrong, 2000; Poole & Granli, 2011). Besides, the trunk may be used in diverse solo and object play such as locomotor play, manipulating an object, spray or splashing water (Lee & Moss, 2014; Nair, 1989; Webber & Lee, 2020). Therefore, the elephants have a prehensile appendage used in many types of behaviour, most of which are essential for elephant survival.

We can perceive the elephant sex influence on its trunk use throughout the sex-related variations on the time spent in types of behaviour that may involve the trunk. Male elephants have larger body sizes, grow faster than females, and therefore have different nutrition needs (Dierenfeld, 2008) and spend more time collecting food than females (Clegg & O'Connor, 2016; Shannon et al., 2006). Sex differences in habitat may also impact this variability in feeding duration (Owen-Smith, 1998). For example, in Kruger National Park, males prefer low tree cover near artificial waterholes and females high tree cover landscapes near permanent rivers (Abraham et al., 2021). Moreover, male elephants, especially adults, play more than females. They play with other males but not with calves, with sparring and wrestling behaviour. Adult female elephants mostly engage in object play, solitary locomotor play and vocalisation. When social playing, it is usually with younger elephants (Lee & Moss, 2014; Webber & Lee, 2020). Shannon and collaborators (2008) found time variability between the sexes for water consumption, with males spending more time at waterholes and rivers. Asian male elephants spend more time than females in mudding, a grooming behaviour (Ahamed, 2015).

However, no study investigated sex differences directly in the use of the trunk in this highly dimorphic species. Male and female elephant trunk use may differ especially in terms of duration and types of behaviour involved. This raises the question of sex influence in elephants on the use of their highly employ prehensile appendage. Moreover, although various activity budgets have been conducted to quantify African savannah elephant behaviour (de Sales et al., 2020; Soltis et al., 2016; Wyatt & Eltringham, 1974), trunk use has never been specifically quantified, except for feeding behaviour in zoo conditions (Lefeuvre et al., 2020).

Therefore, this study aims to add to the knowledge of trunk use and to test trunk use differences between the sexes. We focalise especially on the time spent in the activities that may involve the trunk and on the time spent using the trunk in these activities.

Material and methods

Field conditions

We carried out this study on African savannah elephants during the first week of February 2020 in the Kruger National Park, South Africa where the elephant population was estimated at 17,000 individuals in 2015 (Ferreira et al., 2017). The park has a gallery-forest environment with open grassland areas. Waterholes and rivers have a consistent presence throughout the park: 80% of the park is in less than five kilometres from a permanent water point (Abraham et al., 2021). We conducted the data collection at the end of the wet season, then hygrometry and temperatures were high and vegetation was luxuriant.

Most of the trunk movements studied are brief, about a few seconds. Besides, the types of behaviour displayed by individuals such as calves last for shorter duration and changed quickly (Revathe et al., 2020). Therefore, we filmed the elephants to obtain a better observational accuracy on short duration actions performed by the trunk.

Water areas have a strong impact on the large herbivore population repartition (Harris et al., 2008; Muposhi et al., 2016) and elephant types of behaviour are more diverse near water: more group reunions (Palmer, 2018), different feeding methods (Tehou et al., 2019) and more various playing behaviour (Lee & Moss, 2014). Thus, we choose to collected behavioural data near small artificial waterholes and near the Pioneer Dam. For the waterhole areas, we filmed from the road over a distance up to 15 kilometers from the Pioneer Dam, with an average of 30 metres from the elephants. For the vast Dam, to cover a large area we filmed from a 20 metres elevated location (Mopani rest camp), and at approximately 100 metres from the elephants. We take each video at a distance from the elephants to avoid any human disturbance. To obtain as much as possible individuals, we collect data on videos at each elephant encounter.

Behavioural repertoire

To highlight sex differences in trunk use within a population of elephants we began by quantifying for each individual the time spent in each activity that may involve the trunk. To contextualise the use of the trunk, it was essential to investigate firstly on these activities, to define them and to quantify their importance on the elephant life. This approach allowed us to examine the relationship between the times spent in an activity that might involve the trunk and the time spent using the trunk in that activity. Therefore, we adapted behavioural repertoires to define and inventory

these activities that could involve the trunk. To obtain a behavioural repertoire on these activities, we relied on data from the literature, including the complete ethogram for wild African savannah elephants (Poole & Granli, 2021), our preliminary fieldwork, and the behavioural repertoire of zoo-living African savannah elephants on trunk use during feeding (Lefeuvre et al. 2020).

Seven categories compose the behavioural repertoire of the activities that may involve the trunk. These categories are feeding, drinking, social, exploration, grooming, solo play and self-directed behaviour (**Table 1.1**). Each behavioural unit included in these categories were described by Poole and Granli (2021) and Lefeuvre and collaborators (2020). The activity categories concern all individuals, regardless of age or sex, although most of the elephants did not perform every activity when observed.

Activity	Description
Feeding	Every movement related to feeding, from foraging with diverse techniques to food ingestion. Plants feeding and milk suckling were both included in this activity, but were studied separately.
Drinking	Every movement related to water suction and consumption. Suction directly with the mouth, or with the trunk to release it into the mouth.
Social	Every movement in order to have a physical contact with a congener, every visual and vocal communication. Social play is included in this activity.
Exploration	Every movement related to the environment exploration, usually with ears and trunk extent toward the explore object/individual. Ground exploration with the trunk while walking is omitted in this activity (difficult to detect for the observer).
Grooming	Every movement in order to cover the elephant body with mud, sand, dust or water. If the elephant submerges itself in water, only the first immersion was included as grooming.
Solo play	Every movement related to lone object play and lone locomotor play, as Lee and Moss in 2014 and Webber and Lee in 2020 defined it for elephants.
Self-directed behaviour	Every movement in order to touch its own body. Mostly brief movements with the trunk or leg directed toward the temples, the mouth, the head, the ears, the stomach or the legs.

Table 1.1 – Categories of elephant activities that may involve the use of the trunk. Every behaviour in each activity was described by Poole and Granli (2021) and Lefeuvre and collaborators (2020).

Ethological quantification in natural habitat

From 7 a.m. to 12 a.m., and from 3 p.m. to 5 p.m., when the elephants are the most active (Rozen-Rechels et al., 2020), we filmed every encounter with elephants if the trunk was visible. Most of the videos include several individuals. In this case the behaviour of each elephant was analysed individually. Thus, no individual selection was made (apart from the shooting sites) and the number of elephants recorded was maximised. A large part of the observed elephants were filmed in the same conditions, near the Pioneer Dam. We recorded the data with Sony FDR-AX 53 cameras and following CNRS guidelines and European Union regulations (Directive 2010/63/EU).

We analysed the behaviour of each elephant that was filmed for at least 10 minutes. This 10-minute period represents the minimum time that the filmed elephants near water spent displaying several activities. The observed elephants that spent less than 10 minutes near water generally focus on only one activity that could involve the trunk, drinking. Moreover, the grown males generally spend more time than the females groups near rivers and waterholes when the water is not a limited resource (Shannon et al., 2008). Therefore, to have a good representation of all the activities display near water, we sample the elephants that were observed at least 10 minutes and until they move out of the water area. Moreover, as no sample suffered from too long period with the animal out of sight, none was discarded based on this criterion. These sample films range from 10 to 97 minutes (mean ± S.D. = 17 ± 15 minutes). The elephant male films range from 10 to 97 minutes (mean ± S.D. = 23 ± 20 minutes), whereas the female films range from 10 to 25 minutes (mean ± S.D. = 13 ± 4 minutes). The mean, standard deviation, median, minimum and maximum values, and first and third quartiles of the film duration of each sex in every age class can be found in the **Appendix 1.1**. These informations indicate how long each elephant has been in proximity of the water points. Each individual was filmed only once over the entire observation period: consequently there is only one observation per individual.

Elephant identification and classifications

To recognise each individual we identified physical characteristics such as tusk profiles and particular identifiable markings such as ear shapes, ear holes and veins, wart shapes or back shapes (Moss, 1996; Webber & Lee, 2020). The tusk profiles specifically were very useful in identifying each individual: tusk presence or not, size, breakage or wearing, curve, opening and symmetry. Therefore, we recorded 91 individualised elephants.

The sex and age class of the observed elephant are detailed in **Table 1.2**. Genitals, breasts, shoulder height, body shape, head shape and tusk shape helped us

to sex-classified the elephants (Moss, 1996). We also used group composition (Poole, 1994) as adult female elephants live in groups with coordinated movements and behaviour (Revathe et al., 2020), and adult males are either alone, in small groups of males, or less often with groups of females. In a few cases, the sex of an individual could not be determined safely. These observations were excluded from the analysis.

Sex / Age	Infant	Juvenile	Subadult	Adult	Large adult	*Total*
Female	0	4	10	24	8	46
Male	3	3	10	24	5	45
Total	3	7	20	48	13	91

Table 1.2 – Sex and age distribution of the 91 observed elephants.

We determined the age of each elephant and categorised them into classes of age. Therefore, we referred to elephants less than one year old as 'infants' and elephants between one and seven years old as 'juveniles'. 'Subadults' represent the elephants between around eight and fifteen years old (Moss, 1996; Poole, 1994). Finally, we referred to grown females and independent males as 'adults', and elephants over 35 years, with marked bodies, as 'large adults' (Moss, 1996). We can evaluate the age of an individual by the shape of the elephant's body and the lack of tusk emergence for infants. Tusk's size and shoulder height also help to determine the age of an elephant, especially males that continue to grow as they age (Shrader et al., 2006). If a young male range independently from female groups, he is no longer a subadult but consider as an adult (Moss & Poole, 1983). The presence of an infant or a juvenile with a female can also help to identify her as an adult and no more a subadult (Moss, 1996).

Video and data analyses

We analysed each video using the software Boris (Friard & Gamba, 2016) to obtain the duration of each activity for each observed elephant at a fine scale. We also collected the time spent using the trunk during each of these activities. We considered that the trunk was used during an activity if it effectively contributes to the activity fulfilment. Therefore, we noted both the time spent in an activity and the time spent using the trunk in this activity. When the elephant was fully involved in an activity in which the trunk is never used, such as resting, the observations were omitted in the analyses. To avoid any bias, the video processing was performed by a single observer who had a good knowledge of the behavioural repertoire and had practised applying

this repertoire before the video processing. Our videos contain a significant amount of time of the activities that may involve the trunk: mean ± S.D. = 8 ± 3 minutes for the females and mean ± S.D. = 18 ± 20 minutes for the males. Therefore, the observed elephants spent a significant amount of their observation time performing the activities analysed in this study. The samples display enough of these activities to be analysed.

Each sample represents an individual. For each sample we calculate the proportion, express in %, by dividing the time spent performing a given activity by the time spent performing all the activities that can involve the trunk. We performed similar calculations with the proportion of time spent using the trunk in each of these activities.

We tested sex differences by age classes for each activity. The number of individuals varies greatly between age classes (Tab. 1) and statistical analyses were limited to class ages with at least eight individuals of each sex (i.e. the subadult class and on the adult class). Data are presented as mean ± S.D. and included all the age classes. For each age class data of males and females were compared using a Fisher-Pitman permutation tests with the 'oneway_test' function of the 'coin' package in R, version 3.6.1 (R Core Team, 2018). We also use the same procedure but for paired data when the proportions of two activities were compared. We also tested sex differences by age classes for trunk use in the activity. As previously stated, individuals did not perform all the focal activities during their observation. Consequently, the statistical analyses were performed only for activities with suitable sample sizes. The sample size for each group is indicated on **Figure 1.3**.

Results

Initial results

We determine, with all the activities duration proportions, that 69.3% of the observation time near waterholes and rivers is spent on performing the activities that may involve the trunk. 59.9% of this time truly involves the trunk. Therefore, when performing only the activities that may involve the trunk, the observed elephants actually used it 86.5% of the observation time.

The pie chart in the **Figure 1.1** shows the distribution of the time spent performing the activities that may involve the trunk. The schematic section details the

proportion of time spent performing each activity with and without the trunk. We can see that the observed elephants spent the majority of their time drinking, then engage in social behaviour and eating. The four other behaviour are less performed. The trunk is almost completely use in the drinking, explore, feeding and self-directed behaviour activities. Its use decrease in the solo play and grooming activities, and the trunk is using the less in the social activity. The most common trunk use behaviour and behaviour without the trunk within the activities are explicit in **Figure 1.1** with the drawings.

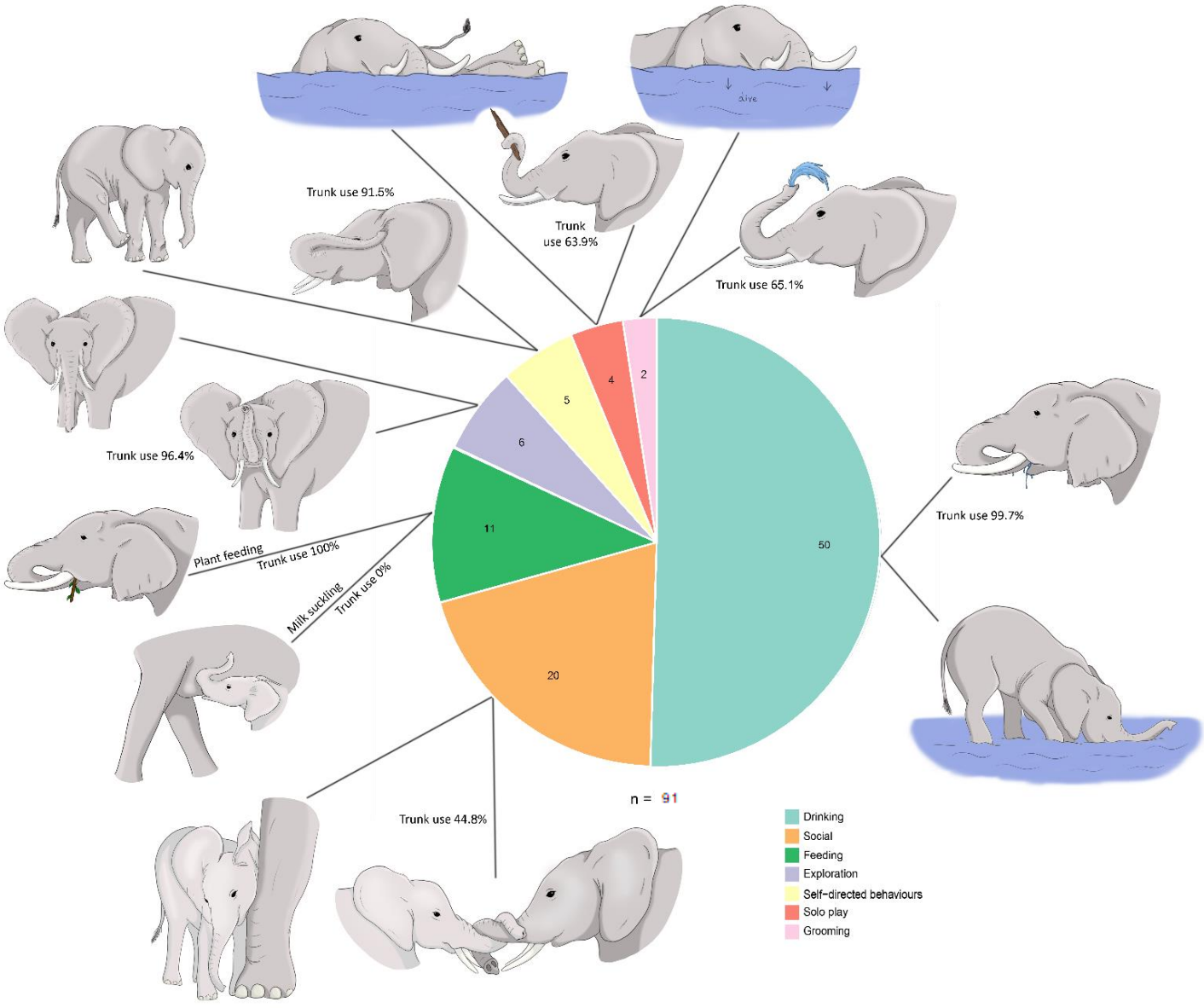


Figure 1.1 – Distribution of the elephant activities that may involve the trunk, combined with trunk use proportions and schematic behaviour within the activities. Distribution in water environment on 91 elephants, expressed in percentages.

Sexual variations in the activities that may involve the trunk

Figure 1.2 displays, per activity, sex and age, the distribution of the time spent performing these activities near the Pioneer Dam. When elephants are near water, they spent most of their time in drinking and social behaviour. Adult males spent significantly more time than adult females in social activity (N_{males} = 22, $N_{females}$ = 21, Z = 4.9367, P <0.001) whereas the females spend more time in drinking than the males (N_{males} = 22, $N_{females}$ = 21, Z = -4.7245, P <0.001). A similar result was observed in large adult animals but could not be tested due to the small sample size. In the other activities, there are no significant differences in the time spent between the males and females (grooming: Z = -1.1363, P = 0.26; feeding: Z = 1.8129, P = 0.07; self-directed: Z = 0.018623, P = 0.99; solo play: Z = -1.8615, P = 0.06; exploration: Z = -0.58738, P = 0.56). In subadults, there was no clear difference between males and females (grooming: Z = -0.73329, P = 0.46; feeding: Z = 1.3749, P = 0.17; self-directed: Z = -0.37082, P = 0.71; solo play: Z = 1.3745, P = 0.17; drinking: Z = -0.19276, P = 0.85; social: Z = -0.92405, P = 0.36; exploration: Z = 0.10295, P = 0.92). However, the subadult males and females spent significantly more time in drinking activity than in the social activity (males: Z = 2.51, P = 0.02; females: Z = 3.005, P = 0.001). When adults, the females also spent significantly more time in drinking than socialising (Z = 4.46, P <0.001). It is contrary to the adult males, who spent more time in the social activity and less in the drinking activity (Z = -2.225, P = 0.02). Therefore, when growing from subadults to adults, there is a change in the major activity for the males (Z = 462.3, P <0.001), but not for the females (Z = 613.9, P = 0.12).

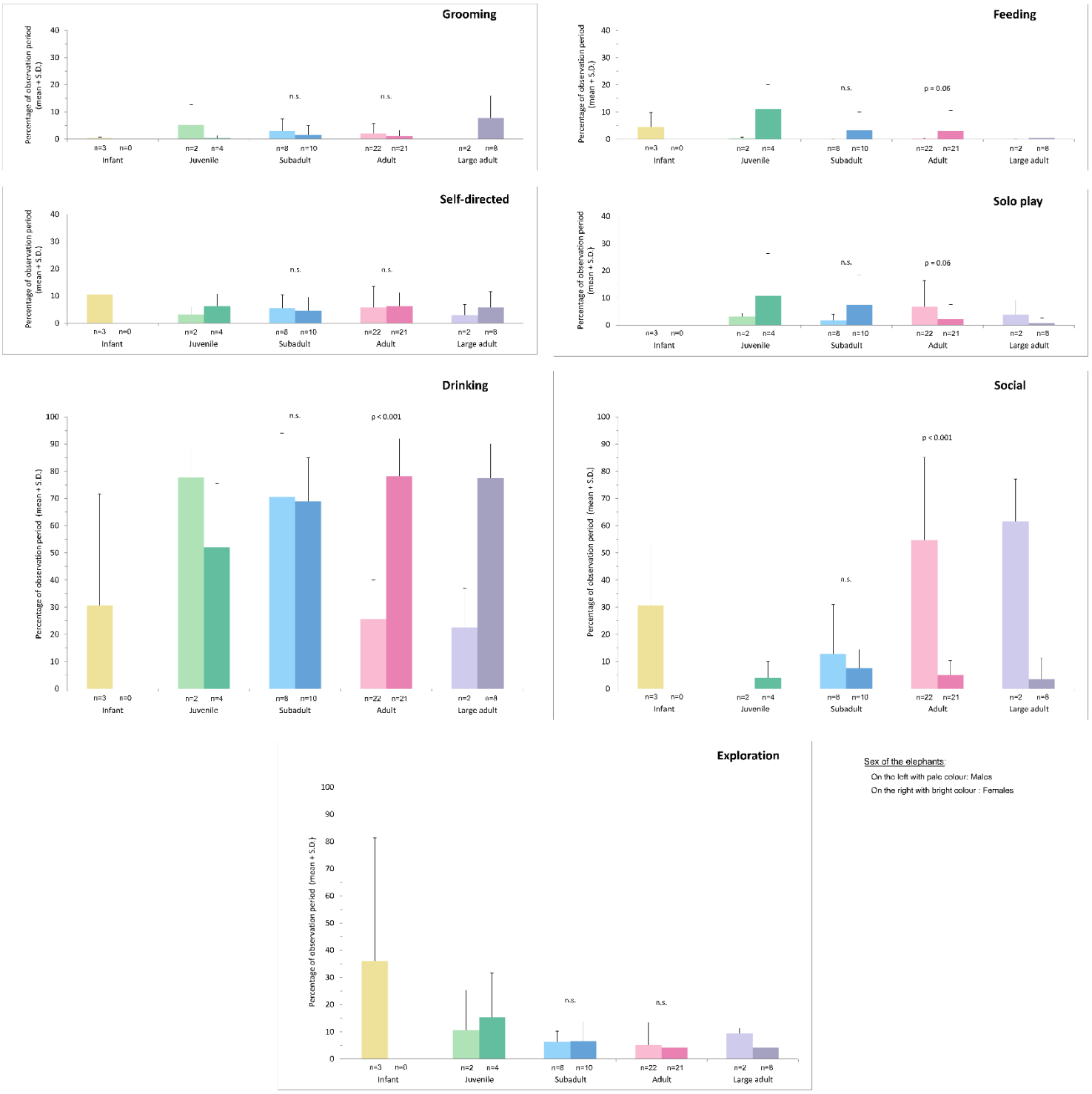


Figure 1.2 – Distribution of the time spent performing activities that may involve the trunk, per sex and in relation to the age of individuals. Distribution near the Pioneer Dam on 80 elephants, expressed in percentages. This figure represents the different means and standard deviation of time spent in each activity, depending on the sex and the age of the elephants. Statistical analyses were limited to subadult and adult class ages. n.s. is for not significant.

Sexual variations in trunk use

As explain in the "Material and methods - Video and data analyses" section, the statistical comparison of the proportions of trunk use between the sexes was possible in only four activities (**Figure 1.3**). During drinking and whatever the age or the sex, the trunk is used most or all of the time (70.6% of the subadult males observed time, 68.9% for the subadult females, 25.7% for the adult males and 78.1% for the adult females) for the subadult and adult, the two age classes with sufficient sample size precluding any statistical analysis. For exploration and self-directed activities, the trunk use is also very high and no statistical difference was detected whatever the age classes (subadults exploration: $Z = 0.86031$, $P = 0.39$; adults exploration: $Z = 0.54076$, $P = 0.59$; subadults self-directed $Z = 0.58539$, $P = 0.56$; adults self-directed $Z = -1.1956$, $P = 0.23$). Trunk use is lower during social activities and the variability greater but male and female did not differ whatever the age class (subadults: $Z = 1.2564$, $P = 0.21$; adults: $Z = -1.3208$, $P = 0.19$).

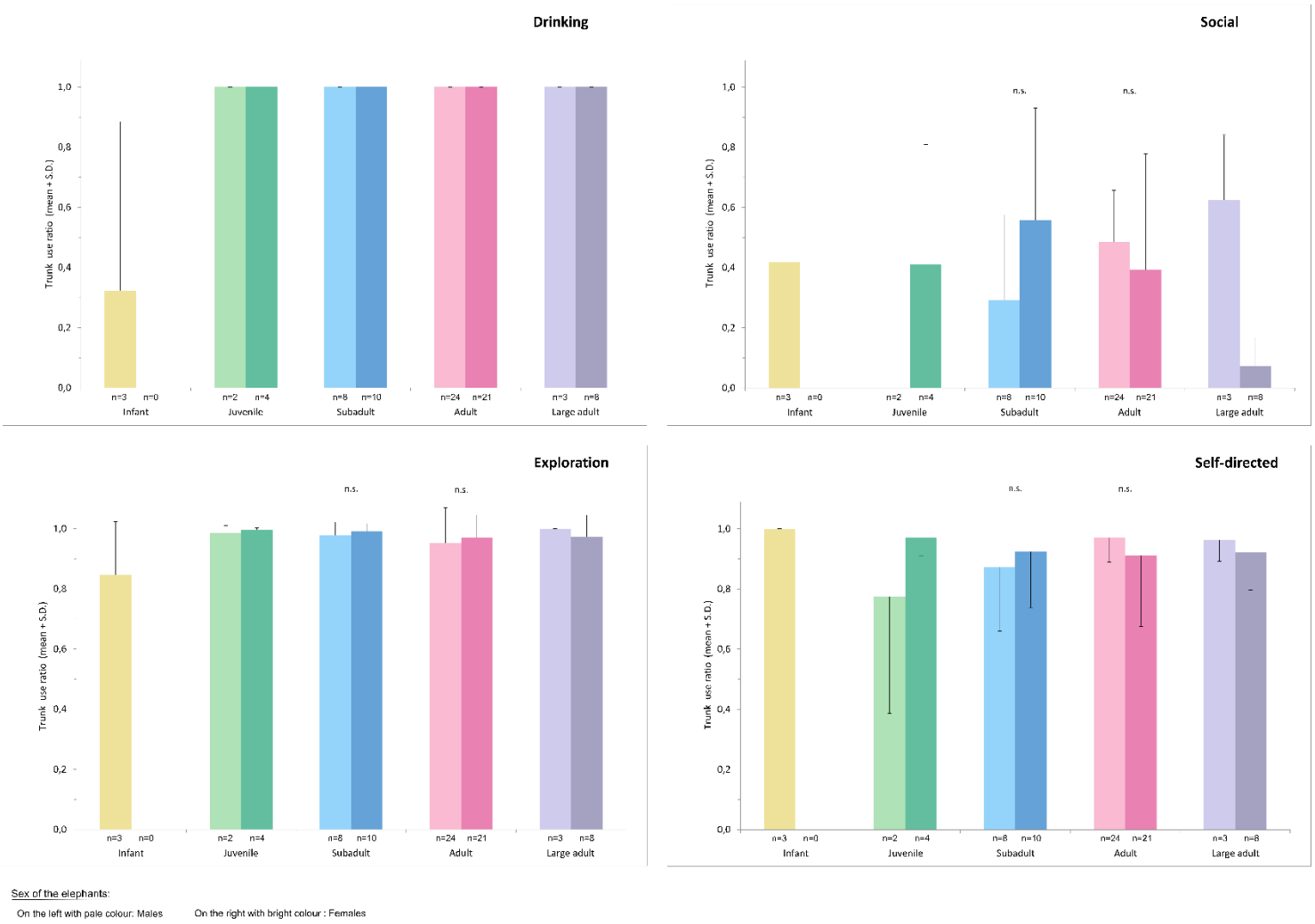


Figure 1.3 – Distribution per sex and age of the time spent using the trunk in each activity. Distribution in water environment on 91 elephants, expressed in percentages. Statistical analyses were limited to subadult and adult class ages. n.s. is for not significant.

Discussion

Activities involving the trunk are essential for the survival of the elephant: they include resource acquisition, environment understanding, body maintenance, well-being, developmental support and social bonding. In studies on primates, we can find similar uses of the prehensile appendage: for food acquisition, to grasp substrates, for grooming and for social cohesion (Jablonski, 2021; Pouydebat et al., 2014a, 2022; Toussaint et al., 2013). Thus, we can assert that the trunk, similar as other prehensile appendages (Sustaita et al., 2013), is fundamental in the animal day-to-day life.

Initial discussion

As shown by our results, the elephants spent most of their observation time performing the activities that may involve the trunk, especially drinking, socialising and eating. These observations differ with the elephants general activity budgets express in the literature, as our observations are focalised on water areas. The elephants are seeking water periodically, every two days in Kruger National Park (De Beer & Van Aarde, 2008). Therefore, when they are close to water, the elephants optimise their time with water-related activities, such as drinking. Male social play may also increase close to rivers, as they were observed using deep water to diversify their play, with behaviour such as swimming and mounting (Lee & Moss, 2014; Webber & Lee, 2020). Moreover, elephants gathering is more important near water (Palmer, 2018) and thus the interactions between individuals are more profuse. To go further, we could compare these results on elephant activities near water areas with data on elephant activities on a more arid region: these activities may differ in a region where water is a scarcer resource.

Sexual variations in the activities that may involve the trunk

Our study highlights that only adult male and female elephants differed in the proportion of time performing two activities that may involve the trunk near waterholes and rivers. Specifically, the females spent significantly less time in social interactions and more time in drinking than the males. This difference concerns the adult but not the subadults, and the large adult seem to follow the same pattern as the adults. Shannon and collaborators (2008) also found time differences between the sexes for water consumption. Because family groups include calves, these groups are more water dependent than the independent males (De Beer & Van Aarde, 2008). They are also more subject to disturbances and risks related to water areas, such as predators (Loveridge, 2006). Therefore, on the contrary to grown males, grown females in family groups go to water areas for a shorter period of time and especially for drinking and grooming (Shannon et al., 2008; Stokke & Du Toit, 2002). Other species with different sexual structures display similar patterns. For example, in the mule deer and bighorn sheep, the lactating and with offspring females spent less time than the males near water areas (Bowyer, 1984; Whiting et al., 2010). We can also find, in elephant literature, similar sociality divergence between the sexes (Baotic & Stoeger, 2017; Shannon et al., 2006). This disparity in social interactions surely occur because grown males and females live in different social structures (Wittemyer et al., 2005), with marked dynamic differences (de Silva & Wittemyer, 2012). Indeed, the grown males do not have the family constraints experienced by the females but have more solitary

lives. The water areas are ideal places for social gatherings and the grown males here especially can interact with grown females for mating and grown males for playing. Lee and Moss (2014) and Webber and Lee (2020) specify that male social play has a tendency to increase close to rivers, as they were observed using deep water to diversify their play, with behaviour such as swimming and mounting. We can find similar results in species under different sexual structures (Meaney et al., 1985). Thus, we can assert that the grown male elephants in our study are more engaged than the females in social behaviour. Therefore, near water, with their different social structures and constraints, the grown males seem to optimise their social interactions whereas the grown females seem to optimise their drinking time. Finally, our data on the other age classes tend toward the same types of behaviour for the grown females and the youngest elephants whatever their sex. In particular, near water, the subadult males have for main activity drinking like the grown females whereas when adults they favour socialising. Therefore, when they reach sexual maturity and change their social environment, the male behaviour changes to prioritise socialising near water. More data on subadult males that are close to leave the family group is nevertheless requested to explore if they may start to display this change of behaviour.

Sexual variations in trunk use

We explored trunk use difference between the sexes. To our knowledge, in other species with a muscular hydrostat as a grasping appendage such as cephalopods, no study explores the differences between the sexes on the use of this grasping appendage. For the observed elephants in our study, both sexes do not significantly differ on trunk use duration on the four major activities. The trunk is used nearly all the time in three of the four major activities near water (drinking, exploration and self-directed behaviour). Its use is fundamental in the elephant day-to-day life as these activities are essential for the elephant survival. However, the trunk may also be used sporadically in other activities such as during social encounters. Its use in this activity varies greatly among individuals. Therefore, its use seems to be related to specific social behaviour such as trunk-twining (Poole & Granli, 2021). Indeed, social behaviour is more diverse than drinking, exploration and self-directed behaviour and usually involve other parts of the body of the elephant as much as the trunk (Poole & Granli, 2021). These results are at least applicable to this context of water environment and the trunk use duration variable studied.

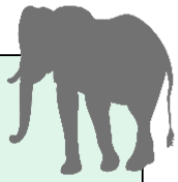
In conclusion, there is sex differences in the time spent in the activities that could involve the trunk. However, we found no specific differences in trunk use between the sexes in the four most common activities, even in the activity with a great

variability among individuals. Therefore, in elephants, sex differences in the time spent in an activity that may involve the trunk does not involve sex differences in the time spent using the trunk. As this study focalises especially on the time spent in trunk use, we could complete these results by exploring the different types of behaviour involve in the activities, such as specific trunk use techniques, and if they are related to the sex and age of the elephants. To go further on the time spent on these behaviour that may involve the trunk, we could investigate other factors. Indeed, we know that elephant behaviour may vary with the temperature and season (Rozen-Rechels et al., 2020; Webber & Lee, 2020), the individual (Bastille-Rousseau & Wittemyer, 2019; Webber & Lee, 2020), the hour of day/night (Wilson et al., 2006) and the physical environment such as the presence of water (Lee & Moss, 2014), food availability (Beekman & Prins, 1989; Guy, 1975) or ground ruggedness (Fullman et al., 2017). Thereby, it could be interesting to widen this study of trunk use variations on these other factors. Especially, as trunk use in feeding was demonstrated to vary a lot among zoo-living individuals (Lefeuvre et al., 2020), we could focalise on trunk use individual differences among wild elephants while feeding.

Appendix

Observed elephants	Sex	Mean	Standard deviation	Minimum value	First quartile	Median	Third quartile	Maximum value
Every elephant	*Females*	774	213	573	620	717	827	1519
	Males	1382	1202	598	722	897	1582	5809
Infants	*Males*	851	227	710	721	731	922	1113
Juveniles	*Females*	747	122	613	696	733	784	908
	Males	659	34	626	642	658	676	694
Subadults	*Females*	751	247	583	598	647	748	1290
	Males	759	119	632	656	747	827	974
Adults	*Females*	785	227	573	621	717	852	1519
	Males	1789	1478	598	810	1261	1734	5809
Large adults	*Females*	787	193	610	642	745	832	1114
	Males	1424	848	704	873	963	1879	2703

Appendix 1.1 – Details per sex of the film duration variations. Every duration is expressed in seconds.



Chapter 1 summary

Title: Variations in trunk use in wild African savannah elephants near water in Kruger National Park: effect of sex.

Background: Grasping and manipulation are fundamental functions for tetrapods. They performed them with diverse form of prehensile appendages, such as hands, feet, mouths. Several studies demonstrated that the use of the hand could be influenced by the animal sex, especially for species with strong sexual dimorphism and segregation. However, no study investigated the influence of the sex on the use of other grasping appendage forms. The elephant, a dimorphic species with a wide use of a grasping appendage, the trunk, is an interesting model to explore the influence of the sex on the use of grasping appendages other than the hand. Moreover, although we know that the elephant trunk is involved in many types of behaviour, its use remains to be quantified.

Methods: To add to the knowledge of trunk use and to highlight trunk use sex differences within a population of elephants, we studied 91 identified wild African savannah elephants (*Loxodonta africana*) near water in the Kruger National Park, South Africa. We investigated, for each age class, the time spent in every activity that may involve the trunk and trunk involvement in these activities, and we explore specifically the differences per sex for these activities and trunk involvement.

Results and discussion: We reveal that the elephants spent most of their observation time near waterholes and rivers using their trunk. Moreover, adult females spend more time than adult males in drinking whereas adult males spend more time in social interactions. There are no such differences for the subadults. The family constraints of the grown females seem to have impacted the behavioural differences found between the sexes. However, there is no sex difference in trunk use duration whatever the age class in the most common activities near water, which are drinking, social, exploration and self-directed behaviour. The sex differences in the time spent by elephants in an activity do not involve sex differences in the time spent using the trunk.

From Chapter 1 to Chapter 2

In Chapter 1, we characterised and quantified elephants' trunk uses with a focus on sex influence. We especially quantified the trunk involvement during a fundamental moment of the elephant's day, its time near water. Although elephant activities near water differ by sex, time spent using the trunk does not. It is therefore possible that parameters other than sex further influence trunk use, and are thus related to grasping and manipulation abilities. To further explore the potential individual variability of trunk grasping and manipulation, we characterised the main grasping and manipulation techniques and the factors that may influence them. This is the subject of Chapter 2.

Chapter 2

Trunk grasping and manipulation techniques in Kruger elephants: effects of tusk profiles

Chapter 2

Trunk grasping and manipulation techniques in Kruger elephants: effects of tusk profiles

Manuscript in preparation

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Key words: elephant, trunk, technique, grasping, manipulation, task, object, individual, tusks

Introduction

Many hands, feet, mouths, tails, trunks or tentacles can grasp or manipulate (Pouydebat & Bardo, 2019; Pouydebat et al., 2022; Sustaita et al., 2013). These skilled movements are widespread in tetrapods and occur mostly for locomotion and food acquisition (Pouydebat et al., 2022; Sustaita et al., 2013). However, the factors that shaped the grasping and manipulative abilities of these prehensile appendages remain unclear (Pouydebat & Bardo, 2019). As these abilities were firstly attributed to primates, most studies in the field focus on the origin and evolution of primate hand grasping and manipulation techniques. Grasping especially may have an adaptive role with the exploitation of the terminal branch habitat in primates. This ecological context requires locomotion and leaping capacities on small branches (Bloch & Boyer, 2002; Nyakatura, 2019; Ravosa & Dagosto, 2007; Szalay & Dagosto, 1988) and foraging capacities for food located on the terminal branches (insect predation and plant exploitation, Bloch & Boyer, 2002; Nyakatura, 2019; Sussman et al., 2013). In this framework, several studies focus on the role of food properties on hand grasping, such as the shape, size, texture and celerity (Ansuini et al., 2008; Pouydebat et al., 2009; Santello et al., 2002; Toussaint et al., 2013). Moreover, it was highlighted that the objects are grasped according to the action planned and its complexity (Ansuini et al., 2006; Bardo et al., 2016). Gorillas (Pouydebat et al., 2010), bonobos (Bardo et al., 2016), and humans (Wong & Whishaw, 2004) grasping and manipulative techniques also differ with the individuals. In particular, the sex, age and individual morphology can affect the use of these techniques (Gérard et al., 2022; Wong & Whishaw, 2004). Similar results were found in non-primate species such as rodents and frogs (Anzeraey et al., 2017; Gholamrezaei & Whishaw, 2009; Ivanco et al., 1996; Nyakatura, 2019; Whishaw & Coles, 1996). These similarities with primates may be due to a common evolutionary origin (Iwaniuk & Wishaw, 2000).

Thereby, there is an effect of the object properties, the task planned, the individual and its inherent features on the grasping and manipulation movements. Exploring the prehensile and manipulative capacities of extant mammals is central to understand the evolutionary mechanisms of movement. Yet, most of the models explored in this research area concern primates, or non-primates with grasping appendages analogues to the hand. The research that focus on other types of grasping appendages, such as the chameleon tails, mostly examine the link between the prehensile capacity and the anatomical features (Luger et al., 2020).

However, muscular hydrostat such as tongues, tentacles and trunks are also commonly used for grasping and manipulate objects. Their grasping and manipulation techniques received increasing attention lately, especially the ones

performed by elephant trunk (Dagenais et al., 2021; Nair, 1989; Lefeuvre et al., 2020, 2021; Schulz et al., 2021, 2022; Wu et al., 2018; Chapter 4 of this dissertation thesis). Indeed, elephant trunks are particularly interesting by their capacities to bend in any direction, elongate and shorten, vacuum up an item, lift heavy masses and grasp precisely with a pinch (Kier & Smith, 1985; Schulz et al., 2021, 2022; Rasmussen & Munger, 1996; Wilson et al., 1991). Moreover, the elephants use their trunks a lot and in a large variety of behaviour (Lefeuvre et al., 2020; Poole & Granli, 2011; Chapter 1 of this dissertation thesis). Most of their foraging behaviour included grasping and manipulation movements, but we can also find these movements in elephants during social interactions and play (Lefeuvre et al., 2020; Poole & Granli, 2021; Webber & Lee, 2020).

Yet, the studies that explored elephant trunk grasping and manipulative abilities did not examine the evolutionary context of these skills. None have investigated the influence of the task planned on elephant trunk grasping and manipulation movements. Object properties influence was only studied on specific grasping techniques with the trunk (Dagenais et al., 2021; Schulz et al., 2021; Wu et al., 2018; Chapter 4 of this dissertation thesis). Inter-individual variability in the use of the trunk techniques was highlighted, but only for the main feeding behaviour and only in non-wild elephants (Lefeuvre et al., 2020). Yet, elephant trunks can be great models for exploring the grasping and manipulation evolutionary questions in tetrapods. Similar as primate hands, the trunk tip of the elephants can preshape (Chapter 4 of this dissertation thesis), probably to increase the grasping success (Pouydebat et al., 2009; Sartori et al., 2013; Peckre et al., 2019a). Moreover, on the contrary of most primate hands, the trunk is not involved in locomotion. Thereby, the evolutionary pattern of trunk grasping and manipulation abilities certainly differ with the primate pattern. It may bring additional information on these evolutionary mechanisms in tetrapods.

In the present study, we aim to characterise the main grasping and manipulation techniques used by the wild elephants with their trunks. We also aim to determine some factors that could make these techniques vary. More precisely, we examine if the grasped object properties, the anticipated task and the individual could have an influence on these techniques. African elephant trunk tip consists of two fingers that let them perform high precision pinch grasping (Hoffmann et al., 2004). On the contrary, Asian elephants have only one finger and seldom perform this pinch (Rasmussen & Munger, 1996). Therefore, in this study, we choose to focalise only on the African savannah elephant (*Loxodonta africana*) grasping and manipulation movements. To do so, we created a detailed catalogue of the techniques by using several criteria to describe them. We determined the main grasping and manipulation

tasks performed by elephants and noted several individual inherent features, which are the sex, age and tusk morphologies. The social environment, i.e. the number of individuals present in the immediate physical surroundings of the focal animal, was analysed too as a potential factor linked to the individual that could influence the techniques. We expected that, similar as Lefeuvre and collaborators (2020) found in captivity, there is a strong inter-individual variability with the grasping and manipulation techniques. We supposed that the tusk profiles are a factor that could explain this variability, especially on the grasping way criterion. We also predicted that the age and the social environment could explain this variability, but not the sex of the elephant (Nair, 1989; Revathe, 2020; Chapter 1 of this dissertation thesis). Moreover, we expected that the object characteristics have an effect on these techniques, similar as for the trunk tip preshaping technique (Chapter 4 of this dissertation thesis). Finally, we also predicted that, alike primates (Ansuini et al., 2006; Bardo et al., 2016), the techniques differ with the anticipated tasks.

Material and methods

Data collect in natural habitat

Data on African savannah elephants were collected in South Africa in the Kruger National Park. The north of the park, where the data were collected, is composed mostly of trees, especially Multistemmed mopane shrubs (Kos et al. 2012; Venter et al., 2003). With this dominance of *Colophospermum mopane*, other woody species are relatively scarce. There is a consistent water presence throughout the park (Abraham et al., 2021). As we collected the data in February 2020, the wet season was ending and the vegetation was luxuriant. Grasses were abundant and the trees were in sheets.

Following the CNRS guidelines and European Union regulations (Directive 2010/63/EU), data were taken in video format at distance with the elephants. The video collect let us obtain observational accuracy as most of the trunk movements are brief, even more when performed by calves (Revathe et al., 2020). No angle of view was prioritised for the data collect. As grown males and family groups differ in their distributions in the Kruger National Park (grown males are more concentrated near artificial waterholes and family groups near permanent rivers, Abraham et al., 2021), we diversify the shooting sites where the videos were taken. Therefore, we collected data from a 20 metres elevated location, in Mopani rest camp, near the Pioneer Dam

and at approximately 100 metres from the elephants. We also collected data from the road near artificial waterholes and in diverse landscapes, over a distance up to 15 kilometers from the rest camp, and with an average of 30 metres from the elephants.

We wanted to study the grasping and manipulation techniques on as much as possible individual. Therefore, we filmed at day light, when the elephants are the most active, in the morning and the end of the afternoon (Rozen-Rechels et al., 2020). The videos were taken with Sony FDR-AX 53 cameras. We filmed at each elephant encounter, when the elephant performed grasping or manipulation with its trunk and when the trunk was clearly visible. Each video last at least 10 minutes and presents a single elephant performing grasping or manipulation behaviour. Then, there is only one video observation per individual, with one or several grasping and manipulation occurrence collected per individual. The observed elephants performed from one to 89 grasping and manipulation types during their observational time.

The techniques, tasks and items

As it was observed that the elephants perform trunk grasping and manipulation mainly in feeding and playing behaviour (Nair, 1989), we focalised the study on the trunk grasping and manipulation that involve these behaviour. Therefore, we explored the main grasping and manipulation tasks that include these behaviour: one playing grasping task that involve congeners grasping, three food grasping tasks and three related food manipulation tasks. These tasks were performed at least by height individuals, more than the median number of herd members (Douglas-Hamilton, 1972; Moss & Poole, 1983). The tasks are described in the **Table 2.1**, and were defined thanks to our preliminary fieldwork observations, the Poole and Granli wild African savannah elephant ethogram (2021), the trunk use behavioural repertoire of captive African savannah elephants during feeding of Lefeuvre and collaborators (2020) and Nair captive Asian elephants feeding descriptions (1989). Other grasping and manipulation tasks in feeding and playing behaviour were sporadically observed but not included in the analyses. For illustration of the bundling and cleaning feeding manipulations, see the videos under the behaviour names “Pack-Grass” and “Sweep-off-Dirt” in the Elephant Ethogram, available at the ElephantVoices website (see Poole & Granli, 2021).

Type of behaviour	Grasping or manipulation	Task	Description
Social play	*Grasping*	Play grasp	Grasp with the trunk a congener of the same group of age and sex for social play
Feeding	*Grasping*	Eating grasp	Grasp with the trunk food items in order to ingest it directly
	Grasping	Bundling grasp	Grasp with the trunk food items in order to bundling it before ingestion
	Manipulation	Bundling	Bundling food items with and on the trunk before ingestion
	Grasping	Cleaning grasp	Grasping with the trunk food items in order to clean it before ingestion
	Manipulation	Cleaning	Clean food items with the trunk (dynamic shaking or slapping) before ingestion
	Manipulation	Adjusting	Manipulate with the trunk food items that are into the mouth to adapt the item position

Table 2.1 – Main grasping and manipulation tasks performed by the elephants.

We also noted the food item, or the part of the elephant body when playing, that were grasped or manipulated. The elephants when playing together, with their trunks, grab regularly different parts of the playing partner body. Grasping the tail and leg is recurrent, and the adult male elephants often grasp the tusks and trunk of their playing partner when wrestle playing (Lee & Moss, 2014; Webber & Lee, 2020). They also eat a large diversity of plants, although, during the wet season, the elephants of the Kruger National Park eat mostly grass (50% of their diet) and ligneous plants (especially Mopane trees, Codron et al., 2006; Kos et al. 2012). Therefore, the elephants in our data grasped and manipulate mostly six types of food items: grasses, leaves, Marula seed pods, barks, small branches (diameter below two centimetres) and branches (diameter upper two centimetres).

Finally, to define the trunk grasping and manipulation techniques, we used four criteria. These four criteria put together enable the characterisation of the techniques. First, we defined the type of grasping, in other words, if the trunk is used with a pinch, a wrap or a torsion (Figure 2.1). This criterion variables were defined by Lefeuvre and collaborators (2020). The African savannah elephants performed a pinch with the fingers of their trunk tips, sometimes helped with a suction (Schulz et al., 2020), and can take the items with the front or side of the trunk tip (Figure 2.1A). They can also perform a wrap of the trunk around an item, with a side or a front wrap

(Figure 2.1B). Moreover, the trunk can grasp an item with a torsion movement, to create a pressure point on the item, usually to break it (Figure 2.1C).

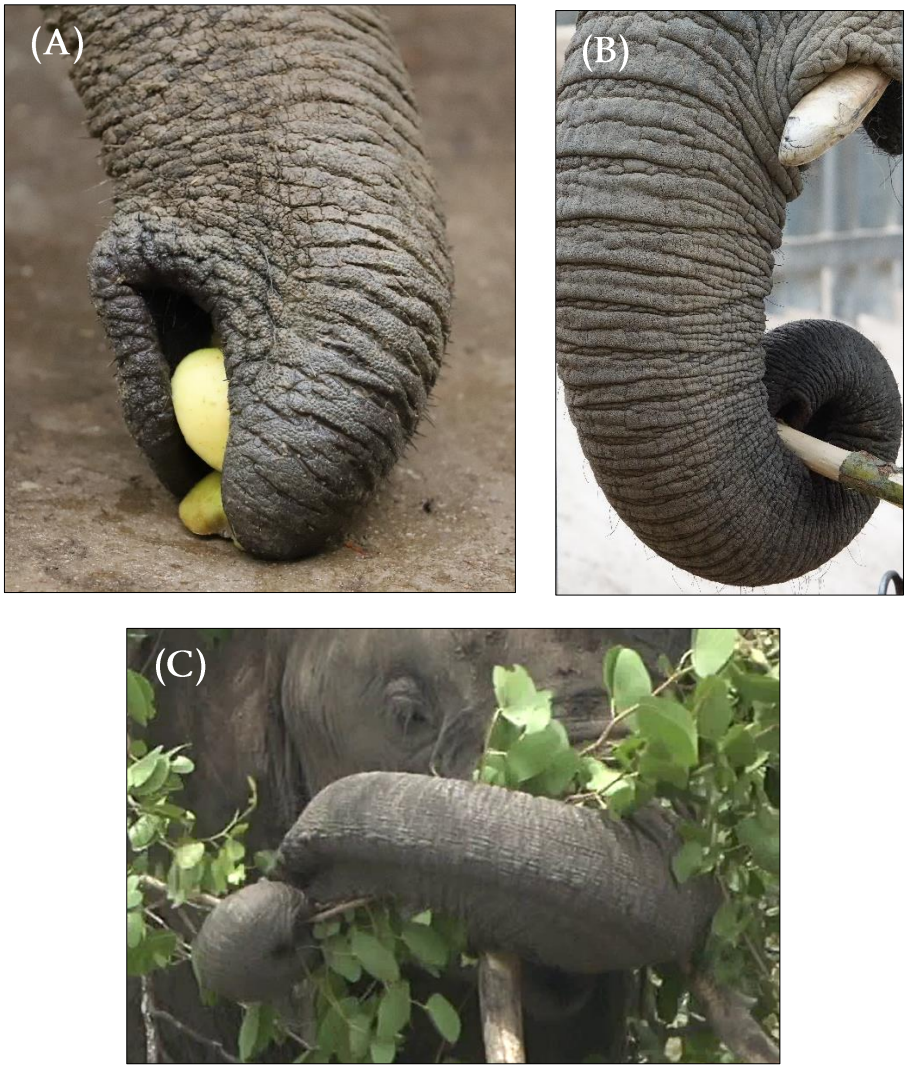


Figure 2.1 – Illustration of the different grasping types: (A) the pinch performed with the fingers of the trunk tip, sometimes helped with a suction; (B) the wrap of the trunk around an item; (C) the torsion of the trunk to create a pressure point on the item. © R. Cornette and J. Soppelsa.

The second criterion of trunk grasping and manipulation techniques is the grasping way. We noted if the trunk grasp the item from the front, the right or the left side (from the elephant perspective). Indeed, elephant trunk lateralisation was observed in feeding, grooming, exploration and social behaviour, during trunk

wrapping but also during the pinch (Giljov et al., 2017; Haakonsson & Semple, 2009; Keerthipriya et al., 2015; Lefeuvre, 2021; Martin & Niemitz, 2003).

The third criterion is the grasping strategy. We defined five strategies to compose this criterion, based on the Poole and Granli wild African savannah elephant ethogram (2021) and the Nair Asian elephants feeding descriptions (1989). The first strategy is "Pluck out", when the elephants used their trunk directly to pluck items out. The second is "Slice-with-foot" and it is when the elephants help their grasping of an item by detaching it with the forefoot, usually with a swinging of the foot to the item. The third strategy, "Strip", is using the trunk to pulling off bark or branches from a tree into long strips, whereas the fourth strategy, "Break", is using the trunk to pulling off and then breaking an item. Finally, the last strategy, "Grasp-food-Bite", describe when the elephant grasp with its trunk a hang-up item (usually branches or leaves from a tree) to approach it to its mouth and to detach it with a bite. For illustration, videos of these strategies are available at the ElephantVoices website, in the Elephant Ethogram (see Poole & Granli, 2021), under respectively the behaviour “Pluck-Leaves”, “Grasp-Kick-Grass”, “Strip-Bark”, “Grasp-Break-Branch” and “Grasp-Branch-Bite”.

The last criterion of trunk grasping and manipulation techniques is the trunk parts used in the movements. We slice the trunk in six parts based on the functional movements of the trunk, movements personally observed in 2020 and observed in Poole and Granli ethogram (2021) videos and descriptions. The first part represents the trunk tip. The sixth one, close to the forehead, is usually used for pulling but not grasping. The other parts were cut depending on how the trunk usually grasps and twists. **Figure 2.2** represents this functional cutting of the trunk in six parts. The grasping and manipulation can occur with one or several parts of the trunk, adjacent or not.

Figure 2.2 – Functional cutting of the parts of the trunk that can be used in the movements. The slice was based on the functional movements of the trunk. The first part represents the trunk tip. Picture © J. Soppelsa.

Animal subjects

We filmed 32 elephants that performed grasping and manipulation. We sex-classified them with their body and head shapes, shoulder heights, tusk shapes, genitals and breasts, and with their group composition, as grown males and females lives in separate types of groups (Moss, 1996; Poole, 1994). The observation data are composed of 14 females, 17 males and one elephant that we could not sex. We also age-categorised the observed elephants with their body and tusk shapes and sizes, especially the males who continue to growth throughout their lives (Shrader et al., 2006). The independency of a new adult male from its family group, or the presence of a calf with a new adult female, were also good age indicators (Moss, 1996; Moss & Poole, 1983). We used five age groups. Infants represent the elephant that had less than one year old. The older calves, from one to seven years old, were the juveniles. We categorised as subadults the older and independent young elephant that had eight to fifteen years old. The adults represent the grown elephants and the large adults were the older adults, over 35 years, with marked bodies (Moss, 1996). The 32 elephants are composed of two infants, four juveniles, five subadults, seventeen adults and four large adults.

For each animal recorded, we determined the social environment, i.e. the number of elephants present in the immediate physical surroundings of the focal animal. We categorised these social environment numbers, based on the elephant social groups. Zero, one, two, three and four elephants around the focal animal represent the first categories. They represent grown males that are alone or in bull groups. The numbers from five to nine elephants around the focal animal were categorised together: family groups are mostly between five and nine individuals. We categorised the number from 10 to 19 individuals together: they represent large family groups and family groups association. Several family groups and occasional adult males composed these group associations. Finally, the numbers from 20 to 40 elephants around the focal animal were regrouped in one category, as these large numbers of elephants reveal large group associations. The social environment composition of the observation data can be found in the appendices (**Appendix 2.1**).

Diverse tusk characteristics were also determined for each elephant. For both tusks of each individual, we noted the presence or absence of the tusk, if the tusk is broken or not, if it is worn or not, if its shape is curved or straight and if its tip point at the trunk, toward the outside or stay straight (the tusk opening). We also noted the size of the tusks based on a five level of size scale. Moreover, we point out if the tusks of the elephants were symmetrical or if one was higher or lower.

With the combination of the criteria of age, sex, tusks profile and particular physical characteristics (body shapes, ear shapes, holes and veins, Moss, 1996; Webber & Lee, 2020), the 32 elephants were recognised individually.

Data analysis

Therefore, we analysed each video and noted, for every grasping or manipulation occurrence, the focus elephant with its sex, age, and social environment and tusk characteristics. We also noted the task, the item involves, the type of grasping, the grasping way, the grasping strategy and the trunk parts used in the movements. This video processing was performed by a single observer to avoid any observer effects.

To explore the tasks repartition performed by the 32 elephants, we calculated the proportion of each task, express in %. To see if the realisation of the feeding grasping tasks (eating grasp, bundling grasp and cleaning grasp) are related to specific individuals, social environments, items or techniques, we performed several Pearson's chi-square tests of independence. We used the "chisq.test" function of the "stats" package in R, version 4.2.0 (R Core Team, 2018) to carry out the tests. A Bonferroni correction was also applied with the function "p.adjust" of the "stats" package. For the

variables related significantly to the task variable, we calculated the Cramer'V correlation to indicate the strength of the association, and we applied a Correspondence Analysis to explore the relationships between the variables. We performed the Cramer'V matrix with the "char_cor" function of the "creditmodel" package and we applied the Correspondence Analysis with the "CA" function of the "FactoMineR" package (2.3 version, Lê et al., 2008), also in R.

In each task, we employed the same procedure to explore the types of items involve, the grasping and manipulation techniques used, the social environment and the type of individuals that performed the task. This procedure enables us to explore the relationships between all these variables in each task, by applying the Pearson's chi-square tests on every interesting variable association. To explore the relationships between the variables, a Multiple Correspondence Analysis was used instead of a Correspondence analysis (with the "MCA" function in the "FactoMineR" package). For a better understanding, several variables in the Multiple Correspondence Analysis plots were present in schematic forms.

Results

The task variations

Among the studied tasks, the grasping and manipulation varied the most when the elephants performed eating grasp (37% of the observations), then bundling grasp (21%) and bundling manipulation (17%). Cleaning manipulation represents 10% of the variations in the observations, whereas it is 7% for cleaning grasp and 5% for play grasp. Finally, the adjusting manipulation task was the less performed and with fewer variations (3% of the observations).

We explored the relationship between the type of task performed by the elephants and the other variables, for the three comparable feeding grasp tasks. The type of task was significantly linked with only one variable, the social environment (Chi-square test: $X^2_{12} = 33.08$, $P' = 0.015$). The type of task was not significantly linked with the other potential factors (the different criteria of the grasping and manipulation techniques, the individual and its inherent features and the item grasped). However, the Cramer'V correlation between the type of task and the social environment is 0.28; with a degree of freedom of 12, this is a large association. The details of this association can be seen in **Figure 2.3**. The cleaning grasp is strongly linked with a social environment of five to nine elephants (one family group). The bundling grasp tends

toward the social environments zero (one lone bull) and five to nine (one family group). The eating grasp is linked with the social environment of four elephants (adult males only) and the one from 10 to 19 (several family groups and adult males), in opposition to the two other grasping tasks.

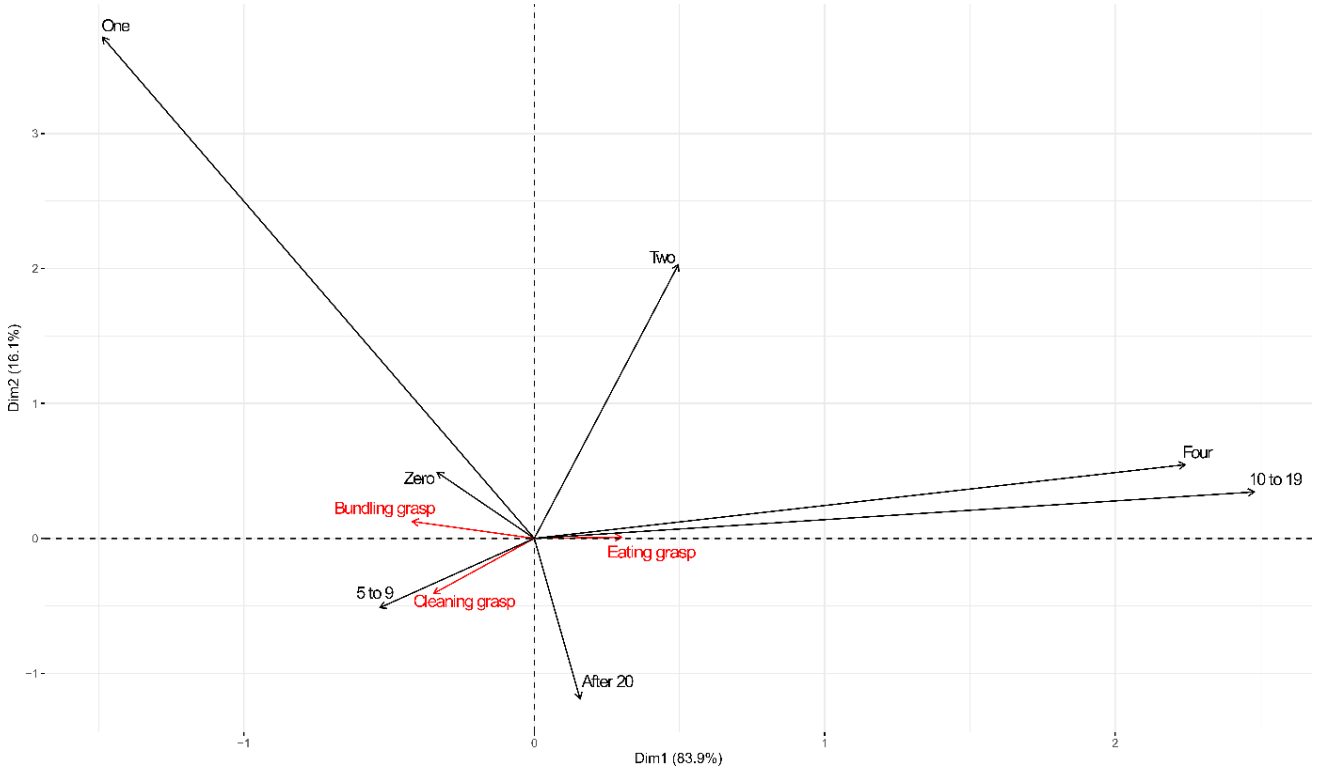


Figure 2.3 – Correspondence Analysis of the relationship during the grasping between feeding grasping tasks and the social environment of the elephant, i.e. the number of elephants present in the immediate physical surroundings of the focal animal. The red arrows represent the three grasping tasks and the black arrows represent the different social environment in which the grasping was performed.

Eating grasp task variations

As the task performed by the observed elephants that display the most variations is the eating grasp, we firstly focalised on this task. We explored all the interesting relationships between all the variables during eating grasp. The **Table 2.2** displays every significant variable association for this task, by presenting only significant Chi-square results. The Cramer'V correlation indications of these significant variable associations can be found in the **Appendix 2.2**. All these Cramer'V indications display large associations (interpretation of these Cramer's V based on the

different degrees of freedom). We can see, in **Table 2.2**, that the item grasped is deeply linked with the social environment and the individual, and with most of the individual inherent features (tusk morphology, sex and age). The grasping type is also associated with the individual and three inherent features which are the size, opening and wear of the tusks. The other associations in this eating grasp task will be explored with the figures above.

Variable 1	Variable 2	Statistic X^2	Degree of freedom	Corrected p value
Item	Tusks size	258.18	40	6.92e-32
Item	Social environment	223.30	30	1.29e-29
Individual	Item	322.64	110	6.01e-21
Item	Tusks opening	164.04	25	1.35e-20
Item	Tusks wear	128.86	15	2.31e-18
Grasping type	Trunk parts	100.99	12	2.31e-14
Item	Grasping strategy	135.47	30	1.53e-13
Item	Tusks break	85.30	10	2.96e-12
Item	Grasping type	82.77	10	9.34e-12
Grasping type	Grasping strategy	80.38	12	2.28e-10
Item	Tusks curve	85.36	15	4.70e-10
Tusks wear	Grasping strategy	73.04	18	8.92e-07
Tusks size	Grasping type	65.05	16	4.69e-06
Item	Age	71.92	20	5.73e-06
Tusks opening	Grasping type	47.19	10	5.67e-05
Tusks symmetry	Grasping way	37.16	6	0.00011
Tusks opening	Grasping way	43.65	10	0.00025
Social environment	Trunk parts	85.11	36	0.00048
Tusks size	Grasping way	49.34	16	0.0019
Item	Sex	28.28	5	0.0021
Tusks wear	Grasping type	29.76	6	0.0028
Item	Trunk parts	67.42	30	0.0069
Tusks size	Grasping strategy	90.97	48	0.012
Individual	Grasping type	81.91	44	0.030

Table 2.2 – Significant Pearson's Chi-square results of different variable associations, for the eating grasp task. The p-values were corrected with a Bonferroni procedure.

Figures 2.4 to 2.7 depict, with Multiple Correspondence Analysis, several details of these significant relationships between the variables. The variables that influence the most the axis of the Multiple Correspondence Analysis plots are grasping type and trunk parts (**Appendix 2.3**).

Figure 2.4 shows the significant relation of the grasping type with the item and with two other trunk grasping techniques criteria (the grasping strategy and the trunk parts). When the elephants performed a torsion as grasping type (green circle), most of the time, they used strip and break grasping strategies, and sometimes with the help of the tusks. This torsion was mostly used for the bark item, and sometimes leaves. The predominant parts of the trunk involved in this grasping type are from 1 to 4 and from 1 to 5. When the elephants performed a pinch as grasping type (pink circle), it was associate mainly with grasp-for-bite and pluck out grasping strategies. The main items grasped are the seed pod and grass items. This pinch is performed with the trunk tip, or the trunk tip and the second part of the trunk. Finally, when the elephants wrap with the trunk (blue circle), slice-with-foot and pluck out grasping strategies are mainly used. The trunk wrap mostly around small branches and branches, but also around leaves and grass. The trunk parts from 1 to 2 or 3 are used, but also from 2 to 4 or 5. Moreover, as the **Table 2.2** displays, there is also a significant link between the grasping strategy variable and the item grasped. As shown in **Figure 2.4**, this relation is like the relation between the item and the grasping type.

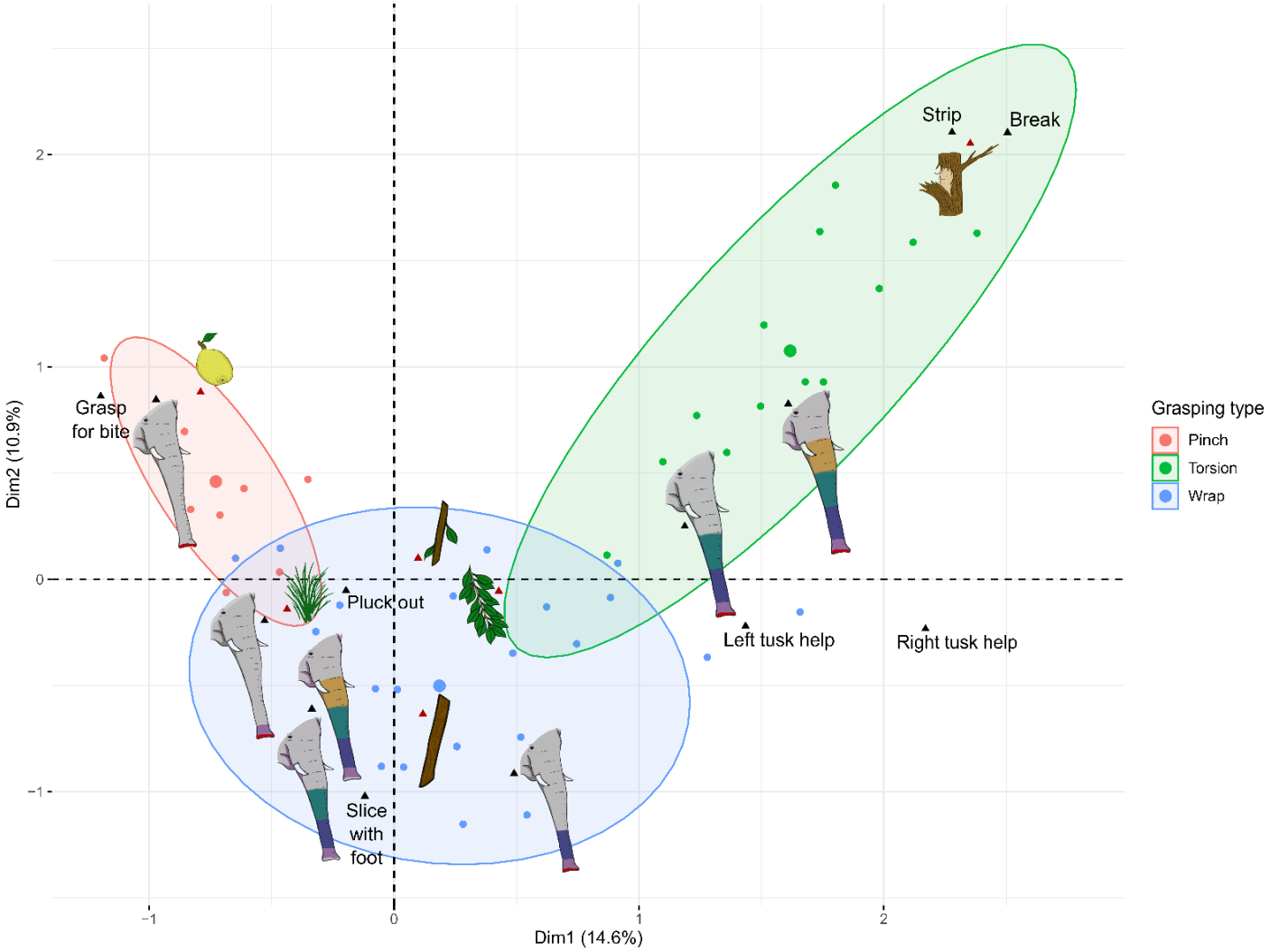


Figure 2.4 – Multiple Correspondence Analysis plot of the variables significantly associated with the grasping type technique criterion, during the eating grasp task. Dots represent every eating grasp task performed by the observed elephants. The schematic shapes represent the different items grasped and the different parts of the trunk involved in the grasp (the coloured parts). Nominal categories of the grasping strategy criterion are displayed in text format, and nominal categories of grasping type can be visualised by the colour of the dots and coloured circles.

Although the grasping strategy does not vary specifically with the individual, it varies with two inherent individual features (**Table 2.2**). **Figure 2.5** displays the details of this relationship between the grasping strategy and the tusks wear and size. In this figure, the grasping strategy nominal categories followed two main outlines. The strip strategy follows the same main outline as the break strategy, represent by the red circle. The grasp-for-bite, slice-with-foot and left tusk help follow the pluck out strategy outline, represent by the green circle. Therefore, the figure reveals that the elephants that used break or strip as grasping strategies have mostly their left tusk wear, plus a tusk with a medium size and the other one with a small size. The other grasping strategies seem not to be linked with any particular tusk wear or tusk size categories.

Similar as the previous figure, **Figure 2.6** represent significant relations between the grasping way technique criterion and three tusk morphology criteria. In this figure, the grasping from the right and the grasping from the face seem not to be linked with specific tusks size, opening or symmetry. However, the elephants that grasp from the left have a medium left tusk size and a smaller right tusk. Both tusks tend toward the left, and the right one is higher.

Finally, in **Figure 2.7**, for the eating grasp, the use of the different trunk parts is significantly related to the social environment and the item. In particular, the use of the parts from 1 to 4 and from 1 to 5 seem to be related to a social environment of four to nine individuals, and a grasping of bark, leaves and small branches. Moreover, the two individuals as social environment occurs when the elephants use only their trunk tip and grasped seed pods.

Figure 2.5 – Multiple Correspondence Analysis plots of the variables significantly associate with the grasping strategy technique criterion, during the eating grasp task. Dots represent every eating grasp task performed by the observed elephants. The schematic shapes represent different tusk wear and different tusk sizes, and the crossed tusks the absence of tusks. Nominal categories of grasping strategy can be visualised by the colour of the dots and coloured circles.

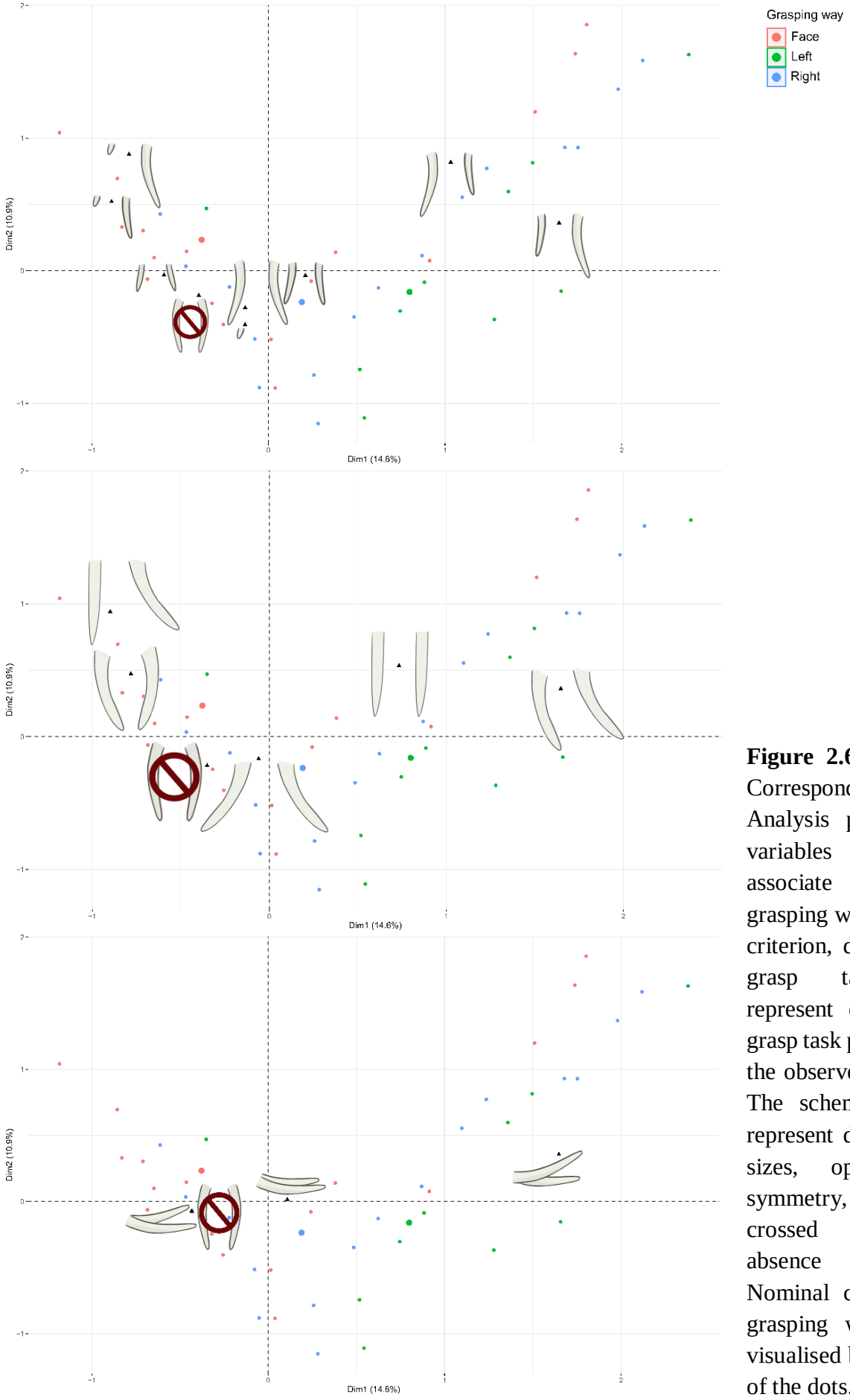


Figure 2.6 – Multiple Correspondence Analysis plots of the variables significantly associate with the grasping way technique criterion, during eating grasp task. Dots represent every eating grasp task performed by the observed elephants. The schematic shapes represent different tusk sizes, opening and symmetry, and the crossed tusks the absence of tusks. Nominal categories of grasping way can be visualised by the colour of the dots.

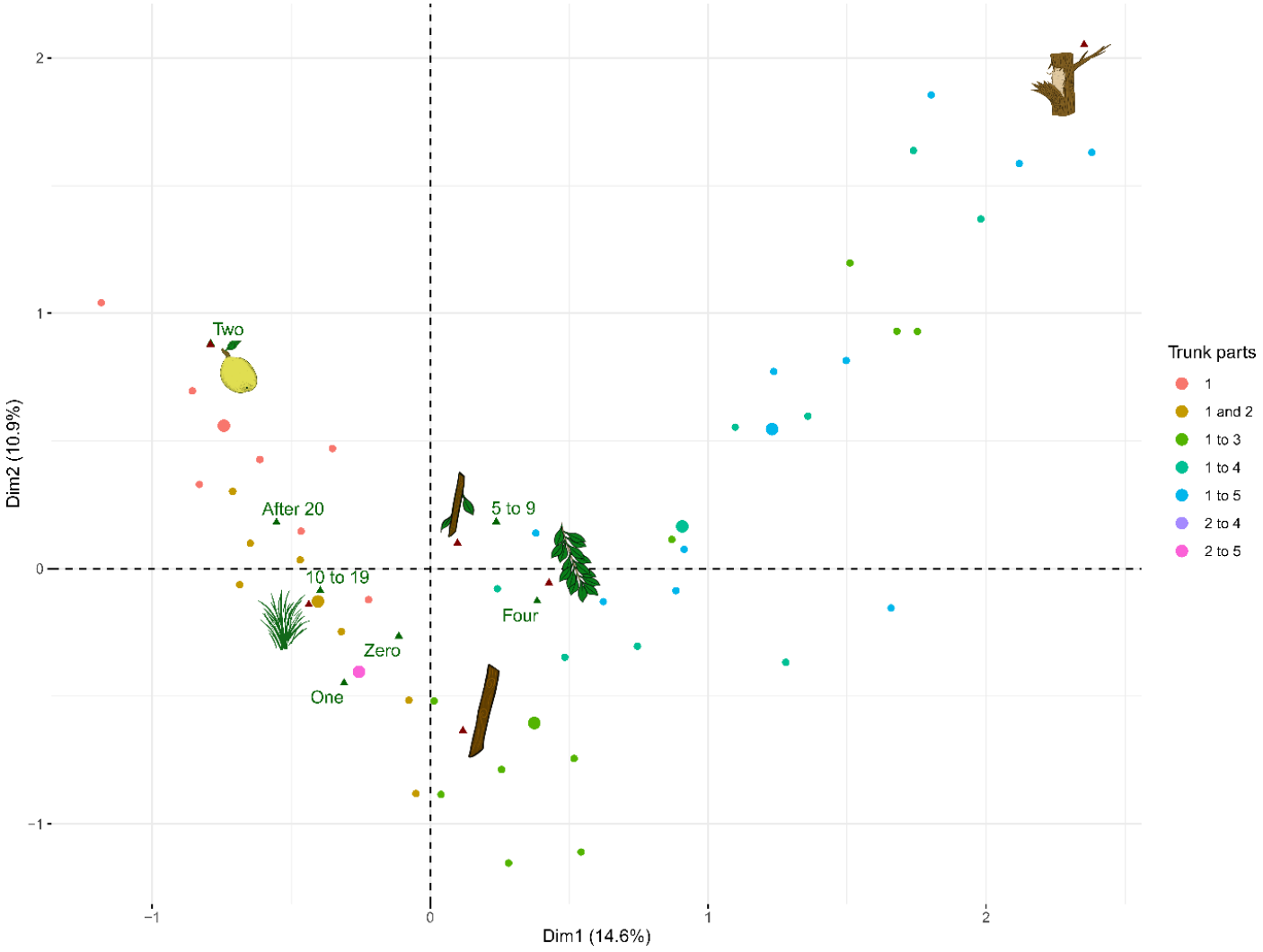


Figure 2.7 – Multiple Correspondence Analysis plot of the variables significantly associate with the trunk parts technique criterion, during eating grasp task. Dots represent every eating grasp task performed by the observed elephants. The schematic shapes represent different items grasped. Nominal categories of the social environment (number of elephants around the focal animal) are displayed in text format, and nominal categories of trunk parts can be visualised by the colour of the dots.

Other grasping and manipulation tasks variations

The variable associations were similarly explored for the other grasping and manipulation tasks. The **Appendices 2.4, 2.5 and 2.6** present respectively the variable association significant Chi-square results for the bundling grasp, the manipulation bundling and the cleaning grasp. For the cleaning and the adjusting manipulations, there is no significant association of the variables. For the play grasp, there is only one significant association, between the item grasped and the wear of the

tusks (X^2_6 = 22.4, P' = 0.039). This association Cramer'V value is 0.79, and indicates a strong association.

Figure 2.8 displays the Cramer'V correlations of the significant variable associations of the bundling grasp, the manipulation bundling and the cleaning grasp. This figure enable, for all the three tasks, the visualisation of all the significant relationships and their correlation strength. All these Cramer'V values also demonstrate large associations.

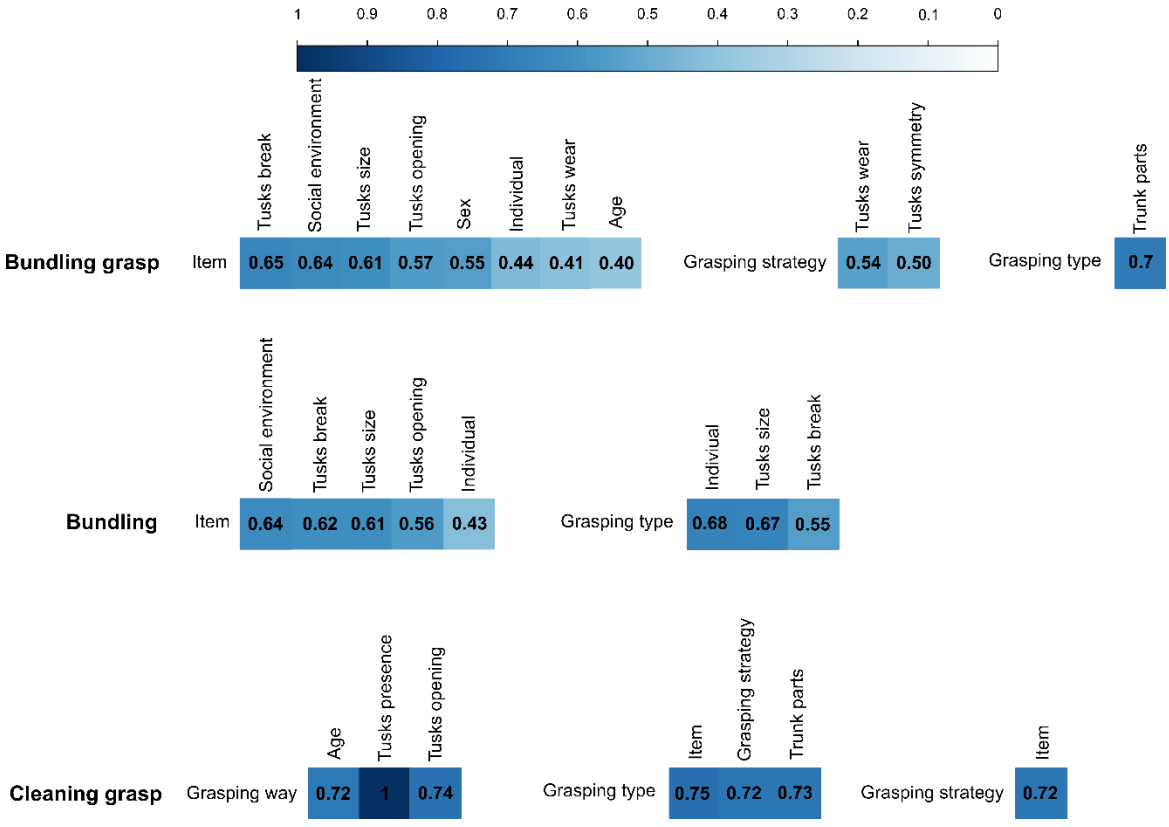


Figure 2.8 – Cramer'V correlation values of the significant variable associations of the bundling grasp, the manipulation bundling and the cleaning grasp tasks.

With the **Figure 2.7** and the Multiple Correspondence Analysis of the bundling grasp (**Appendix 2.7**), we can develop on the trunk techniques and variations when performing this task. Similar as for the eating grasp, the item grasped is deeply linked with the social environment, the individual, and several of its inherent features (sex, age and diverse tusk morphologies). The grasping strategy also varies with two inherent individual features, the tusk wear and the tusk symmetry, but not with the

individual. Indeed, the elephant that performed a slice-with-foot strategy generally have their right tusk lower and damaged. Also similar as when performing an eating grasp, when using a pinch for grasping type, the trunk parts that are used are the trunk tip with or without the second part. When the elephants wrap, they use several parts of their trunk: the second part only, the second and the third parts, the first to the third parts or the first to the fourth parts.

For the bundling manipulation, with the **Figure 2.8**, we can see a similar pattern as the previous tasks, on the linked between the object grasped, the social environment and the individual, plus three inherent individual features (tusks morphology). The individual (and its tusk size and break) also have a link with the type of grasping.

The cleaning grasp show both similar and different patterns to the other grasp tasks. **Figure 2.8** and **Appendix 2.8** display these tendencies. First, the elephants that we observed grasping from the left were only juvenile with no tusks, unlike the other grasping tasks. However, other patterns are similar to the two other grasping type. The grasping strategy is deeply linked with the item grasped. When performing a torsion as grasping type, the elephants that performed the cleaning grasp also grasped mostly bark with a strip strategy and with the 1 to 4 trunk parts. When wrapping, they mostly grasped leaves and grasses, with a pluck out strategy and with the trunk parts from 1 to 2 or 3. Moreover, when using a pinch, the elephants mostly grasped grasses and branches with a slice-with-foot strategy and with the trunk tip or the trunk tip and the second part.

Finally, when performing a play grasp, the elephants that grasped the leg of their play partner mostly had their left tusk wear. The ones that grasped the tail had both their tusks damaged, and the ones that grasped the trunk and tusks of their partner had their own tusks not wear (**Appendix 2.9**).

Discussion

In this study, we firstly highlighted that the tasks are not performed equally. The choice of the performed feeding grasp task seemed to be especially dependent on the social environment. The feeding grasp techniques with the trunk were characterised, depending on the task and the different joint association of trunk parts, grasping type, way and strategy. The bundling manipulation techniques were also

characterised similarly, but no techniques were found for the cleaning and the adjusting manipulation.

We revealed that there are different techniques with the trunk depending on the item grasped, when the elephants grasped for eating directly and grasped for cleaning the item before ingestion. The parts of the trunk used during eating grasp especially depended on the item grasped and the social environment. Moreover, there is a strong individual variation of the type of item grasp in two food grasping tasks (eating and bundling) and one manipulation task (bundling). However, inter-individual variations on trunk techniques only occurred for two tasks, eating grasp and bundling manipulation, and only on the type of grasping technique criterion. The sex of the elephant especially did not have any effect on the techniques studied, and the age was linked with only one trunk technique criterion in one task, the grasping way during cleaning grasp. Nevertheless, the tusk morphologies seemed to have affected the use of the grasping strategy technique criterion, especially the tusks wear and symmetry during bundling grasp, and the tusks wear and size during eating grasp. Concerning the only non-feeding movements we studied, we revealed that, when the grown male elephants play, they grasped different parts of the body of their play partner, depending on their own tusks wear.

Task variations

In our study, the tasks were carried out uniformly: the eating grasp especially was the most performed task, and with more diversity of individuals, items grasped and technique features. Nair (1989) also highlighted, in Asian elephants, that elephants grasp more often food to place it directly in the mouth rather than cleaning it before. On the contrary of the bundling and cleaning grasps, the eating grasp is not followed by a manipulation task. The bundling and cleaning grasps probably require specific movements to prepare the manipulation to come, and are therefore more complex. In primates, it was highlighted that the task complexity affects the grasping techniques (Pouydebat et al., 2010; Sabbatini et al., 2016; Weir, 1994), and in zoo elephants, the inter-individual variability in feeding behaviour decrease with the task complexity (Lefeuvre et al., 2020). Therefore, we can assume that this is also the case in the wild elephants, for the three feeding grasping tasks studied in this chapter. The eating grasp, by its simplicity, is easily performed by all the individuals, more often than the other grasps, for grasping a better diversity of items, and display more movement variability.

Moreover, we highlighted that this difference in the feeding grasp tasks are also directly links with the social environment where the task was performed. The cleaning

grasp is mostly used by elephants grouped in lone family herds (5 to 9 elephants). Besides, the other complex grasp, the bundling grasp, was also performed mostly by family herds and lone grown males. In these social environments, there is less social pressure and constraints on resource access (Louw et al., 2021). The elephants can therefore perform more complex tasks that are usually more time consuming. This hypothesis is strengthened by our results on the eating grasp: this simpler task was used when the social environment indicates bull associations and family herd associations (higher social constraints). In addition, as the complex grasp tasks were realised mostly by members of family herds, we could presume that their realisation result of transmission within the herd (Fishlock et al., 2016). To test this hypothesis, we need to complete the data on these specific tasks on more individual and to perform a longitudinal study.

The trunk techniques

We characterised the feeding grasp techniques, with their similarities and differences. For the three feeding grasp tasks, the trunk parts used when pinch grasping are the same. The trunk parts used when wrapping are also similar. Moreover, during eating and cleaning grasp, both tasks displayed conjoint use of the wrapping and pluck out strategy, and conjoint use of torsion and strip strategy, with the first four parts of the trunk. These similar technique features used for the grasping tasks certainly constitute basic movements. These basic movements are therefore frequently used for various tasks, as Dagenais et al. depicted (2021).

Besides, the eating and bundling grasps usually involved more trunk parts than the cleaning grasp. During the cleaning manipulation that generally follows this grasp, the food item was mostly always held just with the trunk tip. Therefore, to rapidly timed the two actions (cleaning grasp and manipulation), the cleaning grasp had to be performed with the trunk tip and few other parts. In addition, the eating grasp displayed more grasping strategy variability, and thus, as previously state, more technical variability due to its simpler nature.

Nevertheless, the feeding grasping tasks were also constituted of other technique features, besides the basic movements described above. The eating and cleaning grasping techniques were also constituted of specific grasping strategies. Therefore, the eating and cleaning grasping techniques were a combination of several grasping type, trunk parts and grasping strategy. However, these strategies differed between the tasks when a pinch was used. During cleaning grasp, the elephants displayed a slice-with-foot grasping strategy. During eating grasp, the grasp-for-bite and pluck out strategies were used. The slice-with-foot strategy is used especially to

uproot plants (Nair, 1989), and these grasped uproot plant usually needs to be clean from remaining soil. Thus, the slice-with-foot strategy is logically mostly use during cleaning grasp. However, this association may highlight elephant habits to plan to clean their food when they grasp it thanks to a slice-with-foot. In addition, Sikes (1971) described the slice-with-foot grasping strategy in African savannah elephants as rare. Yet, it was the second most used grasping strategy that was recorded in our data, after the pluck out strategy. To explain this divergence, we could hypothesise that the use of the slice-with-foot strategy may not be widespread in African savannah elephants, but inherent to specific elephant populations. To test it, further observations have to be recorded on elephant food grasping strategies, in several populations.

However, for the bundling grasp, we highlighted no other specific technique. For this task realisation, only the conjoint used of different trunk parts and types of grasping was displayed. Therefore, this task may require less specific movements for its realisation, such as specific grasping way or strategy, compared to the two other feeding grasp tasks. This complex task is then certainly performed with precise but few and elementary movements, in accordance with the finding of Dagenais and collaborators (2021). Furthermore, we did not find any particular technique used with the trunk for the three feeding manipulations and for the play grasp. Therefore, for these manipulations and this play grasp, the technique criteria used in this study cannot reveal any technique.

Technique variations with the item

As shown by our results, the techniques used during eating and cleaning grasps vary with the type of item grasped. For both tasks, techniques involving torsion were mostly employed to grasp bark and leaves, techniques with wrap mostly to grasp leaves and grasses and techniques with a pinch for grasping grasses. Besides, the type of item grasped is more diverse with the eating grasp task. As previously state, this task is simpler and therefore display more variability in terms of items that could be grasped. In the observed elephants, the grasping techniques were probably adjusted to the diverse food item properties, i.e. their size, shape, weight, mobility and consistency, similar as for other species (Christel, 1993; Marzke et al., 2015; Peckre et al., 2019a; Pouydebat et al., 2009; Reghem et al., 2011). Dagenais and collaborators (2021) found similar results with elephant trunk, as they reveal that the size and weight of the item induce transitions in grasping techniques. The elephant grasping technique repertoire seems adapted to the properties of the food. This brings new information on the ecological context that may have shaped the food grasping abilities in elephants. However, we did not find any link between the item grasped and the

technique features used for the bundling grasp, the play grasp and the three feeding manipulations. The item properties may affect the grasping techniques, but it is dependent on the task performed. To go further, as no specific technique was highlighted for the three feeding manipulations and the play grasp, we could explore the item properties links with other techniques criteria that the ones we explored.

Moreover, we revealed that the trunk parts used during eating grasp, related to the item, are directly dependent on the social environment. Particularly, in a social environment that corresponds to a bull group or a family herd, almost all the trunk parts (from 1 to 4 or 5) were used for grasping bark, leaves and small branches. These food items, as they require to be pulled out from a tree, were associated with most of the trunk parts to perform this difficult grasp. Moreover, bull group and family herd alone are usually related to low social constraints with less pressure on the resources (Louw et al., 2021). We can therefore hypothesise that the choice to grasp these food items, and thus to perform a difficult grasp, is directly related to social pressure and constraints on resource access in elephants. To develop this hypothesis, we have to explore the grasping techniques and related items in elephants under higher social constraints, for example in an arid area where the competition for resources is harder (Fuller et al., 2021; O'Connell-Rodwell et al., 2011). The other remarkable link between the three variables (item, trunk parts and social environment) is that the elephants that grasped seed pods did it only with the trunk tip in a social environment of two individuals. This result is probably linked with an observational bias, as we observed only one elephant grasped seed pods.

Inter-individual variability

First of all, we revealed that there is a strong individual variation on the item grasp, but only during eating and bundling grasp and bundling manipulation tasks. This variability may highlight individual food preferences (Franz et al., 2010; Howes et al., 2020; Koirala et al., 2016), especially given that the sense of smell is performed by the trunk. The other manipulation tasks and the cleaning grasp were performed mainly on one item, the grasses, whatever the individual. Thereby, these few inter-individual differences probably reveal the specificity of these tasks, as a similar pattern (task use for a unique item) is used across the individuals.

There was also a strong inter-individual variability on one technique criterion, the type of grasping, during eating grasp and bundling manipulation tasks. As both tasks usually enable more movement variability, an individual choice between performing a pinch or a wrap can be made by the elephant during these tasks. This individual choice could be linked to individual preferences, but also to individual

trunk morphological features that could make a wrap or a pinch easier (Christel & Billard, 2002; Martin & Niemitz, 2003; Sustaita et al., 2013). For example, an elephant that has short trunk tip digital extensions may perform more wraps than pinch, as the pinch could be harder to perform than with longer digital extensions. Study particularly this effect of the digital extension length on elephant grasping techniques could be interesting to understand better the complexity of grasping with the trunk in elephants.

The other technique criteria (other than the type of grasping) displayed variations related to individual inherent features. As we hypothesised, the sex of the elephant did not have any link with the techniques studied. These results are concordant with our previous results (Chapter 1 of this dissertation thesis), as we demonstrated that the trunk use duration does not differ with the sex of the individual. However, we revealed that the age is linked to the grasping way during cleaning grasp. More precisely, we highlighted that the only juvenile that performed this grasp and which do not have tusks yet, is the only individual that grasped from the left when performing a cleaning grasp. This grasping task is complex due to the precise manipulation that follows. Thereby, this grip certainly requires precise movements, more than the other studied grasping task. A strong coordination is necessary for the realisation of precise movements, and a strong specialisation increases the coordination. Therefore, a strong lateralisation is probably necessary for the cleaning grasp realisation. Moreover, it was demonstrated that the right bias in elephant grasping is strong and occur very early in the elephant lives (Giljov et al., 2017, 2018; Keerthipriya et al., 2015; Lefeuvre et al., 2021; Revathe et al., 2020). Thus, we can hypothesise that the observed juvenile that grasped from the left may have already developed a left bias trunk lateralisation. This result goes along with the previous studies that also hypothesis that the elephant trunk lateralisation does not develop with age.

Moreover, the tusk morphologies too are linked with the trunk techniques. Specifically, the grasping strategy changed with the elephant tusks wear and symmetry during bundling grasp, and tusks wear and size during eating grasp. During the bundling grasp, the elephants that had their right tusks lower and damaged, used more a slice-with-foot strategy than the other elephants. By its lower position, the right tusk is more inclined to be used during foraging, and thus damaged (Bielert et al., 2018). Yet, the tusks presence, size and positions are genetic characteristics (Campbell-Staton et al., 2021; Jachmann et al., 1995). The lower position of the right tusk can thereby reflect a family herd in our observation. We can suppose that the members of this herd was the only observed individuals that perform the slice-with-foot strategy during bundling grasp. Indeed, we suppose before that this strategy is

inherent to specific elephant populations, and therefore it can result from a transmission throughout the herds for specific tasks. Moreover, during eating grasp, the elephant that performed break and strip strategies had their left tusk wear and a smaller tusk (left or right). Similar has for the bundling grasp, the wear on the left tusk may reveal its higher use in the elephant life, and therefore the existence of a side bias for the use of the tusks in elephants, maybe related to the trunk lateralisation (Bielert et al., 2018; Giljov et al., 2017; Keerthipriya et al., 2015; Lefeuvre et al., 2021). The small tusk, as a genetic feature, may also indicate family elephants that may use more of the break and strip strategies.

In addition, also during eating grasp, the observed elephants that performed the left side grasping, had their right tusk small, directed toward the trunk and high. This specific right tusk profile certainly obstructs trunk movements toward the right, and thus trunk movements toward the left are easier to perform. This difference between the individual in grasping way was even more visible, as most of the observed individual performed a non-lateralised grasping or a right grasping, similar as what was found in the literature (Giljov et al., 2017; Keerthipriya et al., 2015; Lefeuvre et al., 2021). Thereby, the tusks profiles may change the food grasping techniques. However, we can also hypothese that, in these elephants that grasp more toward the left, these movements let the right tusks grow more freely, with less obstruction and can lead to these specific right tusk profile. This is the first time that the link of tusk profiles and trunk grasping techniques was revealed. These results indicate the importance for further studies on elephant trunk abilities to consider the tusks morphologies too.

Finally, concerning the only non-feeding movement we studied, we highlighted that, during play grasp, the parts of the congener body that are grasped change with the tusk wear of the elephants that grasp (tail and legs are grasped when the elephant has damaged tusks, trunk and tusks with not wear tusks). This play grasp corresponds to a play between grown and independent males only. This could be explained by the fact that, during play, when male elephants grasp the trunk and tusks of their partners, it is usually during a wrestling interaction (Lee & Moss, 2014; Webber & Lee, 2020). With wrestling interactions, the tusks are subjected to impacts that could damage them. Then, we can hypothesise that the elephants with damaged tusks engage themselves less in wrestling interactions to preserve their tusks and more in pursuit interactions (Lee & Moss, 2014; Webber & Lee, 2020). To go further, more data on play patterns and tusks profiles have to be collected.

All these results must be tempered by a potential intra individual effect, as all our individuals were observed only once each. Thus, to ensure our results, more data could be collected on these specific individuals.

Conclusion

In conclusion, the tasks were performed uniformly, depending mostly on their complexity, and the social constraints for the feeding grasp tasks. As most of these tasks were complex and some were related to specific herds, they are probably a result of transmission. In this study, we characterised the feeding grasp techniques, and we highlighted the basic movements shared by these tasks. There is no such techniques for the manipulations studied. The grasping techniques differed with the tasks, as we described the different variability of the techniques depending on the specificity required by the tasks. Thus, elephants likely grasp differently depending on what they are plain to do with the item just after grasping it. These technique realisations also are probably related to population-level and even herd-level.

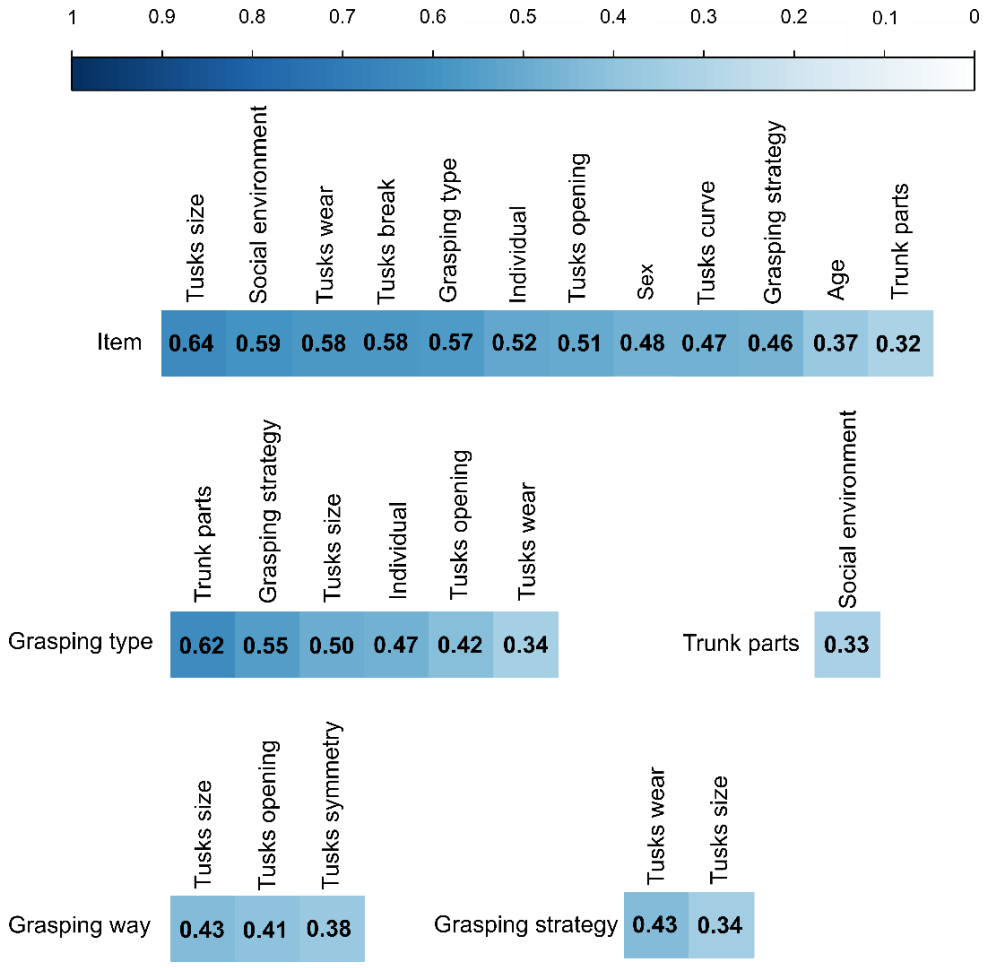
Our results also highlighted other factors that make these trunk grasping and manipulation techniques vary. First, we revealed that, as hypothesise and similar as previous studies, the food grasping techniques are adapted to the food properties and dependent on the task realised. Moreover, in the feeding tasks that are not related to specific food, there was strong individual variations on the item grasp, certainly revealing individual food preferences. Secondly, the techniques used for grasping and manipulate did vary with the individual in several tasks. Especially, as expected, we did not reveal any sex effect on the trunk techniques. We also did not reveal any age effect, as the only significant link we found between age and technique was certainly directly related to the individual, as the lateralisation of the trunk is likely not link with age development. In addition, the tusk morphologies also had an effect on the trunk grasping techniques, and especially the grasping way. Indeed, the technique used may vary to facilitate a feeding grasp obstruct by specific tusk profiles, or to preserve damaged tusks during play.

Therefore, in wild African savannah elephants, the task and its complexity, the item grasped and its properties and the individual with its tusk profile do have a link with trunk grasping and manipulation techniques. These results bring new information on the morphological and ecological contexts that may have shaped the grasping and manipulation abilities in elephants. They also highlight for further studies the importance to take into consideration the tusks morphologies when exploring elephant trunk abilities. To understand more broadly the evolutionary patterns that shaped elephant grasping and manipulation abilities, it would be interesting to complete the data on more individual, in several populations that live under diverse social constraints, and on other techniques criteria that the ones we explored. Moreover, to reveal the rearing effects on these grasping and manipulation techniques, a longitudinal study could be done.

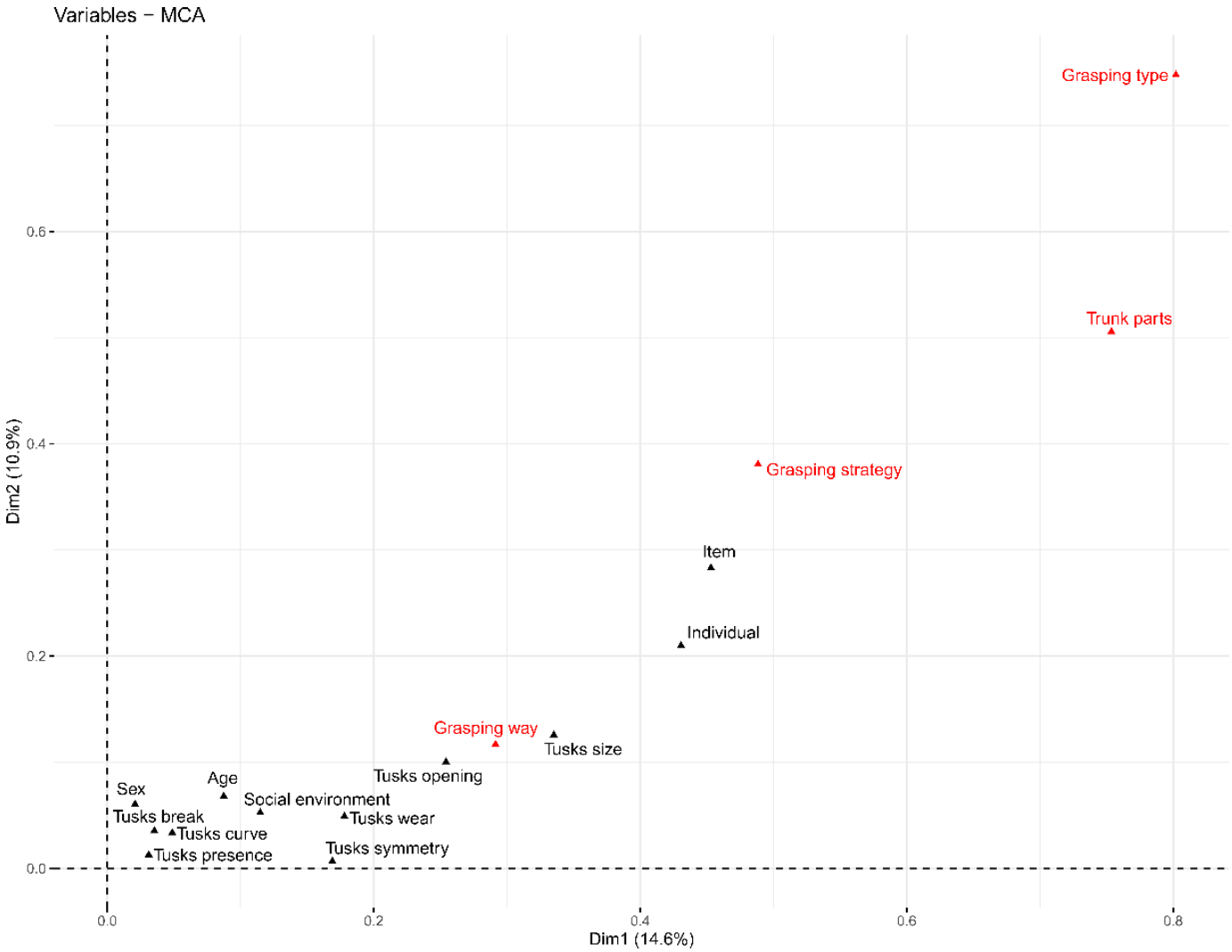
Appendices

Social environment	0	1	2	3	4	5 to 9	10 to 19	20 to 40	Total
Number of elephants	1	2	1	1	2	11	4	10	32

Appendix 2.1 – Social environment distribution of the 32 observed elephants.



Appendix 2.2 – Cramer'V correlation indications of all the significant variable associations for the eating grasp task.



Appendix 2.3 – Multiple Correspondence Analysis variables representation, for the eating grasp task.

Variable 1	Variable 2	Statistic X	df	Corrected p value
Item	Social environment	119.28	20	2.52e-14
Item	Tusks opening	94.77	20	6.97e-10
Item	Tusks size	109.08	28	1.06e-09
Item	Tusks break	61.85	8	1.31e-08
Individual	Item	119.28	52	2.18e-05
Grasping type	Trunk parts	35.90	5	6.46e-05
Tusks wear	Grasping strategy	21.64	3	0.0050
Item	Sex	22.39	4	0.011
Item	Tusks wear	36.82	12	0.016
Tusks symmetry	Grasping strategy	17.93	3	0.030
Item	Age	34.80	12	0.033

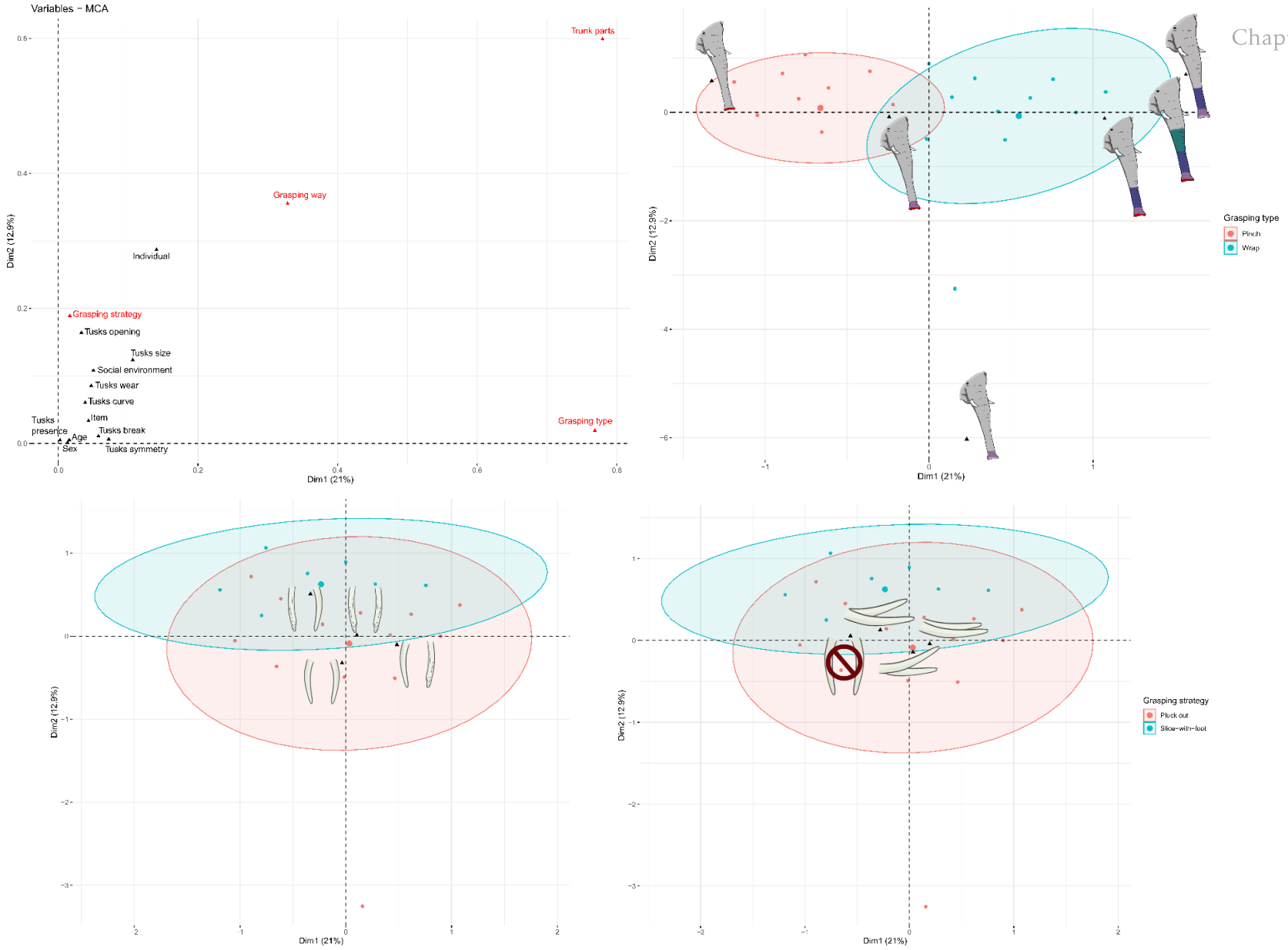
Appendix 2.4 – Significant Pearson's Chi-square results of different variable associations for the bundling grasp task. The p-values were corrected with a Bonferroni procedure.

Variable 1	Variable 2	Statistic X	df	Corrected p value
Item	Social environment	92.17	20	1.55e-09
Item	Tusks opening	71.93	20	4.39e-06
Item	Tusks size	84.98	28	5.92e-06
Item	Tusks break	43.36	8	3.76e-05
Individual	Item	106.18	56	0.0030
Individual	Grasping type	43.63	14	0.0034
Tusks break	Grasping type	17.43	2	0.0082
Tusks size	Grasping type	25.40	7	0.0323

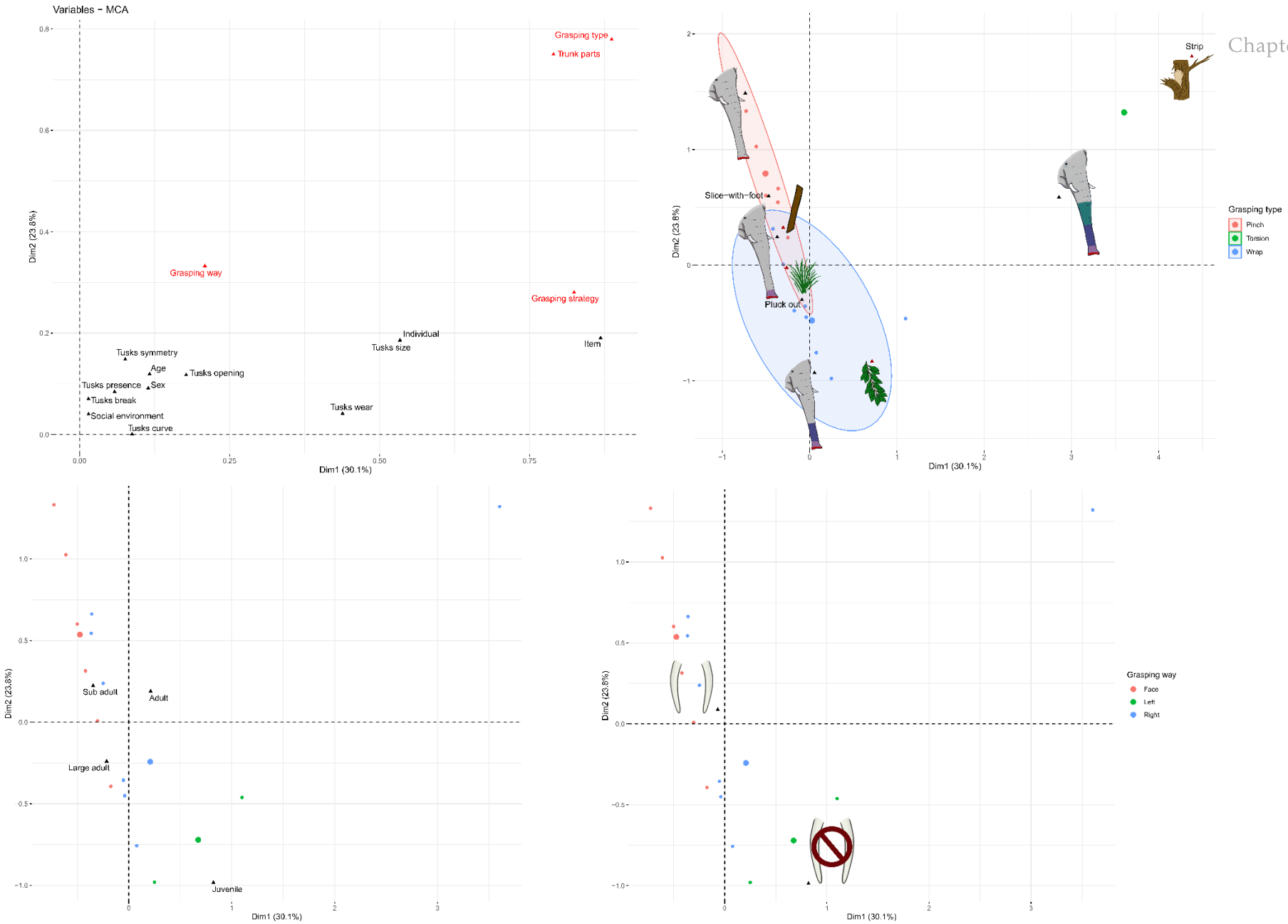
Appendix 2.5 – Significant Pearson's Chi-square results of different variable associations for the bundling manipulation task. The p-values were corrected with a Bonferroni procedure.

Variable 1	Variable 2	Statistic X	df	Corrected p value
Tusks presence	Grasping way	25	2	0.00024
Grasping type	Grasping strategy	26.04	4	0.0020
Item	Grasping type	28.13	6	0.0058
Tusks opening	Grasping way	27.51	6	0.0076
Grasping type	Trunk parts	26.30	6	0.013
Item	Grasping strategy	26.19	6	0.013
Age	Grasping way	25.75	6	0.016

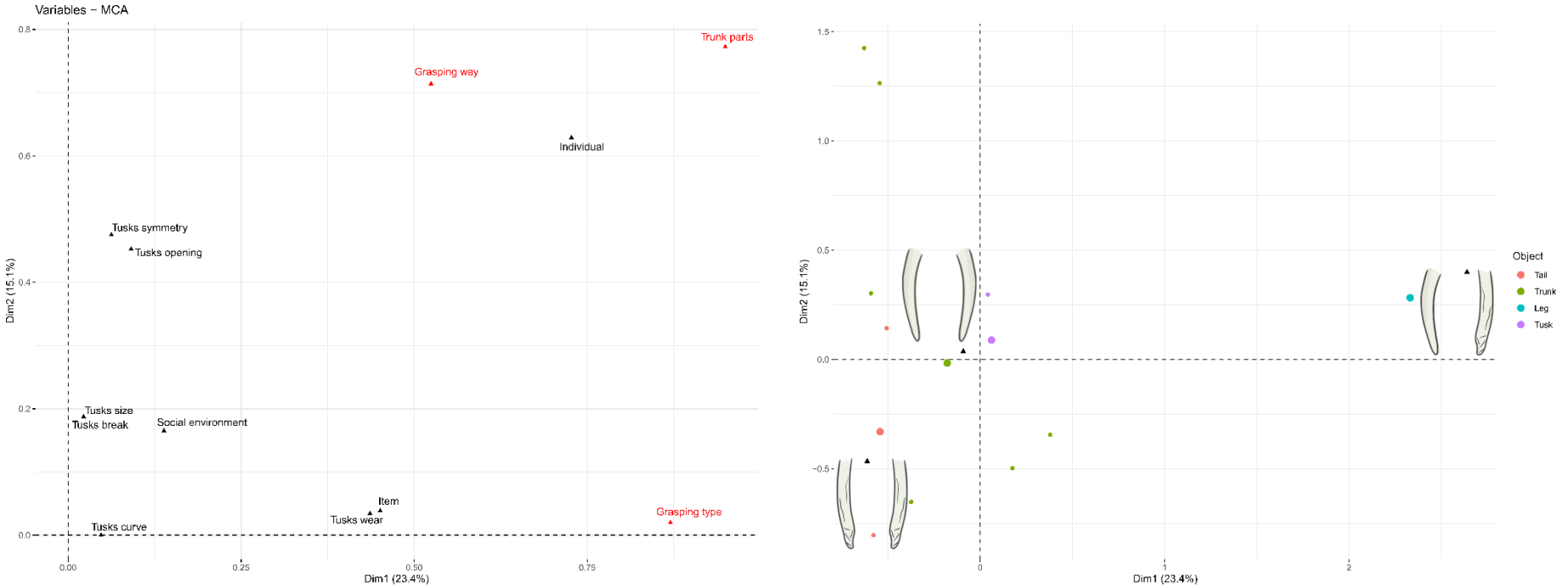
Appendix 2.6 – Significant Pearson's Chi-square results of different variable associations for the cleaning grasp task. The p-values were corrected with a Bonferroni procedure.



Appendix 2.7 – Multiple Correspondence Analysis plots of the variables significantly associates during the bundling grasp task. Dots represent every eating grasp task performed by the observed elephants. The schematic shapes represent different trunk parts and tusks morphologies, and the crossed tusks the absence of tusks. Nominal categories of the grasping type and strategy can be visualised by the colour of the dots and the coloured circles.

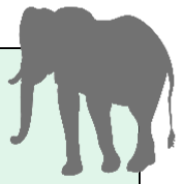


Appendix 2.8 – Multiple Correspondence Analysis plots of the variables significantly associates during the cleaning grasp task. Dots represent every eating grasp task performed by the observed elephants. The schematic shapes represent different trunk parts, items and tusks presence, and the crossed tusks the absence of tusks. Nominal categories of the grasping type and way can be visualised by the colour of the dots and the coloured circles.



Appendix 2.9 – Multiple Correspondence Analysis plots of the variables significantly associates during the play grasp task. Dots represent every play grasp task performed by the observed elephants. The schematic shapes represent different tusk wear. Nominal categories of the item grasped can be visualised by the colour of the dots.

Chapter 2 summary



Title: Trunk grasping and manipulation techniques in Kruger elephants: effects of tusk profiles.

Background: The grasping and manipulation abilities are fundamental for tetrapods, but data on the factors that shaped them are not abundant. Although several studies focus on the influence of object properties, task, and individual on grasping and manipulation movements, most focus on a single form of prehensile appendage: the hand. Yet, in various species, foot, mouth, tail, tentacle or trunk can also grasp and manipulate, but data on these prehensile appendage abilities are scarce. The elephant trunk is a highly used muscular hydrostat, with high flexibility, mobility as well as precise and strong grasping capacities. This is therefore an interesting prehensile appendage to explore the evolutionary context of grasping and manipulative abilities.

Methods: We investigated the link between the elephant trunk grasping and manipulative techniques and the object, the task, the individual and its sex, age, tusks morphology and social environment. To do so, we identified and observed 32 wild African savannah elephants (*Loxodonta africana*) from the Kruger National Park, South Africa. We determined the grasping and manipulative techniques with four factors inherent to the trunk functioning.

Results and discussion: The main feeding grasp techniques were characterised and we highlighted the basic movements shared in every main feeding grasping task, but no specific technique was found. We hypothesis that there is probably a population-level and a herd-level for the realisation of these techniques. They also differ with the tasks and the object, and vary with the individual for several tasks. There is particularly a tusk morphology effect on the trunk techniques. These results add knowledge on the morphological and ecological contexts that may have shaped the elephant grasping and manipulation abilities. The tusks morphology effect on trunk techniques especially shed light on the importance for further studies to take into consideration the tusks when exploring elephant trunk abilities.

From Chapter 2 to Chapter 3

In Chapter 2, we characterised the main trunk grasping and manipulation techniques and the related individual variations. Although no specific technique was found for the manipulation tasks, the elephants do perform diverse techniques for grasping. We highlighted that these techniques may differ according to the grasping task, the item grasped and the individual, particularly if the tusk profiles differ greatly. These findings highlight morphological and ecological patterns that may influence the grasping abilities evolution in elephants, but much remains to be explored. Therefore, to pursue the main questions of this thesis and apprehend adaptations in trunk use, we explored the variability of trunk grasping and manipulation techniques, but this time in different habitats. Chapter 3 explores this variability between two populations, one living in a woody vegetation dominated by *Colophospermum mopane*, the other in an arid habitat.

Chapter 3

Effect of the habitat (Etosha vs Kruger) on trunk grasping and manipulation techniques in African savannah elephants

Chapter 3

Effect of the habitat (Etosha vs Kruger) on trunk grasping and manipulation techniques in African savannah elephants

Manuscript in preparation

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Key words: elephant, trunk, technique, grasping, manipulation, population, habitat, tusks, task, object

Introduction

Food grasping and manipulation have been central to the survival of species (Pouydebat et al., 2022; Sustaita et al., 2013). In many animals with hands, such as primates and rodents, techniques for grasping and manipulating objects vary according to their properties and the task being performed (Pouydebat et al., 2014a). Indeed, the size (Pouydebat et al., 2009, 2011; Reghem et al., 2011) and mobility of the object (Peckre et al., 2019a, 2019b; Toussaint et al., 2015), affect grasping techniques in various primate and rodent species (Bardo et al., 2015; Boulinguez-Ambroise et al., 2020; Ivanco et al., 1996; Peckre et al., 2016; Pouydebat et al., 2010, 2014b; Whishaw and Coles, 1996). Links between grasping techniques and morphological parameters such as segments lengths of the limb have also been quantified (Bardo et al., 2018; Boulinguez-Ambroise et al., 2019; Thomas et al., 2016). Moreover, grasping and manipulation differences can be found at different scales. Indeed, inter-individual differences during tool manipulation have been identified in apes (Bardo et al., 2016, 2017), and inter-population differences in behaviour usually involving grasping and manipulation movements were also highlighted in several species (Cronin et al., 2014; Srinivasaiah et al., 2012; Sueur et al., 2011).

As the evolutionary mechanisms of prehensile and manipulative capacities in tetrapods remain unclear (Pouydebat & Bardo, 2019), exploring the factors that shaped grasping and manipulation techniques is essential to better understand the origin and evolution of these functions. Exploring grasping and manipulation techniques at the population-level can shed light on the learning, ecological and morphological patterns that may influence these movements. Indeed, behavioural variation between populations is likely to be the result of social learning, traditions, environmental conditions and local morphologies beyond genetics (Cronin et al., 2014; Gaechter et al., 2010; Lamba & Mace, 2011; Langergraber et al., 2011).

However, most of the studies that explored grasping and manipulation techniques and related factors concern the hands of primates and rodents. Yet, some species that do not have adapted hands for grasping can manipulate objects with great precision using other organs, such as several birds with their beaks (Brunon et al., 2014) or elephants with their trunks (Hart et al., 2001). The elephant trunk, as muscular hydrostat, is particularly interesting for its absence of a skeletal support system which gives it a high degree of freedom of movements (Lefeuvre et al., 2020), with complex and highly controlled movements. For example, elephants can extend, bend and twist their trunks, allowing them to hold heavy loads, as well as grasp tiny objects with great precision (Fowler & Mikota, 2006; Kier & Smith, 1985; Shoshani, 1998; Yang et al., 2006). This highly sensitive multitasking organ is also involved in a

wide repertoire of behaviour such as feeding, watering, environmental exploration, vocalisation, social behaviour, tool making and tool use (Fowler & Mikota, 2006; Haakonsson & Semple, 2009; Hart et al., 2001; Rasmussen & Munger, 1996; Shoshani, 1998; Yang et al., 2006). Several studies on captive elephants have demonstrated links between objects and grasping and manipulation techniques during feeding, depending mainly on the quantity and characteristics of the food grasped, such as its structure and size (Dagenais et al., 2021; Racine, 1980; Schulz et al., 2021; Wu et al., 2018). For example, small objects, easily held in the distal part of the proboscis, were pinched, while wrapping is mostly employed with larger objects (Racine, 1980).

Although this variety of studies, none has explored whether the variability of grasping and manipulation techniques with the trunk between populations, or the links between these inter-population functional differences and the object or task. However, the elephant is a great model for exploring these inter-population differences. Indeed, the African savannah elephant (*Loxodonta africana*) in particular, is regularly found in 23 countries in sub-Saharan Africa, over a wide latitudinal range between the desert in Mali and the southern temperate zones in South Africa (Gobush et al., 2021a). This species occupy a variety of habitats ranging from montane forests, Miombo and Mopane woodlands, savannah and grasslands to arid deserts, but also a wide altitudinal range from mountain slopes to ocean beaches (Gobush et al., 2021a). There is therefore a diversity of ecological context between different African savannah elephant populations throughout the African continent. Moreover, *Loxodonta africana* has a generalist herbivorous diet (Owen-Smith & Chafota, 2012) consisting mainly of grasses, lianas and plants, and sometimes termite mounds, soil deposits and salt-rich waterholes for mineral supplements (Mwangi et al., 2004; Weir, 1969). During the dry season, its diet also includes leaves and bark, and varies greatly between populations and with habitat (Codron et al., 2006; Estes, 1999; Sach et al., 2019). Elephants' life history also differs with the populations (Shrader et al., 2010), and they are known to display several regional morphological variations, specifically concerning their tusks and ears (Hanks, 1972). Thus, diversity of habitats, diets, life histories and morphologies, regarding the populations, are all factors in exploring inter-population differences in grasping and manipulation techniques.

In this context, we investigated several questions concerning African savannah elephants. On the one hand, we examined if trunk grasping and manipulation techniques vary between populations. On the other hand, we explored if these variations could be linked to the task performed, the habitat and the morphology of the tusks. To do this, we compared the frequencies of use of feeding grasping and manipulation technique modalities between two populations living in two locations, for different foods and tasks. Two distinct locations allowing the observation of

different habitats: an arid study site in Etosha National Park in Namibia and an area with consistent water presence in Kruger National Park in South Africa. The two elephant populations are known to differ in terms of life history and tusk morphologies (Shrader et al., 2010; Steenkamp et al., 2007; Whyte & Hall-Martin, 2018). Since in Chapter 2 we demonstrated that tusks are related to trunk grasping techniques, we decided here to characterise and compare the tusks profiles of these two populations. We hypothesised that, between these two populations, trunk grasping and manipulation techniques differ, certainly as an effect of habitat and tusk morphology differences.

Material and methods

Study areas

We conducted the data collection in two parks, at the end of the wet season that brings high hygrometry and temperatures and thus lush vegetation.

First, we carried out this study on African savannah elephants during the last week of January 2020 in the Etosha National Park. With an area of 22,935 km2, this animal sanctuary is located in north-central Namibia in the Kunene region. Central Etosha received an average annual rainfall of 358 mm (Okaukuejo station, 1954–2020), with most rain falling between January and February. Precipitation in 2020 was around 440 mm at Okaukuejo station (Huang et al., 2021). There is a west-east rainfall gradient, increasing from an annual average of 200 to 450 mm (Huang et al., 2021). These differences are exacerbated by the effects of evaporation. Evaporative water losses in the east represent 4–5 times the annual rainfall, whereas these represent as much as 10 times the annual rainfall in the west (Mendelsohn et al., 2013). The average monthly temperature maximum recorded in south of Etosha park where we collected our data is 35°C in October–December (1975–2004; Turner et al, 2013). The size of the African elephant population in Etosha was estimated to be around 2,800 in 2018 and 0.153 elephant per km^2 (Craig et al., 2021). This protected area corresponds to an arid to semi-arid savannah with woody vegetation (De Villiers & Kok, 1988). The individuals were filmed in an area between Aus and Olifantsbad in three different locations: Aus which is a very open water body, a mud point near Aus and along the road between Olifantsbad and the mud point. This woodland area, south of the Etosha Pan and extending westwards, is bushveld dominated by *Colophospermum mopane*, *Combretum apiculatum* and *Terminalia prunioides*. The soil is a calcrete litho soil.

The herb stratum is poorly developed because of the calcrete, generally in a coarsely fractured form when superficial. The more important herbs are *Enneapogon desvauxii, E. cenchroides, Aristida adscensionis, Eragrostis nindensis, Euphorbia inaequilatera, Tragus berteronianus, Oropetium capense, Tribulus terrestris, Kohautia azurea, Indigojera charleriana, Eragrostis annulata* and *Geigeria odontoptera*. These extensive grasslands are grazed extensively during the rainy season by large numbers of herbivores. During the long dry season, the animals are forced to concentrate near the waterholes, mostly along the southern edge of the Pan, and these regions become severely overgrazed (Le Roux et al., 1988).

The remains of the data were collected during the first week of February 2020 in the gallery forests and open grasslands of the Kruger National Park in South Africa. Average rainfall varies between 375 mm and 500 mm per year (Shingwedzi station, 1977–2018). The average annual temperature recorded was 31°C in 2017 and February was the warmest month at 35°C (Dube & Nhamo, 2020). The elephant population of the park was estimated at 17,000 individuals in 2015 and 39 elephants per km^2 at our data collect area (Ferreira et al., 2017; Louw et al., 2021). We collected the data in the north of the park in Mopane forests and bushes (Kos et al. 2012; Venter et al., 2003). The woody vegetation of this landscape is dominated by Multistemmed mopane shrubs, one to two metres in height. As many as 600 of these shrubs can occur per hectare. The absolute dominance of Colophospermum mopane results in other woody species being relatively scarce. Individual species that occur are the following: *Combretum imberbe, Euphorbia guerichiana, Grewia bicolor, Commiphora glandulosa, Acacia exuvialis, Combretum apiculatum, Lannea stuhlmannii, Acacia nigrescens, Dalbergia melanoxylon, Lonchocarpus capassa, Sclerocarya caffra, Ozoroa engleri, Securinega virosa, Grewia villosa, Albizia harveyi, Acacia tortilis, Ehretia rigida, Combretum mossambicense, Maerua parvifolia, Combretum hereroense* and *Dichrostachys cinerea subsp. africana*. The soils in this landscape structurally consist of flat to concave plains with several marshes. The geological rock formations upon which this landscape developed are basalt and the soils usually have a high clay content (Gertenbach, 1983). As water is present throughout the park and elephant feeding methods are more diverse near water (Abraham et al., 2021; Tehou et al., 2019), we collected behavioural data mostly nearby small artificial waterholes and nearby the Pioneer Dam. For the vast Dam, we filmed from the Mopani rest camp, in an elevated location, approximately 20 metres, to cover a large area. For the waterhole and grasslands areas, we filmed from the road, over a distance up to 15 kilometers from the rest camp.

In summary, the study sites between Kruger and Etosha parks have a similar annual average temperature and the same woody vegetation. However, Etosha sites

present flatter ground, with limestone soil. The rainfall is lower and waterholes are less deep and smaller. Finally, the vegetation is sparser and lower than in the Kruger sites. To make this article easier to read, we have used the terms "Etosha or Kruger elephants" instead of "specimens observed at the study sites in Etosha or Kruger parks". As these parks are made up of very diverse landscapes, we compared here two different environments and not the parks as a whole.

Quantification in natural habitat

To avoid any human disturbance, we took the data at distance with the elephants in video format, approximately 100 metres from the elephants nearby the Pioneer Dam and an average of 30 metres with the videos from the road. We followed the CNRS guidelines and European Union regulations (Directive 2010/63/EU). We recorded with Sony FDR-AX 53 cameras in the morning and the end of the afternoon, when the elephants are the most active (Rozen-Rechels et al., 2020). The videos enable observational accuracy on the brief trunk movements. Each elephant encounter was filmed when the elephant performed grasping or manipulation with a clearly visible trunk. Moreover, most of the videos include several individuals. In this case, the behaviour of each elephant was analysed individually, to avoid individual selection and to maximise the number of elephants recorded. The tracked animals were filmed continuously until they left the view.

Elephant identification

We identified each individual with its particular physical characteristics such as ear shapes, ear holes and veins, wart shapes or back shapes (Moss, 1996; Webber & Lee, 2020). The tusks characteristics were also good indicators for recognition. For each elephant, both tusks were described in detail. **Figure 3.1** displays the illustrations of several of these tusks details. We defined if the tusk was present or not, its potential fracture and its curve or straight shape. We looked for the opening of the tusk, in other words, if its tip point at the trunk or toward the outside, or stay straight. We also noted if both tusks were symmetrical or if one was higher. Finally, we defined the size of the tusk with four levels: emergent tusk, small, medium and large.

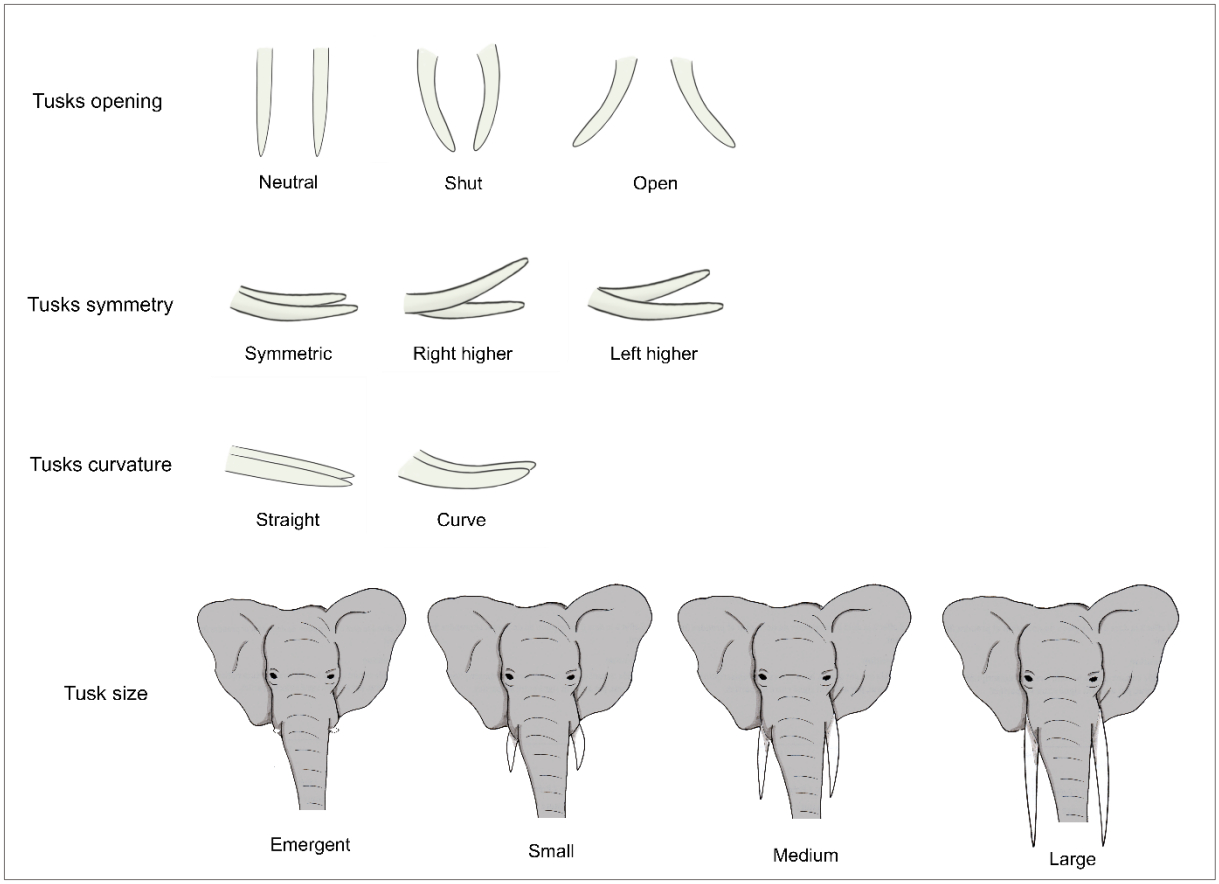


Figure 3.1 – Illustrations of the observed elephant tusks symmetry, opening, curvature and size modalities (tusk presence and tusk fracture not illustrated).

The observed elephants were also sex-classified, based on their genitals, breasts, shoulder height, body shape, head shape, tusk shape and group composition (Moss, 1996; Poole, 1994). The determination of the sex enabled easier identification of the individuals, but as we did not find significant sex effect on trunk grasping and manipulation techniques in Chapter 2, it was not considered in the analyses. However, we did find a significant link of the age with these techniques in Chapter 2, therefore we age-classified the individuals, both for elephant identification and for the analyses. We determined the class of age of each elephant using the literature: "infants" referred to elephants less than one year old, "juveniles" referred to elephants less than seven-year-old, "subadults" represent the elephants between around eight and fifteen years old (Moss, 1996; Poole, 1994). "Adults" referred to grown females and independent males and finally "large adults" referred to elephants over 35 years old, with marked bodies (Moss, 1996). We used the body shape, the tusk size or absence, the shoulder height, the independency of a male and a calf with a female to evaluate the age of the

elephants (Moss, 1996; Moss & Poole, 1983; Shrader et al., 2006). Due to the small amount of data available, especially in Etosha National Park, the different classes were grouped into only two categories for analysis: juveniles (infants and juveniles) and adults (subadults, adults and large adults).

We therefore observed and recognised individually 70 elephants with the combination of the criteria of age, sex, tusks profile and particular physical characteristics. These observed elephants were divided in the two age categories: we identified 62 adults, with 47 from Kruger Park and 15 from Etosha Park, and 8 juveniles, with six from Kruger Park and two from Etosha Park. The information collected on the tusks of the 62 observed adults were used to characterise the tusk profiles of the elephants depending on their population. Among the 70 observed elephants, 43 performed the grasping and manipulation tasks we observed sufficiently to be kept for the analyses. The sex and age categories of these 43 observed elephants are detailed in **Table 3.1**.

Park	Sex/Age	Juvenile	Adult	Total
Etosha	Males	0	7	**13**
	Females	0	4	
	Undetermined	2	0	
Kruger	Males	2	11	**30**
	Females	2	13	
	Undetermined	2	0	

Table 3.1 – Sex and age distribution of the observed elephants which performed grasping and/or manipulation with their trunk.

The techniques, tasks and items

This study focused on the feeding behaviour because elephants perform grasping and manipulation thanks to the trunk mainly in this activity (Nair, 1989). We therefore explored the grasping and manipulation tasks most commonly observed during the fieldwork, described in **Table 3.2**. The tasks were defined thanks to our

preliminary fieldwork observations, the Poole and Granli wild African savannah elephant ethogram (2021), the trunk use behavioural repertoire of captive African savannah elephants during feeding of Lefeuvre et al. (2020) and Nair captive Asian elephants feeding descriptions (1989). These tasks are the same as the task studied in Chapter 2, but are less numerous as we do not observe the elephants from Etosha Park performed the other tasks sufficiently to keep them to analyses. For illustration of the bundling manipulation, see the video under the behaviour names "Pack-Grass" in the Elephant Ethogram, available at the ElephantVoices website (see Poole & Granli, 2021).

Grasping or manipulation	Task	Description
Grasping	Eating grasp	Grasp with the trunk food items in order to ingest it directly
Grasping	Bundling grasp	Grasp with the trunk food items in order to bundling it before ingestion
Manipulation	Bundling manipulation	Bundling food items with and on the trunk before ingestion

Table 3.2 – Main grasping and manipulation tasks performed by the elephants from Kruger and Etosha National Parks.

Furthermore, we noted the food items that were grasped or manipulated. Elephants eat a large diversity of plants but the proportion of grass in their diet increase in the wet season, when individuals are less restricted by water availability (Sukumar, 2003; Codron et al., 2006; van Aarde et al., 2006). The individuals of the Kruger National Park eat mostly grass (50% of their diet), and ligneous plants (especially Mopane trees, Codron et al., 2006; Kos et al., 2012). Similarly, elephants in Etosha prefer areas with high grass biomass (Tsalyuk et al., 2019). Therefore, the two food items considered in this study that are grasped by both population are grasses and small branches (diameter below two centimetres).

Finally, to define the trunk grasping and manipulation techniques, we used three criteria. These criteria were also used in Chapter 2. The first criterion is the type

of grasping, i.e. the pinch with the fingers of the trunk tip, the wrap around an item, or the torsion of the trunk to create a pressure point on the item (Lefeuvre et al., 2020). Illustrations of these grasping types can be seen in Chapter 2 (**see Figure 2.1**). The second criterion is the grasping way, with an item grasped from the front, the right or the left side from the elephant perspective, whenever the elephant performed a pinch, wrap or torsion (Giljov et al., 2017; Haakonsson & Semple, 2009; Keerthipriya et al., 2015; Lefeuvre, 2021; Martin & Niemitz, 2003). Finally, the last criterion is the trunk parts used in the movements. We slice the trunk in six parts based on the functional movements of the trunk, similar as in Chapter 2 (**see Figure 2.1 for a precise schematic description of the six parts**). The first part is the trunk tip, the last is close to the forehead and the four others are related to the trunk grasping and twist functioning.

Data analyses

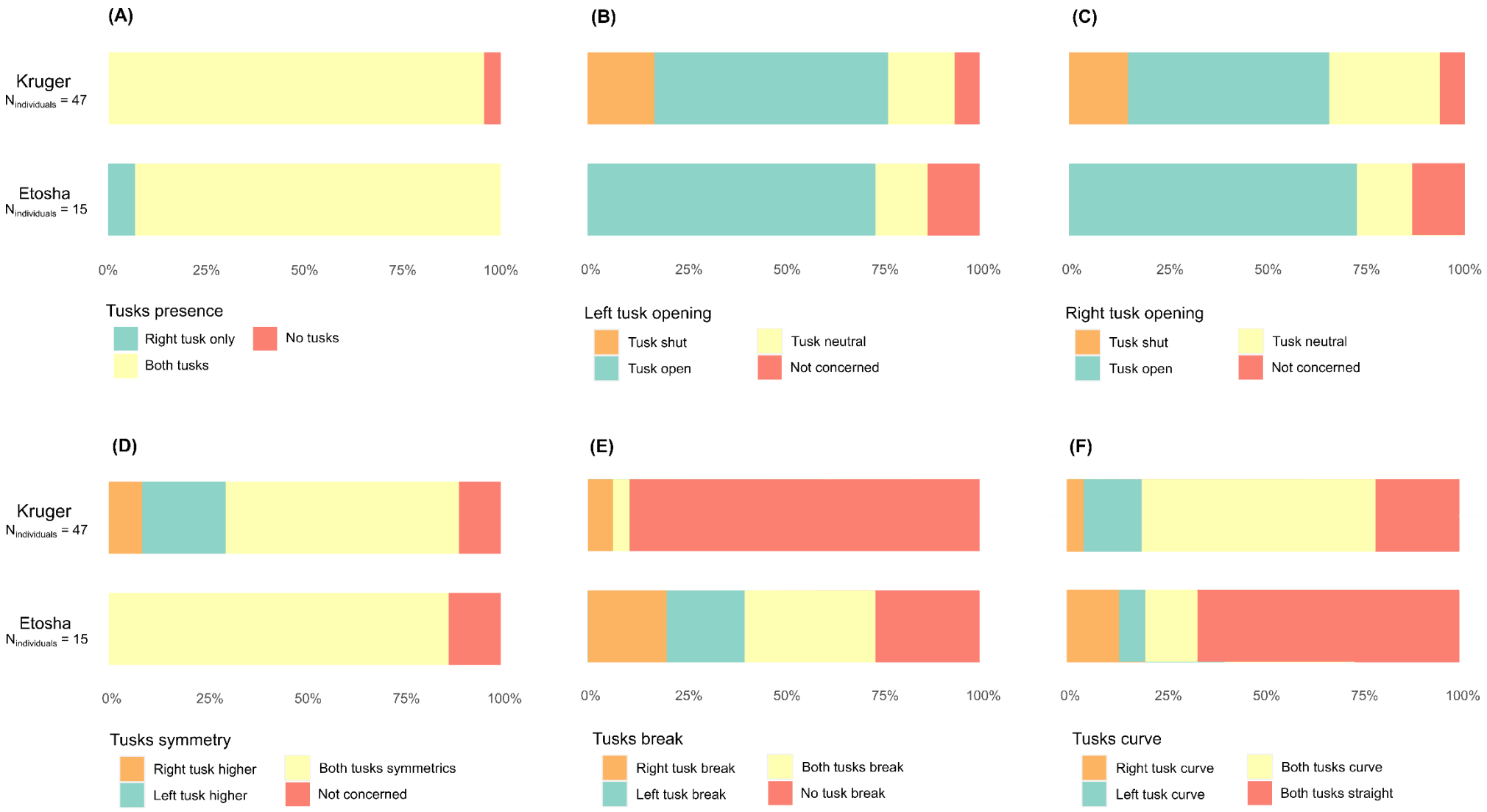
We analysed each video and noted, for every grasping or manipulation occurrence, the focus elephant with its age and its tusk characteristics, and the park where the animal was observed. We also noted the task, the item involved, the type of grasping, the grasping way and the trunk parts used in the movements.

The aim of this paper was to analyse the differences in trunk use between the two parks in a feeding context. To do so, the percentages of each of the modalities of the trunk grasping and manipulation techniques (type of grasping, grasping way and trunk parts used in the movements) were calculated for each possible task/item combination. In order to perform statistical tests on the data, only combinations with at least five observations were kept. Thus, we kept in adults the eating grasp of grass and small branches and the grass bundling grasp and manipulation. In juveniles, we kept the eating grasp of grass only. Next, the distribution of the modalities was compared between parks using several Pearson's chi-square tests of independence, in adults and juveniles independently. We used the "chisq.test" function of the "stats" package in R, version 4.2.0 (R Core Team, 2018) to carry out the tests. A Bonferroni correction was also applied with the function "p.adjust" of the "stats" package. The different modalities describing the tusks profiles were compared between parks in the same way. To illustrate the differences between parks, barplots were made on the tusks profiles modalities and the trunk techniques for each task/item combination.

Results

Tusks profiles

Firstly, the tusks profiles of the adult Kruger elephants and the adult Etosha elephants were characterised and compared. The results show that the majority of the elephants had their two tusks, and there is no significant difference between Kruger and Etosha Park (**Figure 3.1A**, Chi-square test: $X^2_2 = 3.779$, $P' = 0.907$). The tusks opening and symmetry also seem to be similar between the parks (Left tusk opening: **Figure 3.1B**, $X^2_3 = 3.672$, $P' = 1$; right tusk opening: **Figure 3.1C**, $X^2_3 = 4.879$, $P' = 1$; tusk symmetry: **Figure 3.1D**, $X^2_3 = 5.803$, $P' = 1$). However, differences between the two parks have been reported concerning the tusks break and curvature (respectively $X^2_3 = 26.118$, $P' < 0.001$; $X^2_3 = 14.336$, $P' < 0.05$). Kruger elephants had less broken and more curved tusks than Etosha elephants (respectively **Figures 3.1E and 3.1F**). Finally, the results also show that the elephants living in the Kruger Park had longer tusks than the elephants living in the Etosha Park (left tusks: **Figure 3.1G**, $X^2_4 = 24.202$, $P' < 0.01$; right tusks: **Figure 3.1H**, $X^2_4 = 17.654$, $P' < 0.05$).


(A)
Kruger
N individuals = 47
Etosha
N individuals = 15
0%
25%
50%
75%
100%
Tusks presence
Right tusk only
No tusks
Both tusks
(B)
Left tusk opening
Tusk shut
Tusk neutral
Tusk open
Not concerned
(C)
Right tusk opening
Tusk shut
Tusk neutral
Tusk open
Not concerned
(D)
Kruger
N individuals = 47
Etosha
N individuals = 15
0%
25%
50%
75%
100%
Tusks symmetry
Right tusk higher
Both tusks symmetrics
Left tusk higher
Not concerned
(E)
Tusks break
Right tusk break
Both tusks break
Left tusk break
No tusk break
(F)
Tusks curve
Right tusk curve
Both tusks curve
Left tusk curve
Both tusks straight

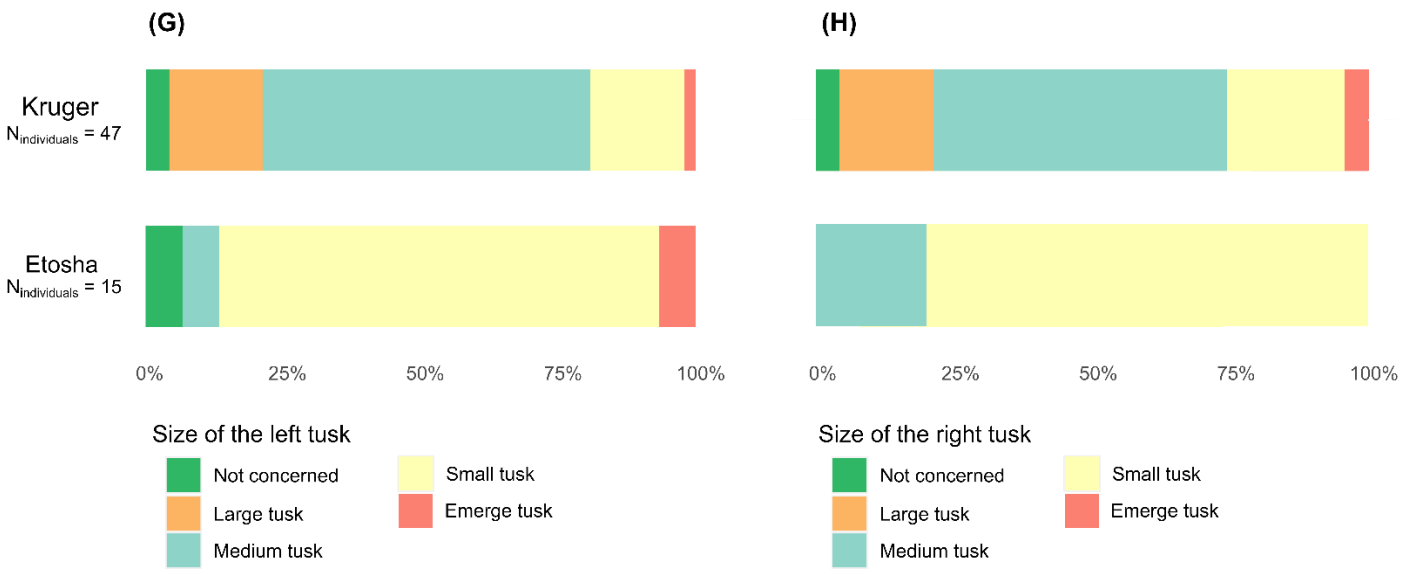


Figure 3.1 – Barplots of the adult elephants' tusks profiles in the Kruger Park and the Etosha Park. The different tusks profile criteria studied are the tusk presence (A), the left (B) and right tusk opening (C), the tusk symmetry (D), the tusk break (E), the tusk curvature (F) and the left (G) and right tusk size (H).

Trunk grasping and manipulating techniques

Several modalities of trunk grasping and manipulating techniques were compared between the two parks. Every task with the item grasped was analysed independently.

First results concern eating grasp when adult individuals grasp grass. The type of grasping is significantly different between Kruger Park and Etosha Park (X^2_1 = 9.786, $P' < 0.05$). Indeed, elephants in the Kruger Park have used more wraps than pinches, whereas elephants in the Etosha Park used as many pinches as they did wraps (**Figure 3.2A**). The grasping way is also significantly different between the two parks ($X^2_2 = 28.997$, $P' < 0.001$). The grasps from the right have been prevalent in the Kruger Park while it is the frontal in the Etosha Park. It may be noted that, in the two parks, the grasps from the left have been less used (**Figure 3.2B**). Lastly, the trunk parts used in the movements are also significantly different between Kruger Park and Etosha Park (X^2_3 = 72.25, $P' < 0.001$). Individuals living in the Kruger Park have used the combination of their trunk tip, second and third trunk parts more than Etosha elephants. On the contrary, individuals living in the Etosha Park have used only the trunk tip part more than Kruger's elephants. The use of the trunk tip with the second

part has been similarly used between the two parks. The combined use of almost all the trunk parts (1 to 5) have only been used in the Kruger (**Figure 3.2C**).

The eating grasp has also been studied in adult individuals for another item, the small branches (**Figure 3.3**). The three trunk grasping technique criteria have shown no significant difference between the parks (grasping type: $X^2_2 = 0.738$, $P' = 1$; grasping way: $X^2_2 = 1.218$, $P' = 1$; trunk parts used: $X^2_4 = 7.360$, $P' = 1$).

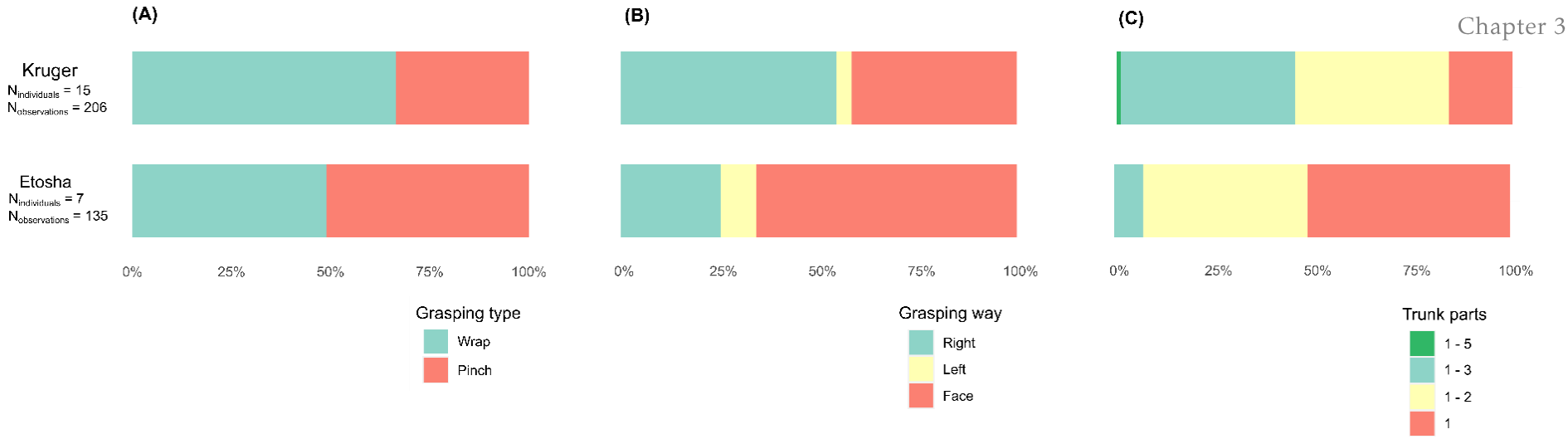


Figure 3.2 – Barplots of trunk eating grasp technique modalities used by adult individuals for grasping grasses in the Kruger Park and the Etosha Park. The modalities studied are the grasping type (A), the grasping way (B) and the trunk parts used (C).

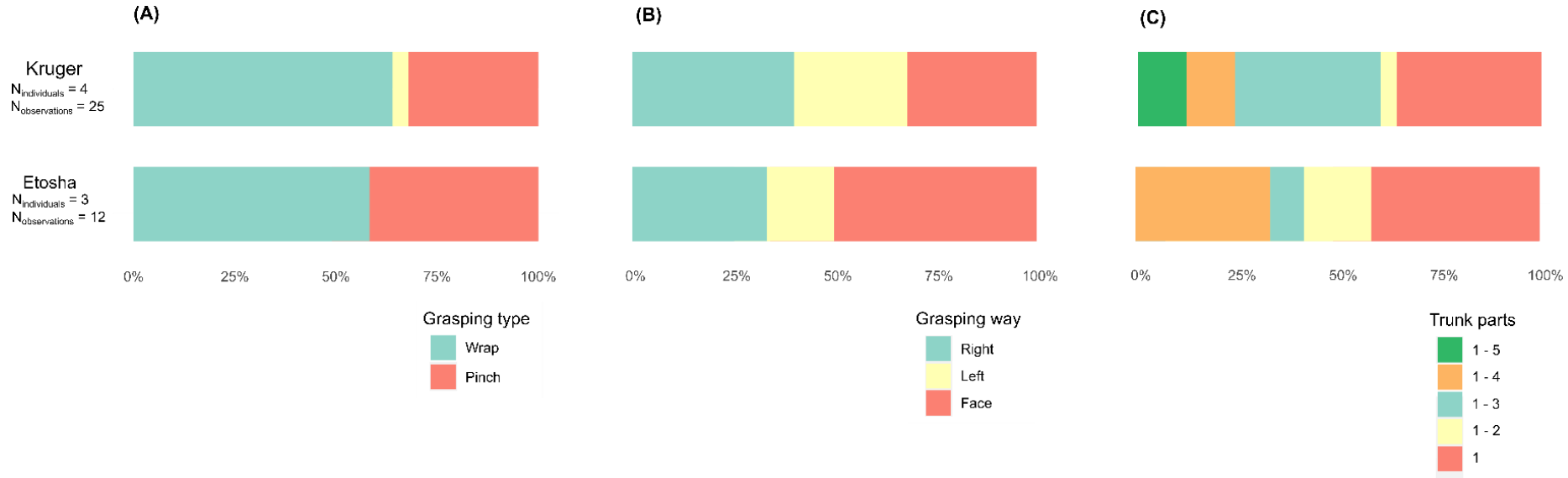


Figure 3.3 – Barplots of trunk eating grasp technique modalities used by adult individuals for grasping small branches in the Kruger Park and the Etosha Park. The modalities studied are the grasping type (A), the grasping way (B) and the trunk parts used (C).

The bundling grasp techniques have also been investigated for the grass in the adult individuals. The type of grasping is significantly different between Kruger Park and Etosha Park ($X^2_1 = 11.941$, $P' < 0.01$). Indeed, in the Etosha Park, the wrap has been more widely used than in the Kruger Park and vice versa for the pinch. However, in the two parks, the elephants have used the wrap more than the pinch (**Figure 3.4A**). The grasping way is also significantly different between the two parks ($X^2_2 = 20.654$, $P' < 0.001$). The three grasping way seems to be used equally in the Kruger Park, whereas, the right way has been in majority, and the left way in minority in the Etosha Park (**Figure 3.4B**). The trunk parts used in the movements are also significantly different between Kruger Park and Etosha Park ($X^2_5 = 54.758$, $P' < 0.001$). The bundling grasps have mostly the first three trunk parts involved together in the Kruger Park and the first two trunk parts in the Etosha Park. The parts from 1 to 4, the second part only and the parts 2 and 3 together have only been used in the Kruger Park (**Figure 3.4C**).

Moreover, the bundling manipulation techniques have been studied for the grass in the adult individuals. The type of grasping is significantly different between Kruger Park and Etosha Park ($X^2_1 = 31.459$, $P' < 0.001$). Indeed, elephants have almost always used the wrap in the Kruger Park, whereas the use of the pinch has been more important in Etosha Park (**Figure 3.5A**). There are also differences in the grasping way between the two parks ($X^2_2 = 51.278$, $P' < 0.001$). The grass was predominantly frontally manipulated in both parks but the results show that manipulation from the right was more observed in Etosha than in Kruger Park. The manipulation from the left was only seen in Kruger Park (**Figure 3.5B**). The trunk parts used in the movements are also significantly different between Kruger Park and Etosha Park ($X^2_6 = 66.964$, $P' < 0.001$). As for the bundling grasps, the bundling manipulation has mostly involved the first three trunk parts together in the Kruger Park and the first two trunk parts in the Etosha Park. The parts from 1 to 5, the second alone and the second with the third parts have only been used in the Kruger Park, whereas the trunk tip alone has only been used in the Etosha Park (**Figure 3.5C**).

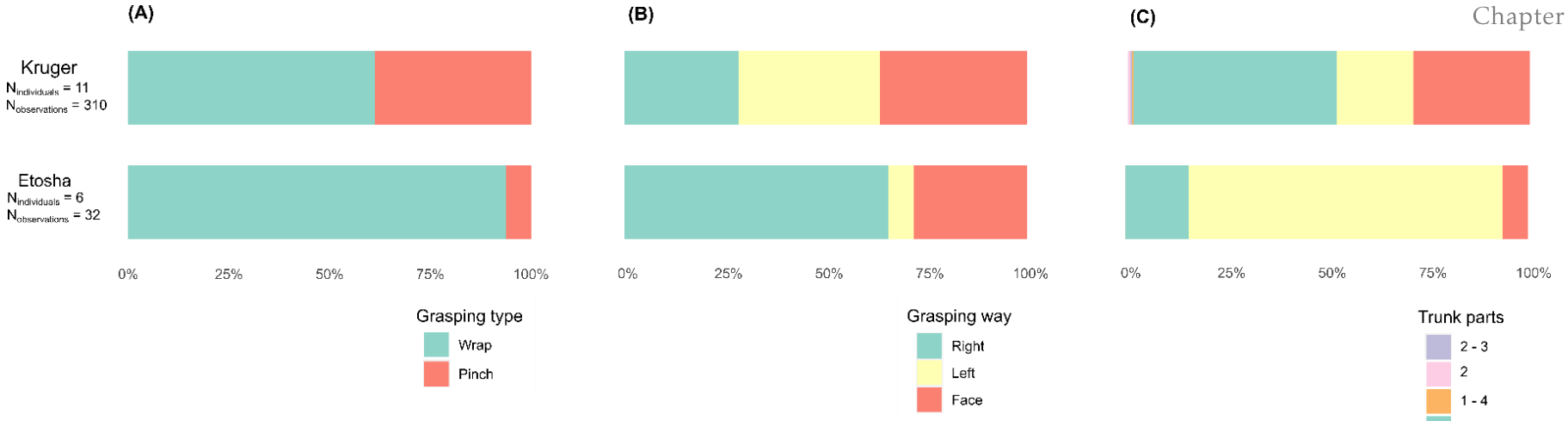


Figure 3.4 – Barplots of trunk bundling grasp technique modalities used by adult individuals for grasping grasses in the Kruger Park and the Etosha Park. The modalities studied are the grasping type (A), the grasping way (B) and the trunk parts used (C).

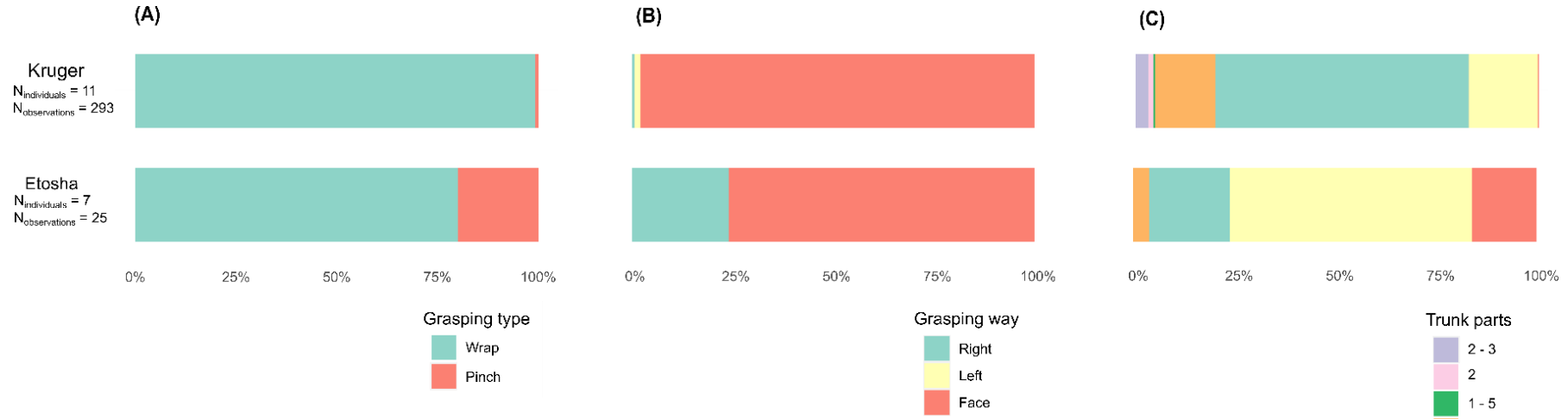


Figure 3.5 – Barplots of trunk bundling manipulation technique modalities used by adult individuals for grasping grasses in the Kruger Park and the Etosha Park. The modalities studied are the grasping type (A), the grasping way (B) and the trunk parts used (C).

Finally, the eating grasps for the grass were analysed in the juvenile individuals (**Figure 3.6**). The three trunk grasping techniques have shown no significant difference between the parks (grasping type: $X^2_1 = 0.002$, $P' = 1$; grasping way: $X^2_2 = 9.521$, $P' = 0.086$; trunk parts used: $X^2_4 = 2.214$, $P' = 1$).

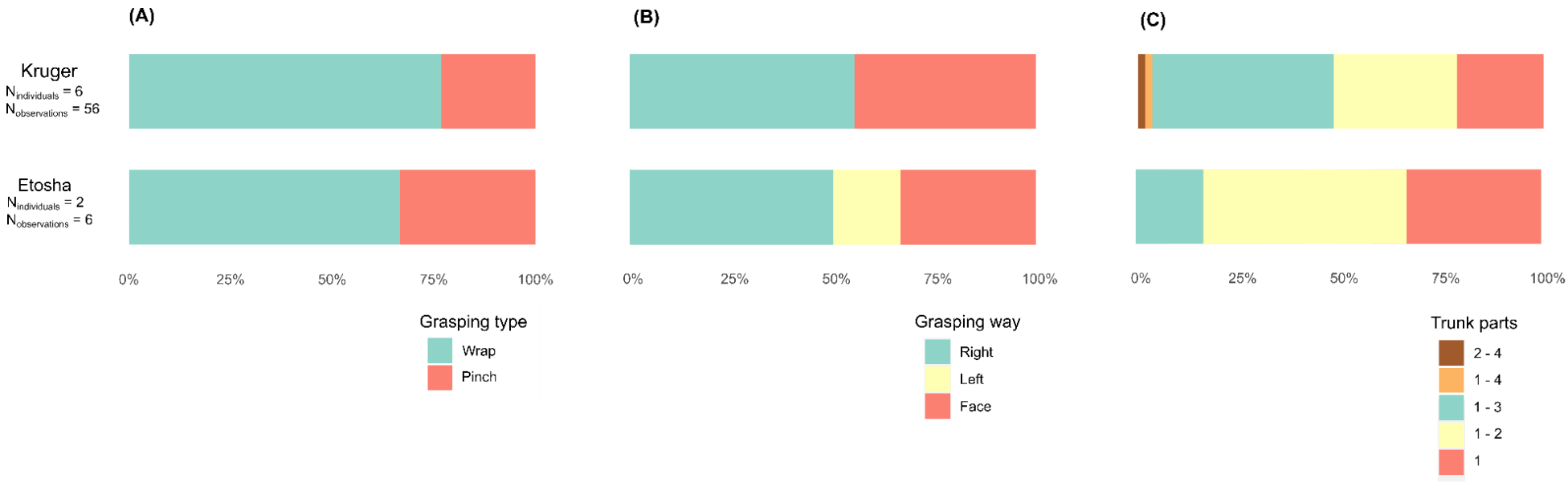


Figure 3.6 – Barplots of trunk eating grasp technique modalities used by juvenile individuals for grasping grasses in the Kruger Park and the Etosha Park. The modalities studied are the grasping type (A), the grasping way (B) and the trunk parts used (C).

Discussion

In this study, we characterised the tusks profiles of the elephants from the Kruger National Park and the elephants from the Etosha National Park. The two population's tusks profiles differed greatly in terms of size, breaking and curvature, with the tusks of the Etosha elephants smaller, more break and curves. However, their tusks symmetry and opening were similar. Moreover, most elephants in both populations displayed two tusks. We also revealed that, in adult elephants, there is different grasping and manipulating techniques with the trunk, and how often they are used depends on the task performed and the item grasped, and in regard to the population. Indeed, the technique modalities used for grasping or manipulate grasses differ between the two park populations in three tasks: the eating grasp, the bundling grasp and the bundling manipulation. However, when the small branches were grasped to eat directly, and when juveniles performed this task with grasses, we did not find any technique difference between the parks.

Tusks profiles

Elephant tusks size, absence and even fractures were explored in different African savannah elephant populations (Bielert et al., 2018; Campbell-Staton et al., 2021; Chiyo et al., 2015; Elder, 1970; Layser & Buss, 1985), including two studies that explored the elephant tusks from the Kruger National Park and Etosha National Park (Steenkamp et al., 2007; Whyte & Hall-Martin, 2018). However, this is the first time that the tusks in these populations were also characterised through their curvature, symmetry and opening.

We highlighted that, similar as Steenkamp and collaborators (2007) found, the elephants from the two Parks had low frequencies of tusklessness. We found a tusklessness below 5% for the Kruger elephants just like Raubenheimer stated in 2000. We did not observe any elephant from Etosha Park with double tusklessness, similarly as Steenkamp et al. (2007). Yet, it was revealed that the tusklessness in elephant populations is directly related to their poaching history for tusks (Campbell-Staton et al., 2021; Chiyo et al., 2015; Heimert, 1994). Thus, we can presume that the low poaching in both parks can explain the low frequencies of tusklessness, on the contrary of other elephant populations that experience strong poaching (Campbell-Staton et al., 2021). This hypothesis is also in agreement with the suggestion of Whyte & Hall-Martin (2018) on the low Kruger elephant tusklessness incidence.

Moreover, the significant tusks breaking differences we found between the two parks are in continuation of the results reported 15 years ago (Steenkamp et al., 2007). However, we found more fractured tusks in both parks. Indeed, in Etosha elephants, they observed 44.4% of tusks fractured while 75% of the elephants we observed had one or both tusks break. In Kruger elephants, these authors observed only 1.64% tusks break while we observed nearby 10% of the elephants with their right tusk or both fractured. However, this difference may be due to the differences in samples, as they observed widen more elephants in both parks, and therefore represented with more accuracy the different tusks profiles. Nevertheless, the strong tusk break difference between the two parks seems steady over time. This difference in tusk fractures may be affected by the environmental differences in the two populations. Indeed, the higher tusk break incidence in African savannah elephants concerns the elephants from Etosha (Steenkamp et al., 2007). We hypothesise that high fluoride ingestion by Etosha elephants, present in quantity in Etosha waterholes and probably related to rainfalls caused crumbly tusks and thus higher chance for breaking (Auer, 1997; Raubenheimer, 1999; Raubenheimer et al., 1998; Steenkamp et al., 2007). Tusks are used for digging (Steenkamp, 2003). Thus, another hypothesis is that the difference in soil composition between the parks may explain the dissimilar tusk fractures. Indeed, a more abrasive or gravelly soil would lead to tusks shorter and being more breakable.

In addition, we found that the tusks sizes differ between the elephants of Kruger National Park and Etosha National Park, as well as their tusks curvatures. The right and left tusks displayed similar patterns of size per park, but the tusks of Etosha elephants were significantly smaller, certainly due to the high friability and break incidence explain above (Whyte & Hall-Martin, 2018). Similarly, the Etosha elephant tusks were less curved, probably due to their smaller size and numerous breaks. With longer size and fewer fractures (Whyte & Hall-Martin, 2018), the tusks from Kruger elephants could display more curvature. However, we did not find any difference in tusk symmetry and opening between the two parks. In both parks, the observed elephants had generally symmetric and open toward the outside tusks. The small variations in tusks symmetry and opening we observed could be linked to individual life history and individual development, and seem not to be reflected at population-level. During the data collect, we saw several herds with same symmetry patterns between the elephants from the same herd. As herds are almost always composed of related individuals, we hypothesis that the variations in tusks symmetry we observed could be inherence genetics reflected at herd-level. Nevertheless, to explore these particular tusks profiles variations, the study has to be carried on larger samples and with information on the herds of the individuals.

Thus, the tusks profiles of both parks were characterised for the first time in detail. The variation is strong between the parks for the tusks size, break and curvature, certainly due to environmental conditions differences such as the concentration of fluoride in water related to rainfalls. These strong morphological variations may lead to differences in trunk grasping and manipulating techniques. This result is in line with Chapter 2 of this dissertation, which showed the importance of tusk profiles in the realisation of these trunk techniques.

Trunk grasping and manipulating techniques

We revealed that the technique modalities used for grasping and manipulate grasses differ between the two park populations. In majority, during eating grasp task and bundling manipulation task, the Etosha elephants used more the pinch than the Kruger elephants. The study sites in Etosha National Park are dry environments, with fewer and lower grasses at the disposal of the elephants compared to the Kruger National Park sites (Kennedy et al., 2003; Sannier et al., 2002). The infrequency of the grasses in Etosha and its lower size, compared to Kruger, probably require a more parsimonious grass collect and the use of a pinch to grasp is more precise (Rasmussen & Munger, 1996). However, this tendency of pinch preference for Etosha elephants changes with the bundling tasks. When they grasped to bundle the food, elephants in both parks displayed mostly wrap, and Etosha elephants even more than the Kruger elephants. Whereas, during bundling manipulation, if Etosha elephants still used more pinches than Kruger elephants, the wrap was predominant in both populations. We can presume that the bundling grasp is a more complex task than the eating grasp, as it certainly requires precise and specific movements to prepare the bundling manipulation to come. Yet, the complexity of the task affects grip variability in primates (Bardo et al., 2017). This task complexity, besides the logical predominant use of wrap to bundle, probably explain the preference of Etosha elephants to wrap instead of pinch. Thus, elephants likely grasp differently depending on what they are plain to do with the item just after grasping it, similar as several primates (Pouydebat et al., 2006). We also highlighted that the torsion technique is not used in all tasks. Indeed, in the Etosha sites, the specimens used torsion only for the eating grasp whereas, in the Kruger sites, individuals used this technique only for the bundling grasp. This difference could be linked to the shape and size of the items grasped or the group's life history.

Moreover, we revealed that the grasping way technique, i.e. the side of the grasping, varied with the task, and this laterality related to the task changed with the park. These results highlight side preferences for grasping and manipulating in the

observed elephants at individual level in both park (Keerthipriya et al., 2015; Lefeuvre et al., 2021). We especially highlighted that there were few left side grasp and manipulation in the observed elephants in both parks. This is consistent with the literature on Asian elephants and captive African savannah elephants, which demonstrated a majority of right bias in food prehension (Giljov et al., 2017, 2018; Keerthipriya et al., 2015; Lefeuvre et al., 2021; Revathe et al., 2020). Thus, this study brings similar information, but for the first time in wild African savannah elephants. However, this bias preference strength seems to vary with the food grasped (here grasses or small branch) and the task, and even change in Kruger elephants when bundling grasp, as they preferred the left side to the right side only for this complex task. As these side preferences changed with the task performed, we can suppose that the lateralisation of the trunk is linked with the task specificity and complexity (Giljov et al., 2017; Lefeuvre et al., 2021). This supposition is consistent with the literature on primates, which revealed a stronger lateralisation when grasping and manipulating mobile food and tools (Laurence et al., 2011; Pouydebat et al., 2010; Regaiolli et al., 2016; Trouillard et al., 2005; see Boulinguez-Ambroise et al., 2022 for a review).

Finally, the trunk parts involved in the realisation of the tasks also differed between the park and depending on the task. These differences in trunk parts per task and park are probably linked with the differences describe above in grasping type, and thus can be explained similarly. Indeed, we demonstrated in Chapter 2 of this dissertation thesis that, when the Kruger elephants grasped for eating directly or grasped to bundle the food, the use of the different trunk parts is strongly related to the different grasping way, with more trunk part involved in wrap grasps than in pinch grasps. Therefore, we can hypothesise that this link is likely the same for the Etosha elephants. To explore this hypothesis, we could also investigate the link between the different techniques criteria in the Etosha elephants, in the same way as we did with the Kruger elephants in Chapter 2.

However, when grasping small branches for eating it directly, the elephants from the two park display similar technique patterns, with similar numbers of grasping way, type and trunk parts modalities used. Therefore, the techniques used in both parks seem similar for this food, on the contrary of the techniques used when grasping grasses. With these results and with the results in Chapter 2 on Kruger's elephants, which revealed the link between the type of food and the grasping techniques, the food properties probably have an effect on the grasping techniques at population levels. These differences in techniques thus could be linked to grasp optimisation depending on the food similar as primates and frogs (Anzeraey et al., 2017; Christel et al., 1998; Peckre et al., 2019; Pouydebat et al., 2009; Reghem et al., 2011; Spinozzi et al., 2004; Toussaint et al., 2013). Likewise, the similarities in

techniques in both populations for grasping small branches may reveal common optimised grasps in elephants for this item. Further work will be to explore this link between the techniques similarities and differences and a potential optimisation.

Therefore, we revealed that the grasping and manipulation techniques with the trunk in elephants varied with the task and the item at population-level. These population-level variations can be explained by ecological factors, as both populations live in different environments and especially face different food varieties and accessibility as describe above (Codron et al., 2006; Estes, 1999; Sach et al., 2019).

The population-level variations in grasping and manipulation techniques can also be a result of differences in social learning. Indeed, in other species such as pigeons, great tits and vervet monkeys, technique transmission is common and generally reflected at population-level (Canteloup et al., 2020; Palameta & Lefebvre, 1985; Thorogood et al., 2018). We can therefore hypothesise that the trunk techniques probably outcome of transmission between elephants, and especially mother and allomothers to calves (Fishlock et al., 2016; Lee, 1987). In addition, the differences in life history between the two populations may also be related to these trunk techniques transmission. There is indeed strong differences in survival rates between the two populations of Kruger and Etosha Parks, with a lower juvenile survival rate in the Etosha population due to the lower food availability (Shrader et al., 2010). The survival rate can then affect the transmission of food grasping and manipulative skills in both populations, as the food availability is not the same.

Moreover, we revealed that the tusks profiles differed greatly between the two populations in terms of size, fracture and curvature, and probably link with the habitat. Yet, tusks profiles and especially the size do have an effect on the trunk grasping and manipulation techniques (Chapter 2 of this dissertation thesis). Thereby, we can suppose that the food grasping and manipulation variations we highlighted between the two populations are directly related to the tusks profiles differences. Indeed, the Kruger elephants, with their longer tusks and various tusks profiles, may have some of their trunk movements obstructed by the tusks. The grasping way especially is related to the tusks morphology in these elephants (Chapter 2). However, the Etosha elephants, with their smaller tusks had probably their trunk movements less obstructed and thus impacted by the tusks. They could therefore display different trunk techniques and more variability than the Kruger elephants. With the evolution of the tusks toward smaller size or even absence due to poaching pressure in numerous elephant populations (Campbell-Staton et al., 2021; Chiyo et al., 2015; Heimert, 1994), African savannah elephants thus could display in the future larger variability in trunk techniques. A long-term study on trunk use in parallel of tusks evolution will be a great way to explore it.

Finally, we also explored the trunk techniques in relation to the age of the elephants. When grasping grasses for eating it directly, the juveniles did not display different techniques patterns depending on the park they were from, on the contrary of the adults. Young elephant tusks are not well developed yet (Raubenheimer, 2000; Whyte & Hall-Martin, 2018); thus, their tusks could not have an influence on their grasping techniques yet (Chapter 2). No population differences in grasping techniques due to the tusk morphologies could be found in juvenile elephants.

All these results must be tempered by the differential number of elephants studied in the two populations, with more elephants studied in Kruger than in Etosha. Moreover, the number of elephants studied is not high enough to disregard a potential individual effect on our data that could influence some of our results. Therefore, to ensure these results, and to explore further the different ecological and morphological factors that could influence the food grasping and manipulation techniques at population-level, more data could be collected in these two elephant populations, and especially the Etosha elephants.

Conclusion

For the first time, elephant tusks profiles from the Kruger National Park and from the Etosha National Park were characterised in detail. The two populations displayed a low incidence of tusklessness, presumably linked with low poaching pressure. The tusks profiles between the populations differed in size, breaking and curvature, in continuity with descriptions of these population tusks years ago. These differences certainly result of environmental factors that caused tusk fragility and low development, but there is a lack of information on these potential factors. High fluoride ingestion level related to the aridity of the habitat may have an effect on tusk sturdiness, as well as the diet of the elephant probably affect the development of the tusks, such as deficiency in mineral salts. Thus, it could be interesting to investigate precisely which elements in elephant diet could be related to its tusk development, tusk frailty and tusk robustness.

Differences in trunk grasping and manipulating techniques in the two populations were also highlighted, and these differences are certainly related to the strong tusk morphological variations of the two populations, as it was revealed before that trunk techniques realisation are related to tusks profiles. The population with smaller tusks displayed more variability in trunk techniques. As there is in elephants an evolution of the tusks toward smaller size due to poaching, elephants may show larger trunk techniques variability in the future. A long-term study on trunk uses in parallel of tusks evolution is then necessary to explore this potential link.

Moreover, we demonstrated that the task and food properties probably have an effect on the grasping and manipulation techniques at population levels. This could reveal an optimisation of the grasps and manipulations depending on the population and related to, besides the tusk morphology, the task complexity, the age of the elephant and the food accessibility. Furthermore, we particularly highlighted that food grasping in wild African savannah elephants was more performed with a right side bias than left, and depending on the task. Enlarge the observations in more elephants could ensure these results and explore further the factors that could shape these variations between populations.

Chapter 3 summary

Title: Effect of the habitat (Etosha vs Kruger) on trunk grasping and manipulation techniques in African savannah elephants.

Background: Food grasping and manipulation is central to the survival of species. The links between grasping and manipulation techniques and morphological parameters, individuals, properties of the object grasped and task performed were studied mostly on primates, rodents, lizards and chameleons. The related inter-population differences were also explored in some of these species to shed light on the learning, ecological and morphological patterns that may influence the prehensile and manipulative capacities. Yet, no study investigated the population-level of grasping and manipulation techniques with a muscular hydrostat and especially the elephant trunk. However, African savannah elephants (*Loxodonta africana*) occupy a variety of habitats, display regional morphological variations and have different life histories depending on the population.

Methods: To examine if and how trunk grasping and manipulation techniques vary with the populations, we quantified and compared these trunk techniques during feeding behaviour in two populations of African savannah elephants. We identified and observed 70 wild African savannah elephants, with 43 that performed the analysed tasks: 13 from the dry savannahs of Etosha National Park in Namibia, and 30 from the gallery forests of Kruger National Park in South Africa. The tusks profiles of the two populations were also characterised and compared.

Results and discussion: The tusks profiles of the Kruger and Etosha elephants differ in size, fracture and curvature, probably due to environmental factors that caused tusk fragility and low development, such as the ingestion level of fluoride. Particularly, the different elements in elephant diets that could be related to tusks morphology have to be explored further. The low incidence of tusklessness in both population could nevertheless be linked with low poaching pressure. We highlighted differences in trunk grasping and manipulating techniques in the two populations, with an effect of the task and food properties at population levels. These variations are probably related to the strong tusk morphological variations between these populations. The population with smaller tusks especially display more technique variability. As elephant tusks seem to involve toward smaller tusks du to poaching, elephants may show larger trunk techniques variability in the future, but a long-term study has to be performed to investigate it.

From Chapter 3 to Chapter 4

In Chapter 3, we highlighted differences in trunk grasping and manipulation technique across distinct populations that live either in gallery forest habitat or arid habitat. We also described the potential implication of the tusks profiles on the techniques at population-level. With the first three chapters, trunk uses and grasping and manipulation techniques were thus distinctly explored and characterised, as well as the potential influences of individuals, populations and habitats on them. As we highlighted that, during grasping tasks, the pinch is an essential technique feature, we explored particularly the characteristics of this precise grip in Chapter 4. African savannah elephant pinch, perform with the two fingers of the trunk tip, can be related to hand high precision grip. Therefore, we can suppose that the trunk may display similar grasping patterns. In Chapter 4, we attempt to determine whether during pinch grasping the trunk tip preshapes like hands. We describe this pinch specific technique and explore what may influence its use among the studied individuals.

Chapter 4

The relationship between distal trunk morphology and object grasping in the African savannah elephant (Loxodonta africana)

Chapter 4

The relationship between distal trunk morphology and object grasping in the African savannah elephant (Loxodonta africana)

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Introduction

Grasping is an essential movement that is widespread among many tetrapod species and plays a fundamental role in feeding, social interactions and locomotion (Pouydebat et al., 2022; Sustaita et al., 2013). Various grasping techniques can be performed with mouths, hands, paws, feet, or trunks (Christel, 1993; Sustaita et al., 2013). For example, elephants often grasp each other's trunks during greeting ceremonies, bonding ceremonies and social play (Poole & Granli, 2011).

Hand grasping, in particular, has been widely studied among primates, including humans, because of their individual fingers and ability to perform complex grasping and manipulation tasks (Christel, 1993; Jones-Engel & Bard, 1996; Napier, 1956; Pouydebat et al., 2011). In primates, objects, including tools and food, are grasped according to their physical properties, such as size, shape, consistency, and mobility, and depending on the action planned (Ansuini et al., 2006, 2008; Chieffi & Gentilucci, 1993; Jeannerod, 1984; Pouydebat et al., 2009; Santello, 2002; Santello et al., 2002).

Many primates preshape their hands according to food properties during grasping, including chimpanzees (Jones-Engel & Bard, 1996; Pouydebat et al., 2009), macaques (MacFarlane & Graziano, 2009; Sartori et al., 2013) and strepsirrhines (Peckre et al., 2019a; Reghem et al., 2011; Toussaint et al., 2013, 2015). However, when reaching to grasp the same object, i.e. when the hand moves toward the same object to be grasped, the general shape of macaque and human hands differ (Roy et al., 2000). In species besides primates, such as rats (Sacrey et al., 2009; Whishaw & Coles, 1996) and frogs (Anzeraey et al., 2017), food properties also affect grasping techniques.

More precisely, during reach-to-grasp movements, the human hand gradually adjusts (Mason et al., 2001; Santello & Soechting, 1998) to accommodate the object contour (Chieffi & Gentilucci, 1993; Jeannerod, 1984; Pellegrino et al., 1989; Supuk et al., 2005). Similar behaviour has been observed for other primate species, such as macaques (Roy et al., 2000; Sartori et al., 2013) and capuchins (Christel & Fragaszy, 2000). The object affordances (i.e. the properties of an object; Sartori et al., 2011) evoke its use and function during grasping.

Preshaping enables increased grasping success (Sartori et al., 2011) and can thus serve as a selective advantage for species or individuals. Preshaping may result from learning or variability in appendage morphology or motor control. While hand preshaping during reach-to-grasp movements in primates is well established, data on other species is scarce. Only rats (Sacrey et al., 2009; Whishaw et al., 1992) and pigeons (Bermejo & Zeigler, 1989) have been studied in terms of their ability to preshape their

paw or beak when grasping an item. Despite the enormous variability in trunk utilisation for grasping objects in elephants (Lefeuvre et al., 2020; Poole & Granli, 2011; Wu et al., 2018; Yasui & Idani, 2017), studies have not yet investigated the potential for elephant trunk preshaping during reach-to-grasp movements.

Elephant trunks are especially interesting appendages due to this grasping variability. Elephants use their trunks in many situations, such as grasping food, congeners or other items in their environment (Ahamed, 2015; Lee & Moss, 2014; Lefeuvre et al., 2020; Poole & Granli, 2011; Yasui & Idani, 2017). The trunk is a muscular hydrostat that does not have hard skeletal elements, similar to cephalopod tentacles and the tongues of many vertebrates; thus, it can bend in any direction, elongate, shorten and lift heavy masses (Kier & Smith, 1985; Wilson et al., 1991). Grasping techniques, mainly including the morphological and kinematic aspects, are well studied in muscular hydrostats (Grasso, 2008; Ritter & Nishikawa, 1995). Elephant grasping has also received increasing attention, especially the techniques that involve the distal part of the trunk (Dagenais et al., 2021; Schulz et al., 2021). Although the most commonly used grasping technique in muscular hydrostats is coiling around the item, elephant trunk tips can also engage in pinch grasping (Rasmussen & Munger, 1996; Wu et al., 2018) as chameleon tongues too (Herrel et al., 2000). Indeed, African elephants can perform precise pinch grasping movements. According to the IUCN, there are two distinct African elephant species: the African savannah elephant (*Loxodonta africana*) and the African forest elephant (*Loxodonta cyclotis*) (Hart et al., 2021). Unlike Asian elephants, which have only one finger at the top of their trunk tip, African elephants can pinch items with high precision between two fingers (one at the bottom and one at the top of the trunk tip; Hoffmann et al., 2004). The grasping capacities of the African elephant trunk tip are sometimes compared to those of appendages of other species, such as the human hand (Hoffmann et al., 2004; Onodera & Philip Hicks, 1999). Despite these interesting grasping capacities, no studies have examined the potential for preshaping in muscular hydrostats to date; thus, none has investigated the potential for preshaping of trunk tips.

In this study, we aimed to understand grasping behaviour in African savannah elephants. As grasping capacities are affected by individual variability in the shape of the appendage, we first investigated whether there were interindividual differences in the trunk tip shape. Then, we determined whether elephants preshape their trunk tips during reach-to-grasp movements toward food items and whether this potential preshaping influences grasping success. Last, we examined whether grasping success increased as the trials progressed and whether all elephants exhibited similar trunk grasping shapes for a given item by the end of the trials.

We predicted that each elephant has a unique distal trunk shape and that preshaping of the trunk tip would occur during reach-to-grasp movements toward food items. We also expected that preshaping of the trunk tip would increase grasping success and that over time an elephant's grasping movements would become more efficient. Finally, we predicted that all individuals would gradually converge toward the same distal trunk shape when reaching to grasp the same object. To test these hypotheses, we quantified and visualised (with geometric morphometric tools) the morphology of the distal part of the trunk during reach-to-grasp movements toward food items for six female African savannah elephants (*Loxodonta africana*; Blumenbach, 1797).

Materials and methods

Subjects and housing

Data presented in this study were collected on six African savannah elephants (*Loxodonta africana*) from the ZooParc of Beauval in Loir-et-Cher, France: Ashanti, Juba, Marjorie, M'Kali, N'Dala and Tana (**Figure 4.1B**). Five of these elephants were approximately 32 years old at the beginning of the experiment; Ashanti was a 16-year-old subadult. Comparisons between the adults and the subadult allowed us to examine the role of experience in trunk preshaping behaviour. All elephants except Ashanti were wild-born. They lived in two groups, each of which had a specific dominance hierarchy. One of the females, N'Dala, had been blind for a year by the time the study commenced. Thus, comparisons between sighted and blind elephants allowed us to assess the importance of visual input for grasping behaviour. The elephant characteristics can be found in **Table 4.1**.

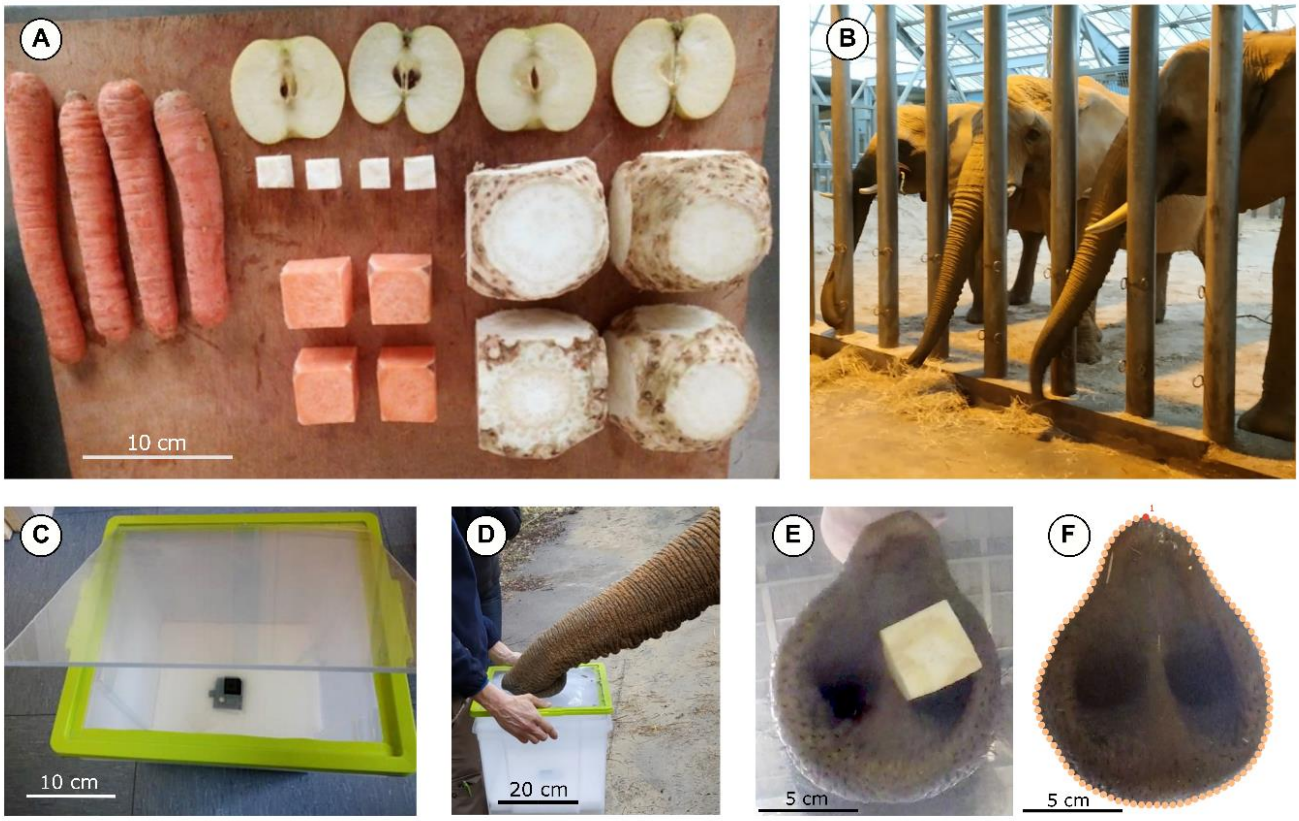


Figure 4.1 – The materials and methods used for the experiments. (A) Examples of food items used for the experiment. Here we presented to the elephant five types of items: carrot, flat apple slice, two centimetre side-length celery cube, four centimetre side-length sweet potato cube and eight centimetre side-length celery cube, with a repeatability of four for each. (B) Three of the six African savannah elephants (*Loxodonta africana*) of the ZooParc of Beauval. (C) The double box system used to film the experiment. It is a double transparent box inlay in one another, the first one contains the camera and polystyrene to maintain it, and the second one had a hole at its bottom for the lens of the camera. (D) The items were put down on the transparent top of the second box and carried in front of the animal. (E) Example of a screenshot of a four-centimetre side-length food cube just before grasp, in order to take the print of the distal part of the trunk. (F) Example of a trunk tip contouring during a grasp. The red dot corresponds to the anatomical landmark at the top of the trunk tip, and the 100 orange dots correspond to the sliding semi-landmarks around the outlines of the distal part. Pictures © M. Lefeuvre and © C. Cornette.

Name	Sex	Age (year)	Hierarchical rank	Origins	Physical particularities
Ashanti	Female	16	Medium rank	Knowsley Safari Park (UK)	Smallest elephant
Juba	Female	32	High rank	Zimbabwe	-
Marjorie	Female	33	High rank	Zimbabwe	Largest elephant
M'Kali	Female	30	Low rank	Namibia	Tall
N'Dala	Female	30	Medium rank	Namibia	Blind, trunk tip deformity
Tana	Female	32	Medium rank	Zimbabwe	-

Table 4.1 – Subjects characteristics. These characteristics include the name of the elephants, their sex, age, hierarchical rank, origin and physical particularities.

The elephants were housed together but were isolated during the experiment. They were tested during their weekly training sessions. Every morning, one elephant was trained to facilitate any future medical interventions; this corresponded to one training session per elephant per week. The elephants were already experienced with grasping food items during these weekly training sessions; thus, they were already experienced with the movements required for the experiment. The running order of these training sessions changed each week. Thus, in total, we conducted five to six experimentation sessions per elephant over six weeks in spring 2019.

Ethical note

As the data were collected by keepers during the weekly elephant training sessions, only standard elephant-keeper interactions occurred, in accordance with zoo security regulations. All procedures were conducted in accordance with the relevant CNRS guidelines and European Union regulations (Directive 2010/63/EU).

Object grasping

The food items used in the experiments were found in the typical diet of captive Beauval elephants and included carrots, apples and celery (Olson, 2004; Ullrey et al., 1997). Three food item types were presented to the elephants: elongated objects with a constant diameter (carrots), flat objects (apple slices, cut horizontally), and cubic objects of three sizes. The objects consisted of diverse vegetables (according to availability), and the three cubic sizes included small cubes (two centimetres per side), medium cubes (four centimetres per side) and large cubes (eight centimetres per side). Food item dimensions are presented in **Table 4.2**. The small cube size was determined by elephant participation: smaller cubes (i.e. one centimetre per side) made the elephants impatient, and experiments with this size were inconclusive. The large cube size was determined according to the maximum size of the largest vegetables (e.g. beetroots and celery). Three to six items of each type were provided during each session (**Figure 4.1A**), depending on vegetable availability, except for the large cubes, which had low availability.

Food item	Dimensions (mm)
Apple slice	75 (diameter)
Carrot	160 (length) * 25 (diameter)
Small cube	20*20*20
Medium cube	40*40*40
Large cube	80*80*80

Table 4.2 – Dimensions of the food items grasped by the elephants. Dimensions in millimetres.

Recordings of grasping movements

To determine the influence of food item characteristics on the trunk tip shape during grasping behaviour, the items were laid out on a double transparent box. The bottom of the first box contained the camera, set in polystyrene, and a second box, with a hole at its bottom for the lens of the camera, was placed over the first box. The top of the second box was a transparent lid (**Figure 4.1C**) where the items were

individually placed. This box-and-camera system was placed on the ground in front of the animal by an animal keeper (**Figure 4.1D**). Therefore, we were able to film all grasping behaviour from below. An example film of a grasping behaviour can be found in the appendices (**Appendix 4.1**).

We recorded the reach-to-grasp movements of each individual with a digital video camera (GoPro7). For each grasp, we took pictures of the distal part of the trunk. We captured these images from the video frames when the elephant first touched the box and when the trunk was flat against the box (**Figure 4.1E**). Other grasping techniques, such as coiling, were removed from the analysis. For each grasping attempt, we also noted when the trunk hit the box near the food but missed the food item. As these grasping attempts require a readjustment of the trunk toward the item, they are directly correlated with the time spent on a grasp. The elephants almost never dropped food items but took longer to grasp them after missing. Therefore, we termed these grasping attempts ``failure before a grasp'' to differentiate them.

Geometric morphometrics and statistical analysis

To describe the shape of the tip of the trunk, we used a 2D geometric morphometric (GM) approach (Adams et al., 2004; Gunz & Mitteroecker, 2013; Rohlf & Marcus, 1993). For each image of the trunk tip, the trunk tip was outlined with tpsDIG2 software, version 2.32 (Rohlf, 2016). To obtain these outlines, we placed an anatomical landmark on the top of each trunk tip and placed 100 sliding semilandmarks on the curves (Gunz & Mitteroecker, 2013) to outline the distal part of the trunk (**Figure 4.1F**). These semilandmarks defined the borders of the trunk tip. Every characteristic (the subject, food item, and number of failures) that might influence the trunk tip contour was annotated. The film in the appendices shows a part of this methodology (video recording of the grasp as well as the landmark and semilandmarks on the trunk tip, **Appendix 4.1**).

We performed a Generalised Procrustes Analysis (GPA) (Rohlf & Slice, 1990), using the ``gpagen'' function of the package ``geomorph'' version 3.2.1 (Adams et al., 2018) in R version 3.6.1 (R Core Team, 2018). This GPA aligned the different distal trunk shapes with a Procrustes superposition to remove the effects of translation, rotation, and scaling. We visualised the GPA using the ``plotTangentSpace'' function and retained 90% of shape variability after reducing the dimensionality of the variables with a principal components analysis (PCA) (Baylac & Frieÿ, 2005). The PCA components were used as shape parameters in the following analyses. To detect significant differences in the shape of the trunk according to the object properties, individual, or number of grasping failures, we performed a MANOVA using the

``manova'' function in R. A MANOVA was also used to detect significant differences in trunk tip shape according to the object properties for each individual.

To optimise and visualise individual differences in trunk tip shapes, canonical variable analysis (CVA) was performed using the ``CVA'' function in the package ``Morpho'' version 2.8 (Schlager, 2017). This CVA was applied to only five of the six elephants because one elephant, N'Dala, had a deformed trunk tip caused by a previous injury. Her trunk tip thus differed from those of the other five. To explore intact trunk tip shapes and obtain the most representative variability between individuals, N'Dala was excluded from this analysis. All other analyses included all six elephants.

A CVA was also performed for each individual to calculate the Mahalanobis distances between food items. These Mahalanobis distance plots revealed the similarity between trunk shapes for grasping different items. The Mahalanobis distances were calculated with the ``hclust'' function in R, plotted in an ``unrooted'' form and then paired with deformation vector fields and deformation isolines of the trunk tip shapes for each object. These thin plate spline (TPS) deformations showed the difference in shape between the mean trunk tip shape for each individual and the mean trunk tip shape per object for each individual. To obtain these TPS deformations, every dot of the mean distal shape outline was slid to the position of the mean distal shape per object. A deformation grid was thus obtained, and the intensity and direction of the deformations were indicated by smooth deformation isolines and deformation vector fields. The deformation isolines indicated the location of the strongest differences in trunk tip shape, and the deformation vector fields showed the direction of these differences. These TPS visualisations were performed with the functions ``tps_arr'' and ``tps_iso'' in the ``Momocs'' package (version 1.3.2) in R (Klingenberg, 2013).

The mean number of grasping failures per individual and per object for all trials were also calculated. Linear regressions were performed to determine the change in the number of failures over time for each individual and each object. The number of failures is shown along all the grasping attempts (all objects included). Finally, a GPA of the trunk tip shapes of all individuals for each object was performed and paired with trajectory plots. These plots were obtained in the Procrustes space by joining for each individual the dots corresponding to the outlines of the first and last grasping movement. We could therefore examine the trajectories of the distal trunk shapes during grasping to see if different individuals' trunk tips converged on similar shapes for the same object.

Results

We obtained a total of 639 grasps from 03:03 h of video from all studied elephants. Of these grasps, trunk tip contouring could be obtained from 491. In the remaining 148 grasps, the trunk either did not lay flat on the box lid or the object or side of the box obscured a part of the trunk tip. The distribution of the 491 grasps among each elephant and food item can be found in **Table 4.3**. The number of grasps was not equivalent for each individual and item type. These differences can be explained by the 148 grasps that were removed and by variation in the availability of vegetables in each session. Similarly, the low number of large-cube grasps is explained by the low availability of vegetables to create this item. Moreover, in the 491 grasps included in the final analysis, M'Kali only interacted once with a large cube; the other interactions between M'Kali and the large cubes occurred in the 148 grasps that were removed.

Number of grasping attempts		**Individual**					
		Ashanti	*Juba*	*Marjorie*	*M'Kali*	*N'Dala*	*Tana*
Food item	*Apple slice*	13	20	21	18	27	26
	Carrot	14	23	15	18	18	17
	Small cube	19	25	23	20	20	20
	Medium cube	15	19	15	20	20	19
	Large cube	4	6	6	1	5	4
Total grasping attempts		65	93	80	77	90	86

Table 4.3 – Number of grasping attempts per individual and per food item. All these grasping were included in the analyses.

Table 4.4 shows the results of the MANOVA on the trunk tip shape just before a grasp (the preshape) and the individual, object and number of failures variables. The trunk tip shape varied according to these variables. First, the distal trunk shape varied significantly by individual and by object ($p<0:05$). The significant association between the distal trunk shape and the individual elephants supports the hypothesis of a unique distal trunk shape. The significant association between the distal trunk shape and the type of object supports the hypothesis of trunk tip preshaping during a reach-

to-grasp movement toward a food item. Thus, the trunk tip shape corresponded to the individual and the type of object. Moreover, the trunk tip shapes for each object were also dependent on the individual elephant. However, there was not a significant association (p>0:05) between the distal trunk shape and the number of failures. Therefore, in this experiment, we were not able to establish a link between distal trunk shape and the number of failures before a successful grasp.

All elephant trunk tip shapes according to	Pillai's Trace	F	df	P-value
Individuals	2.67	93.12	5	2.2e-16 ***
Objects	0.10	1.79	5	0.0051 **
Individuals * objects	0.35	1.23	20	0.0363 *
Number of failures	0.12	1.10	9	0.2873

Table 4.4 – Results of the variance analyses MANOVA performed on all the individuals trunk tip shapes just before a grasp and some variables.

Individual differences

As seen in **Table 4.4**, trunk tip shapes differed according to the individuals. Interindividual variability in the distal trunk shape during food item grasping is shown in **Figure 4.2**. This CVA of the elephant trunk tip shape during food item grasping included only five of the six elephants because one elephant, N'Dala, had a deformed trunk tip; therefore, she was not included in this analysis. Each point in **Figure 4.2** represents a grasp, each colour represents an individual, and the shape at the end of each axis represents the shape of the maximum (red) and minimum (blue) trunk tip.

In **Figure 4.2**, all distal trunk shapes are distinctly grouped by individual. Although Juba's (light blue) and Marjorie's points (orange), are grouped together, their distal trunk shapes were still very different from each other. There were pronounced individual differences in the distal trunk shape between elephants.

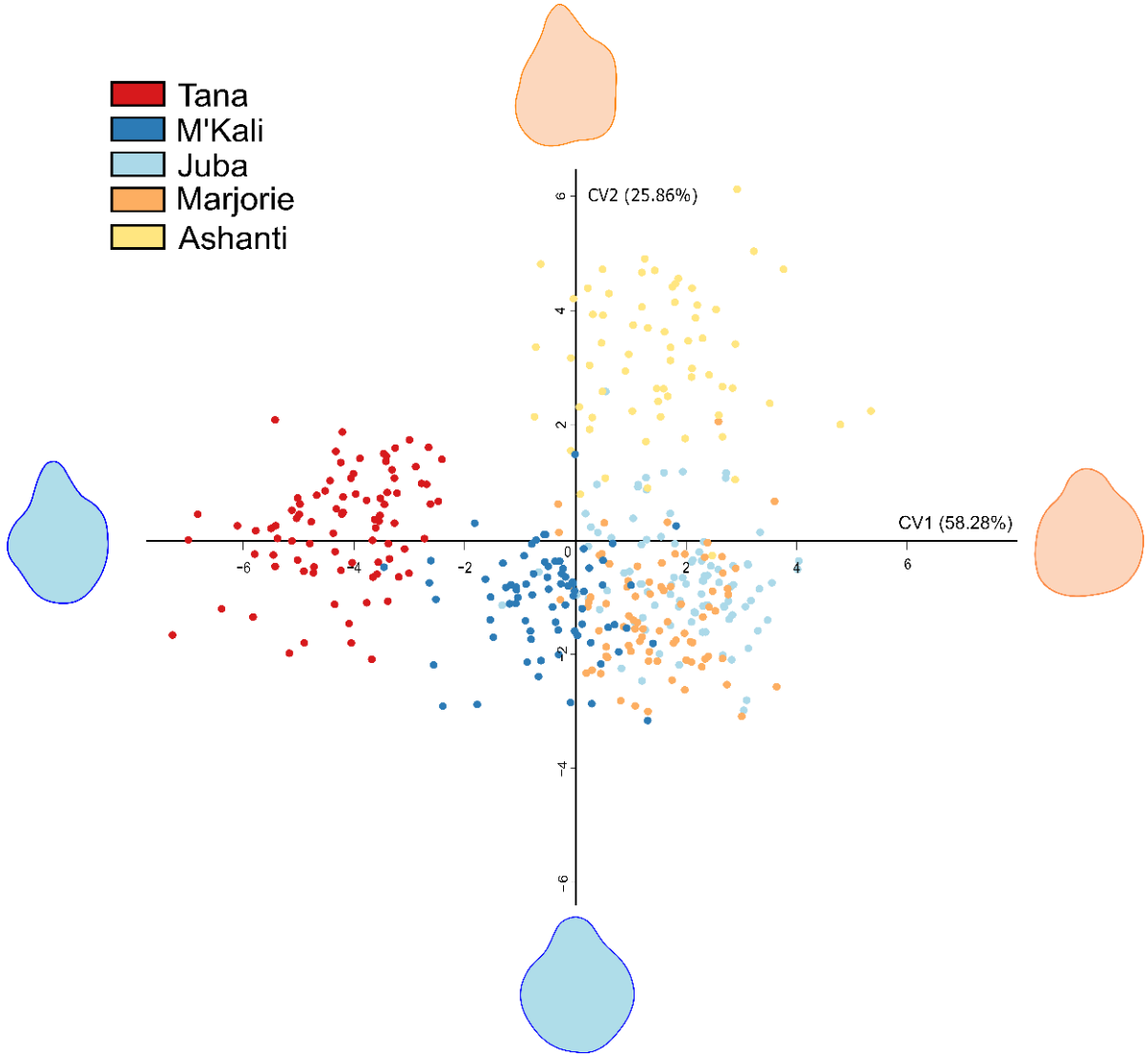


Figure 4.2 – Canonical Variate Analysis visualisation of five elephant trunk tip shapes during food grasp. Each point represents a grasp, each colour an individual, and each end of the axis the maximum (red) and minimum (blue) distal part shapes.

Trunk shapes and object characteristics

Table 4.4 shows that the trunk tip shape varied according to the type of object grasped and the individual elephant. Some of the studied elephants preshaped their trunk tip according to the object properties. The results of the MANOVA on the trunk tip shape just before a grasp, performed per individual and according to the type of object, are shown in **Table 4.5**. The trunk tip shape significantly differed according to the type of object for M'Kali, Juba and Marjorie; thus, there was a significant effect of object properties on trunk tip preshaping. The three other elephants, N'Dala (the blind elephant), Ashanti (the subadult) and Tana, did not preshape their trunk tip according

to the food item properties. Thus, only half of the sampled individuals had specific tip trunk shapes associated with object properties.

Trunk tip shapes according to objects per individuals	Pillai's Trace	F	df	P-value
M'Kali	0.49	2.29	3	0.0028 **
Juba	0.50	1.76	4	0.0113 *
Marjorie	0.34	1.79	4	0.0311 *
N'Dala	0.48	1.22	4	0.1848
Ashanti	0.51	1.20	4	0.2289
Tana	0.28	0.85	4	0.6762

Table 4.5 – Results of the variance analyses MANOVA performed per individuals on the trunk tip shapes just before a grasp according to objects.

Specifically, **Figures 4.3, 4.4 and 4.5** display the trunk tip shapes of M'Kali (**Figure 4.3**), Juba (**Figure 4.4**) and Marjorie (**Figure 4.5**) and their variance according to the object properties. As M'Kali only interacted with the large cube once in the analysed grasps, her trunk tip shape associated with the large cube is not included in the figure. These three Mahalanobis distance plots paired with thin plate spline deformation visualisations represent the three individuals who preshape their trunks according to the object properties. The TPS deformations are the differences between the mean distal trunk shape for each object and the general mean shape, for each individual. The isoline visualisations show the location of these deformations: the red parts indicate areas with the greatest deformation, and the blue parts indicate areas with the lowest deformation. The deformation vector field visualisations show the directions of these deformations.

In **Figure 4.3**, it can be seen that M'Kali preshaped her trunk tip differently according to the type of food item she reached to grasp. As the Mahalanobis distances show, her trunk tip shape was similar when grasping apple slices and small cubes but different when grasping carrots or medium cubes. For the apple slices and small cubes, the deformations (indicated in red) were mostly on the sides of the trunk tip, and the vectors on these sides point toward the centre of the trunk tip. Thus, when grasping

apple slices and small cubes, M'Kali's trunk tip was more elongated than usual. More specifically, when grasping apple slices, her trunk tip was more oval, and the top of the trunk tip was thicker; the shape of her trunk tip was similar when grasping small cubes but narrower in area. When grasping carrots, her trunk tip was more circular than usual, with a sharp top to the trunk tip, as indicated by the vector directions and isoline colours. Finally, when grasping medium cubes, M'Kali's trunk tip shape isoline visualisation was mainly blue. This trunk tip shape was similar to the usual shape, with only three small areas of difference, creating a slightly more rounded shape.

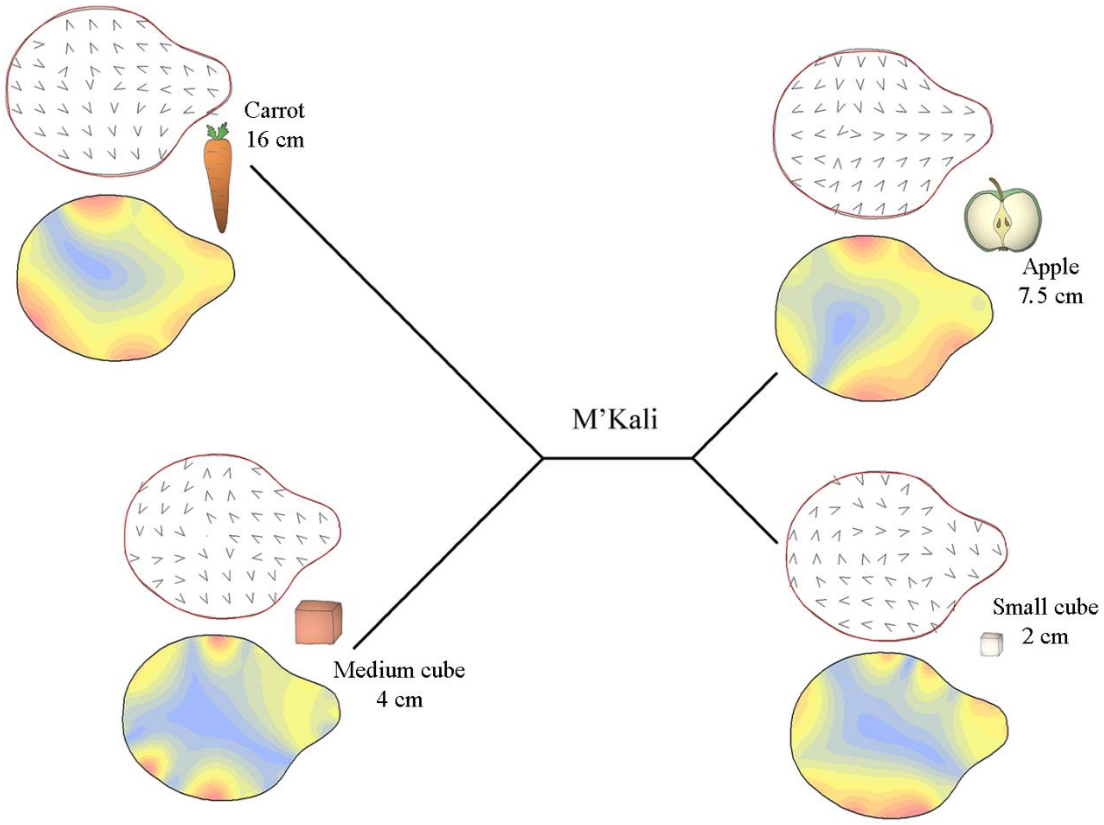


Figure 4.3 – Mahalanobis distance plots paired with thin plate splines deformation visualisations (vectors field deformations and isolines deformations) of trunk tip according to the object grasp, for M'Kali. These Mahalanobis distance plots show through discriminant space the similarity between the different distal shapes obtained per object. The Thin Plate Splines deformations specify where and how the differences in form are on the distal shapes. Red parts of the isolines deformations reveal where the distal shapes change the most, and the blue parts where they change the least. Arrows on the vectors field deformations show in which direction the deformations occur.

Figure 4.4 shows how the distal part of Juba's trunk was preshaped according to the type of food item grasped. Her trunk tip shape was similar when grasping small cubes and medium cubes but different when grasping carrots and apple slices. Moreover, as the Mahalanobis distances show, her trunk tip shape completely differed from the others shapes when grasping large cubes. As the deformation vector field and isoline visualisations for the periphery of the distal trunk shape show, her distal trunk shape became more circular than usual and the top of the trunk tip became thinner. When grasping other food items, the top of the trunk tip was thicker. Still according to the vector field and the isoline colours, when grasping small and medium cubes, Juba's trunk tip shape was slightly more circular than usual, especially on the left side for small cubes and the right side for medium cubes. When grasping carrots, her trunk tip shape was close to usual but thicker on the top right side of the trunk tip. Finally, when grasping apple slices, the general shape of the trunk tip was more oval than usual.

Figure 4.5 displays how Marjorie's trunk tip preshape differed according to the type of food item. Similar to M'Kali, her trunk tip shape was similar when grasping apple slices and small cubes but different when grasping carrots, medium cubes and large cubes. From the vector field and isoline colours of each object's distal trunk shape, we can see that when grasping apple slices and small cubes, Marjorie's distal trunk shape was more oval than usual, with differences on the left and bottom right of the trunk tip. Moreover, the top of the trunk tip was thicker than usual, especially on the left side. When grasping the three other types of food (carrots, medium cubes and large cubes), the top of Marjorie's trunk tip was thinner. The distal trunk shape was also more rounded than usual, especially on the right side when grasping medium cubes, on the bottom right side when grasping large cubes, and on the left side when grasping carrots.

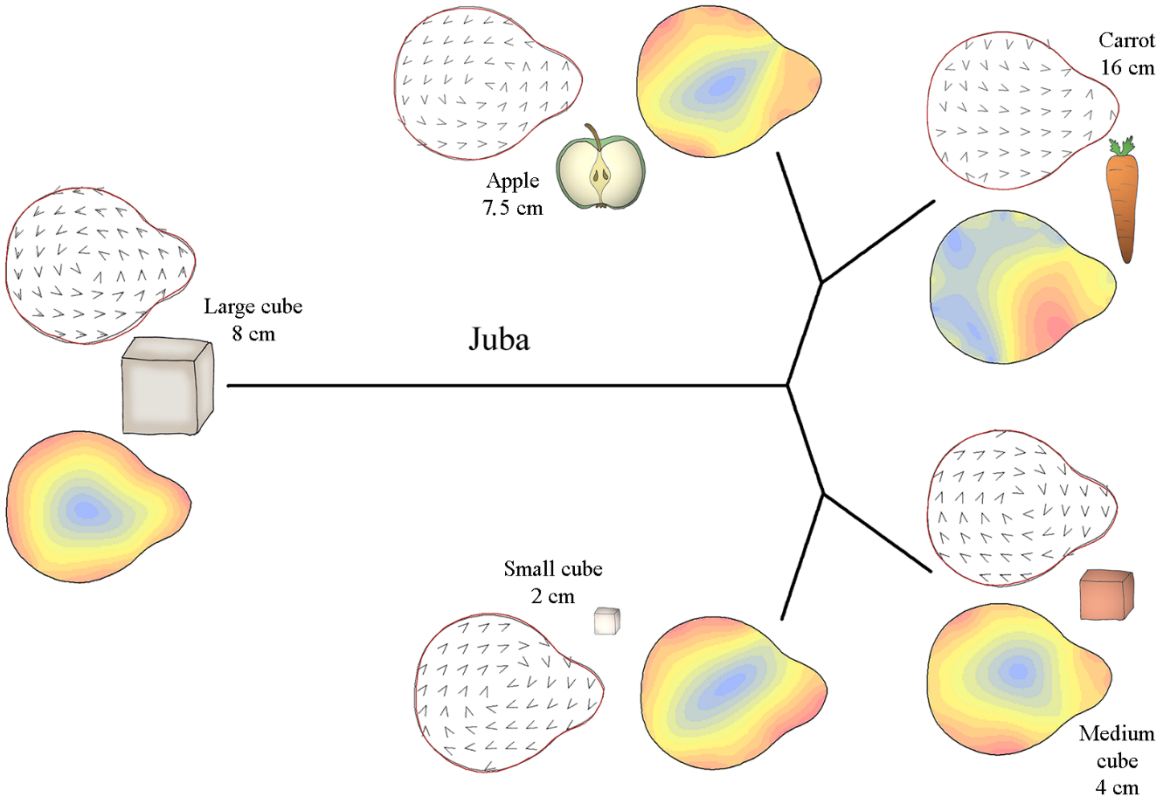


Figure 4.4 – Mahalanobis distance plots paired with thin plate splines deformation visualisations (vectors field deformations and isolines deformations) of trunk tip according to the object grasp, for Juba. These Mahalanobis distance plots show through discriminant space the similarity between the different distal shapes obtained per object. The Thin Plate Splines deformations specify where and how the differences in form are on the distal shapes. Red parts of the isolines deformations reveal where the distal shapes change the most, and the blue parts where they change the least. Arrows on the vectors field deformations show in which direction the deformations occur.

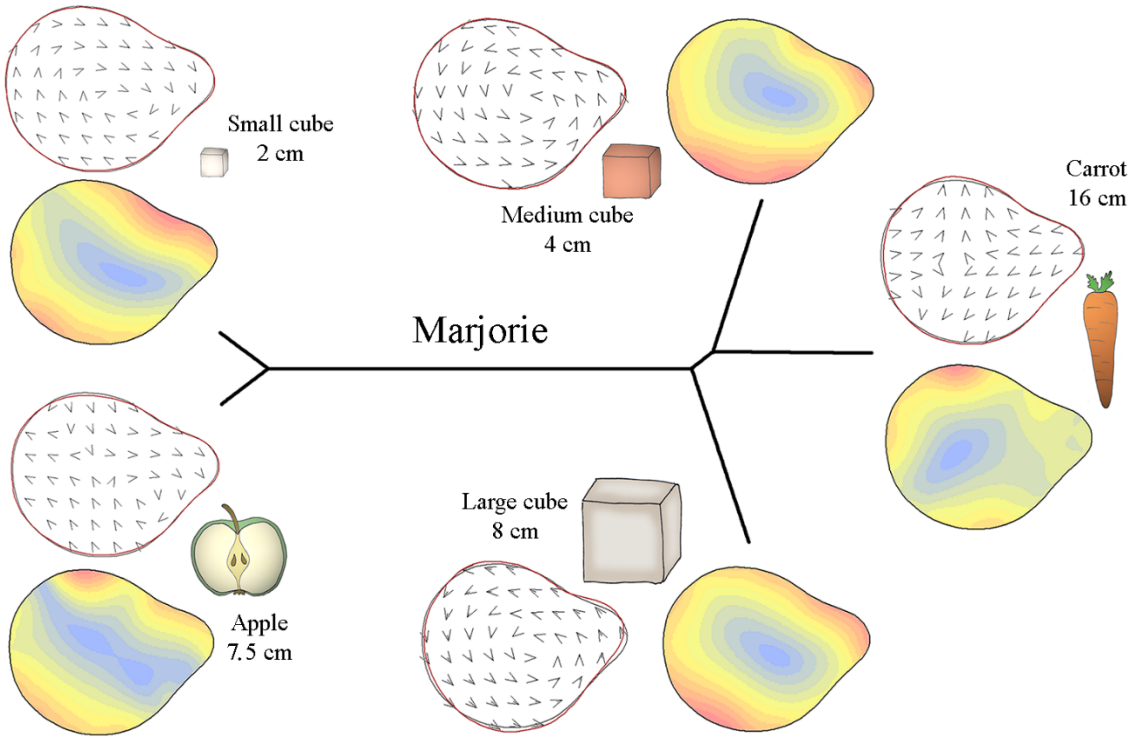


Figure 4.5 – Mahalanobis distance plots paired with thin plate splines deformation visualisations (vectors field deformations and isolines deformations) of trunk tip according to the object grasp, for Marjorie. These Mahalanobis distance plots show through discriminant space the similarity between the different distal shapes obtained per object. The Thin Plate Splines deformations specify where and how the differences in form are on the distal shapes. Red parts of the isolines deformations reveal where the distal shapes change the most, and the blue parts where they change the least. Arrows on the vectors field deformations show in which direction the deformations occur.

Thus, M'Kali and Marjorie had more circular and thin-topped trunk tips when grasping carrots and medium cubes, while the top of the trunk tip was thicker for Juba. When grasping apple slices, the three elephants had more oval and thick-topped trunk tips. For M'Kali and Marjorie, the trunk tip shape when grasping small cubes was similar to that when grasping apple slices, but for Juba, the trunk tip shape was more circular. Finally, Marjorie and Juba had the same distal trunk shape when grasping large cubes: circular with a thin top.

The trunk tip shapes differed according to the type of object and individual, but the three elephants had many similarities in distal trunk shape for grasping the

same object. M'Kali and Marjorie had the same trunk tip shapes when grasping the same objects. Juba tended to have the same shape as well with some food items, but her distal trunk shape also differed for other items, such as small cubes. Taken together, these results indicate that there are both similarities and individual differences in trunk tip preshape in the three elephants.

The distal part of the trunk was also preshaped in a way that matched the type of food item in these three elephants. A rounder trunk tip allowed it to better conform to the contours of food items such as carrots and medium and large cubes, with the sides of the trunk tip matching the edges of the items. Small cubes and flat apple slices, which were more difficult to grasp, required a more oval distal trunk shape to apply maximal surface area to the item. The more difficult the object was to grasp, the more oval the trunk tip shape was. Conversely, if the object offered more grip, as is the case for carrots, the distal trunk shape was closer to the shape of the object.

Grasping success

Table 4.4 shows that trunk tip shape did not differ according to the number of failures before a successful grasp, namely, when the trunk hit the box but missed the food. There was no link between the distal trunk preshape and the number of failures for these individuals. Regardless of the number of failures before a successful grasp, the trunk tip was preshaped just before a grasp. Moreover, **Table 4.6** represents the mean number of failures per individual and per object for all the grasping attempts. Focusing on the individuals, the elephants that failed the most before a successful grasp were M'Kali and N'Dala, while Ashanti and Juba had the fewest failures. The three elephants that had the best grasping success (Ashanti, Juba and Tana) were not necessarily the same elephants that preshaped their trunk tip according to the object properties (M'Kali, Juba and Marjorie). Additionally, for these individuals, a distal trunk preshape in accordance with the object properties was not linked with the success of a grasping attempt.

The objects section of **Table 4.6** displays the success of grasping attempts in general, including the mean number of failures per object for all grasping attempts. Failure was less likely when the elephants attempted to grasp large cubes and carrots and more likely when they attempted to grasp apple slices and small cubes. Overall, grasps were more efficient for large and thick food items.

Variables		Number of failures: mean
Individual	Ashanti	0.98
	Juba	1.10
	Tana	1.18
	Marjorie	1.27
	N'Dala	1.43
	M'Kali	1.91
Object	Large cube	0.82
	Carrot	0.89
	Medium cube	1.24
	Apple slice	1.54
	Small cube	1.79

Table 4.6 – Mean of number of failures per individuals and per objects for all the grasping attempts. The mean number of failures before a successful grasp, for each individual and for each object, on all grasping attempts, were calculated and are presented in this table.

However, over time (and with an increasing number of trials), the number of grasping failures consistently increased or decreased depending on the individual and objects concerned. **Figure 4.6** shows the change in the number of failures on different grasping attempts for each individual and object pair. M'Kali and Ashanti had fewer failures with all food items as the trials progressed, notably improving their success of grasping small cubes (M'Kali) and carrots (Ashanti). At the beginning of the experiment, M'Kali had the most failures in grasping the small cubes of all elephants studied, but her number of failures quickly decreased as the trials progressed. Tana, Juba, Marjorie and N'Dala had fewer failures for most food items as the trials progressed, except for grasping carrots (Tana), apple slices and large cubes (Juba), apple slices and carrots (Marjorie), and apple slices and medium cubes (N'Dala). In particular, Juba had more failures in grasping the large cubes and fewer failures in grasping carrots as the trials progressed. Marjorie had the largest decrease in failures when grasping medium cubes, while N'Dala had the largest increase in failures when grasping medium cubes and the largest decrease in failures when grasping small cubes. All the studied elephants improved in grasping efficiency over time, with all or the majority of the food items. However, each elephant improved on different objects.

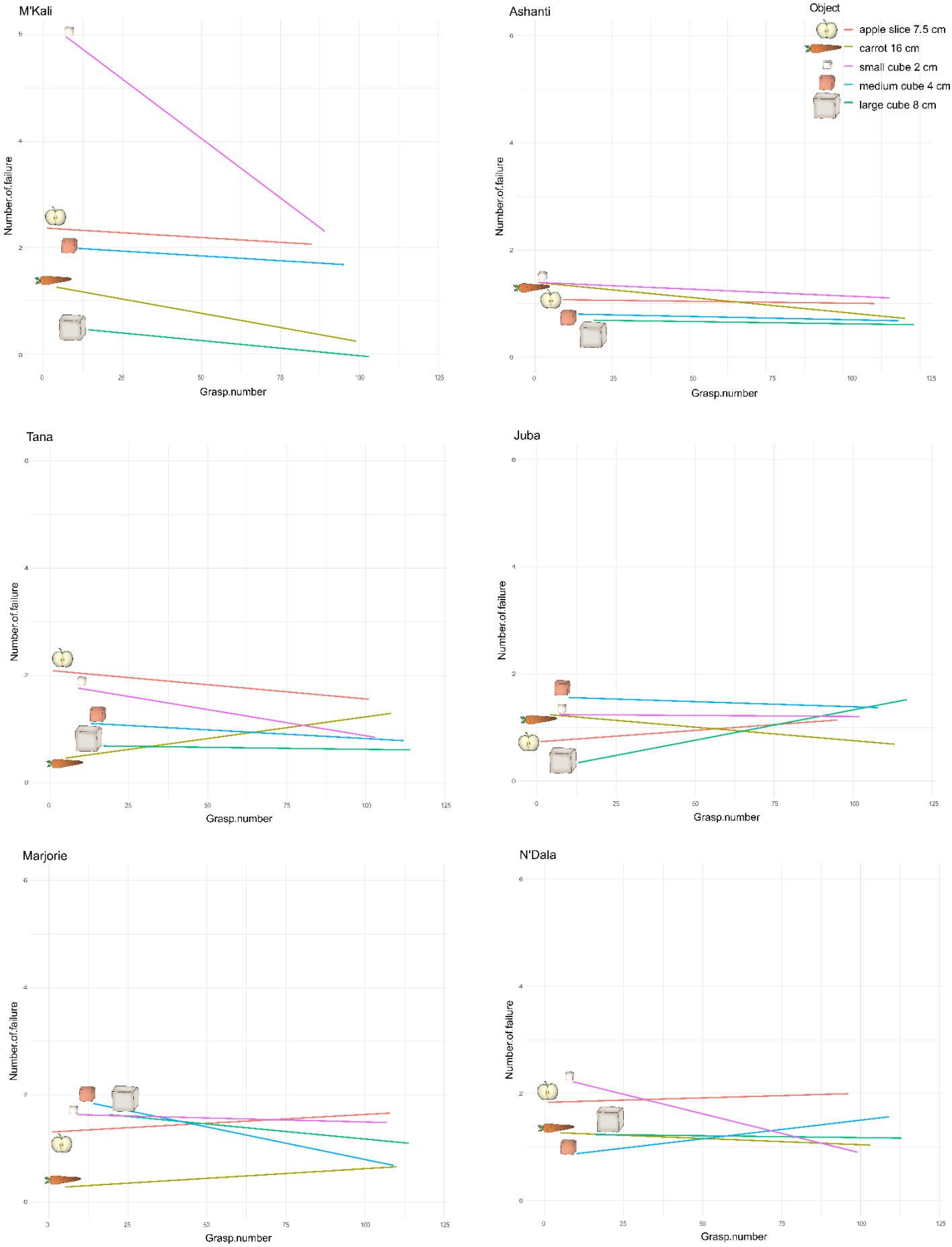

M'Kali
Ashanti
Tana
Juba
Marjorie
N'Dala
Number.of.failure
Grasp.number
Object
apple slice 7.5 cm
carrot 16 cm
small cube 2 cm
medium cube 4 cm
large cube 8 cm

Figure 4.6 – Number of failures along the grasping per individual and object. The x-axes correspond to all the grasping perform over time by an individual, with all the objects. As we introduce the objects to the elephants one after the other each week, each object first grasp number then depends on when the elephant was first introduces to the object in its attempts. The y-axes represent the number of failures before a successful grasp, namely when the trunk hit the box but missed the food. The straight lines show these number of failure tendency along the attempts and per object, for each individual.

Finally, we investigated whether the trunk tip shapes of all the individuals converged when grasping the same object by examining the trajectories of distal trunk shapes over time. **Figure 4.7** displays these trajectories for all studied elephants when grasping medium cubes. The trajectories when grasping the other types of food items are provided in the **appendices**. In **Figure 4.7**, each individual distal trunk shape when grasping medium cubes changed over time. However, no individual preshape clearly trended in the same direction. Thus, their trajectories when grasping medium cubes did not converge. The results were similar for the trajectories when grasping other food items. Taken together, these results did not indicate a convergence of individual distal trunk shapes when elephants grasped the same type of object.

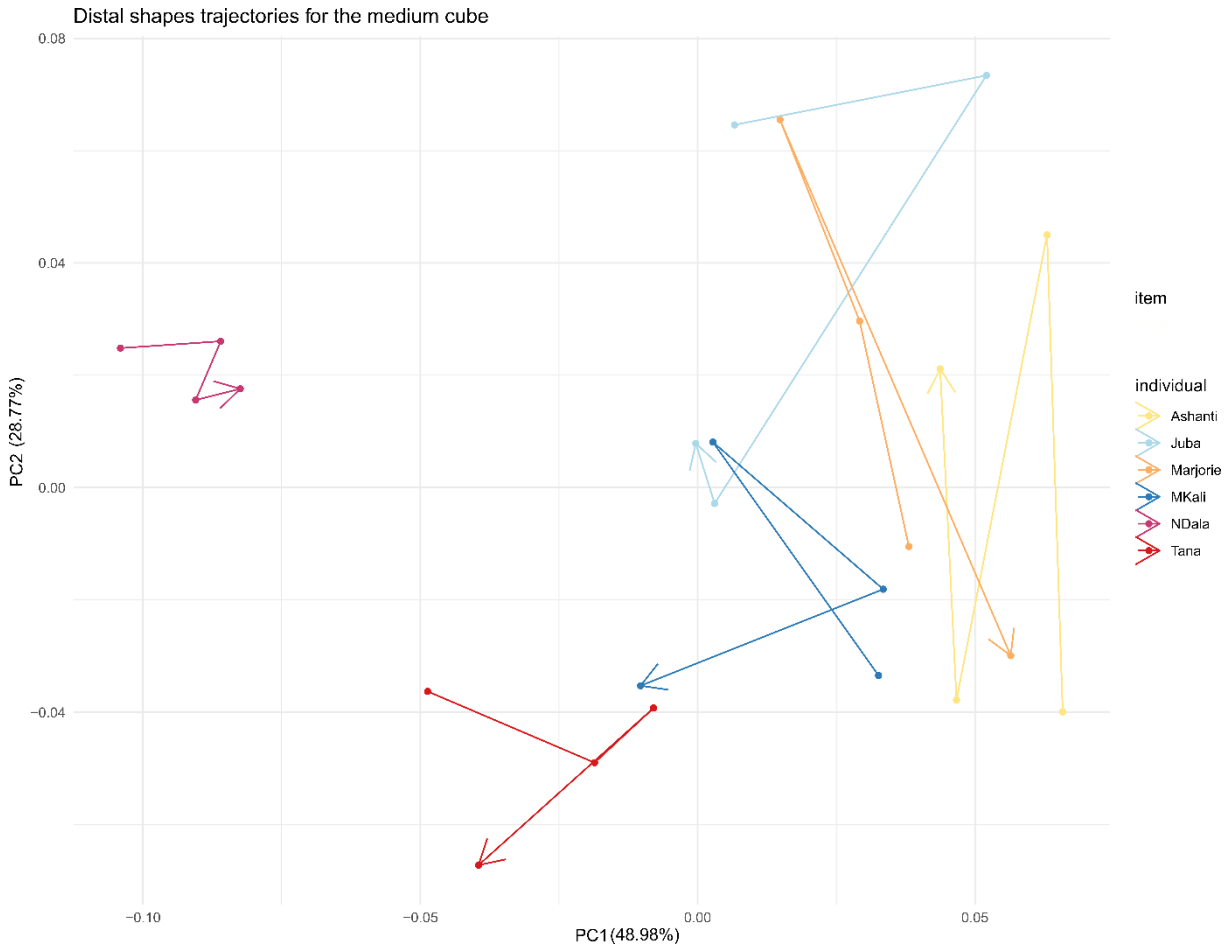


Figure 4.7 – Distal shapes trajectories of all the individuals when grasping a medium cube.

Discussion

We found that elephants preshaped their trunk tip in reach-to-grasp movements toward food items according to the characteristics of the different food items. Preshaping varied between individuals, which each had a unique distal trunk shape, but was not linked to grasping success.

Individual differences

As shown by our results, all the elephants in our study had a unique trunk tip shape. Similar results are found in the human literature: individual and interpopulation variation in human hand shapes are well documented (Králík et al., 2014) and have a real impact on hand utilisation and related abilities. For example, some sports modify and intensify these individual differences in hand shape, which confers an advantage for certain hand shapes in these disciplines (Barut et al., 2008; Fallahi & Jadidian, 2011). Thus, we assume the same applies to elephants: different trunk tip shapes may lead to different reach and grasping skills in individuals. These individual differences may influence (and predict) individual grasping performances.

Trunk tip shapes and object characteristics

We highlighted a significant effect of food item properties on the trunk tip preshape of three out of the six elephants. M'Kali, Juba and Marjorie adjusted the shape of their trunk tip according to the object properties, consistent with findings of preshaping in the hands or paws of other species (Chieffi & Gentilucci, 1993; Christel & Fragaszy, 2000; Roy et al., 2000; Sacrey et al., 2009; Sartori et al., 2013). These elephants also showed similar distal trunk preshapes for almost all the types of food items in our experiment; the preshapes matched the shape of the food and its difficulty to grasp. This adaptation of trunk tip shape may allow individuals to grasp more efficiently. Comparable results are found in studies on hand or paw preshaping according to object properties (Christel, 1993; Pouydebat et al., 2011). In animals such as primates, preshaping sometimes provides more appropriate and optimal grasping (Christel, 1993; Pellegrino et al., 1989; Pouydebat et al., 2009; Supuk et al., 2005).

Interestingly, preshaping of the trunk tip according to the object properties does not occur in all elephants, as half of our sample did not show any trunk tip shape adaptation. Although the preshaping of hands or paws is found in many primates and rats (Napier, 1993; Sacrey & Whishaw, 2012), it is not always widespread in all subjects. Preshaping can result from individual differences in hand, paw or trunk tip morphology but may also be the result of individual variability in motor control.

Moreover, the group of elephants that did not preshape their trunk according to the food item properties included the blind elephant. According to Jeannerod, preshaping is controlled by visuomotor channels and, more precisely, by visual data of the object shape (Jeannerod, 1981, 1988). Weir, (1994) corroborated this idea. In humans, a grasping movement without visual feedback will have an increased hand aperture (Sacrey & Whishaw, 2012; Tipper et al., 2006; Uno et al., 1993; Winges et al., 2003). Although Santello and collaborators (2002) showed that continuous visual

feedback from the object or the hand is not necessary for adequate preshaping, a degree of visual input remains essential. Some primates and other animals cannot preshape their hands or paws because of vision impairments (Uno et al., 1993; Tipper et al., 2006; Winges et al., 2003). This may be the case for the blind elephant, N'Dala, which did not exhibit trunk tip preshaping in accordance with the properties of the object grasped. To verify this hypothesis, the experiment could be redone with entirely blind grasping tests for all subjects. However, like the other elephants, N'Dala still managed to grasp all the food items. These results confirm the idea that vision, one of elephants' less-used senses (O'Connell-Rodwell, 2007; Plotnik et al., 2013; Poole & Granli, 2011), is not necessary for grasping food items with the trunk.

The subadult elephant, Ashanti, also did not exhibit trunk tip preshaping according to the properties of the food item. This may be due to her relatively young age and interactions with other elephants; in some species young and subadult individuals do not exhibit preshaping or use adult grasping techniques (Butterworth & Itakura, 1998; Forssberg et al., 1991; Le Brazidec et al., 2017; Pouydebat et al., 2011). Thus, preshaping of the trunk tip according to the object properties may result from learning.

Grasping success

We did not find a link between the trunk tip shape just before a grasp and the number of failures before a successful grasp. Moreover, unlike what we hypothesised and what is found in other species (Christel, 1993; Supuk et al., 2005), preshaping the trunk tip did not increase grasping success. Therefore, trunk tip preshaping may not confer a selective advantage in terms of reducing the number of failures before a successful grasp for these elephants.

Although grasping is logically more efficient with large and thick food items, all the studied elephants improved in grasping efficiency over time, each with different objects. This result suggests that each individual developed, over the trials, her own grasping strategies to increase grasping success. This individuality of grasping success for individual-object pairs might indicate taste preferences. Individuals may be motivated to improve grasping success for foods that they prefer and may be less motivated when they find the food less appealing. These differences in grasping success can also be explained by the constraints of the experiment: we could not control the posture of the elephant in front of the box or the position of the head relative to the bars. The elephants may have experienced different visual obstructions while grasping the food items; however, N'Dala, the blind elephant, did not have significantly lower grasping success than two of the elephants that preshaped

their trunk tip according to the object properties (Marjorie and Juba). Thus, vision may have little importance to grasping success of specific objects by individuals. As olfaction is essential in elephant life (Plotnik et al., 2013, 2019; Polla et al., 2018), we assume that elephant trunk grasping success depends more on olfaction than on vision.

Finally, in contrast to our hypothesis, individuals' distal trunk shapes did not converge when grasping the same object. Although the three individuals who preshaped their trunk tip according to the object properties tended to have the same general shape when grasping the same type of object (more oval or more rounded), over time, they did not develop similar grasping shapes. This was also true for the three other elephants. In the studied elephants, there was no general convergence of trunk tip shape over time to optimise grasping success.

Conclusion

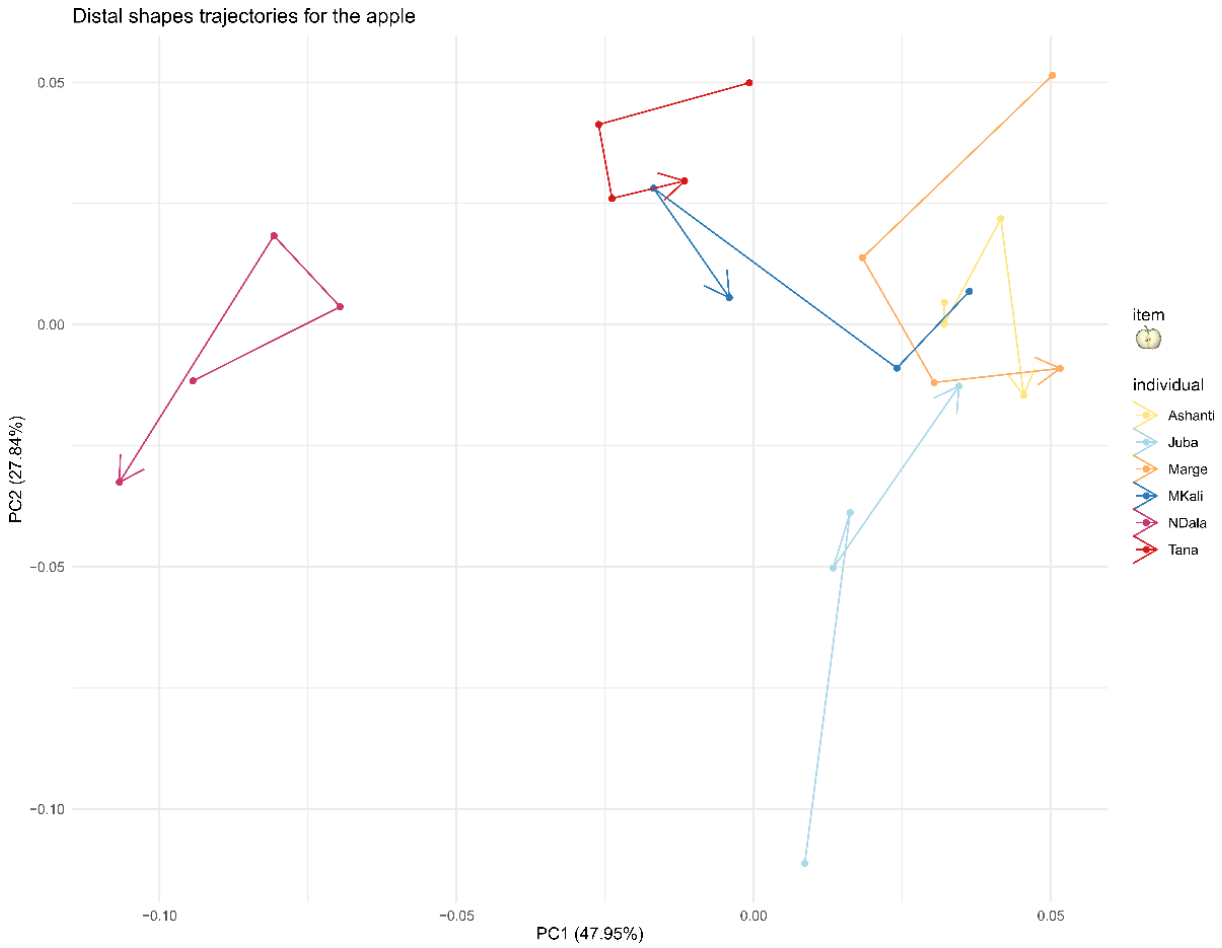
To conclude, our results indicate that three out of the six studied African savannah elephants adjusted their distal trunk shape to that of the object. Preshaping varied depending on the individual, each of whom had a unique distal trunk shape. This study is the first time that preshaping has been demonstrated with a muscular hydrostat, in other words, with a grasping appendage that has no joints. Grasping techniques can be similar even if the grasping appendage operates in a completely different way. We found that the blind elephant could grasp but did not optimally preshape its trunk. This finding reveals that elephant trunk grasping success may depend more on olfaction than on vision, but preshaping during reach-to-grasp movements is probably, as in other species, mostly controlled by visuomotor channels. Moreover, as the blind elephant had a similar increase in success grasping objects as the other elephants, we assumed that grasping success did not depend only on vision. Preshaping may also result from learning, as one of the other elephants that did not exhibit optimal preshaping was a subadult. The third elephant in this group, Tana, did not show an optimal preshaping. This may be due to her life's history, such as experience or learning during development. It would be interesting to investigate further, perhaps by conducting a developmental preshaping study. However, preshaping of the trunk tip did not increase grasping success and thus may not confer a selective advantage in these elephants. We observed increases in grasping success that differed according to objects and individuals, probably influenced by learning and food taste preferences.

Finally, our study was based on a sample of six African savannah elephants. It would be interesting to increase the sample size and to carry out a similar study in Asian elephants, which have only one finger on their trunk, to understand preshaping strategies in elephants more broadly.

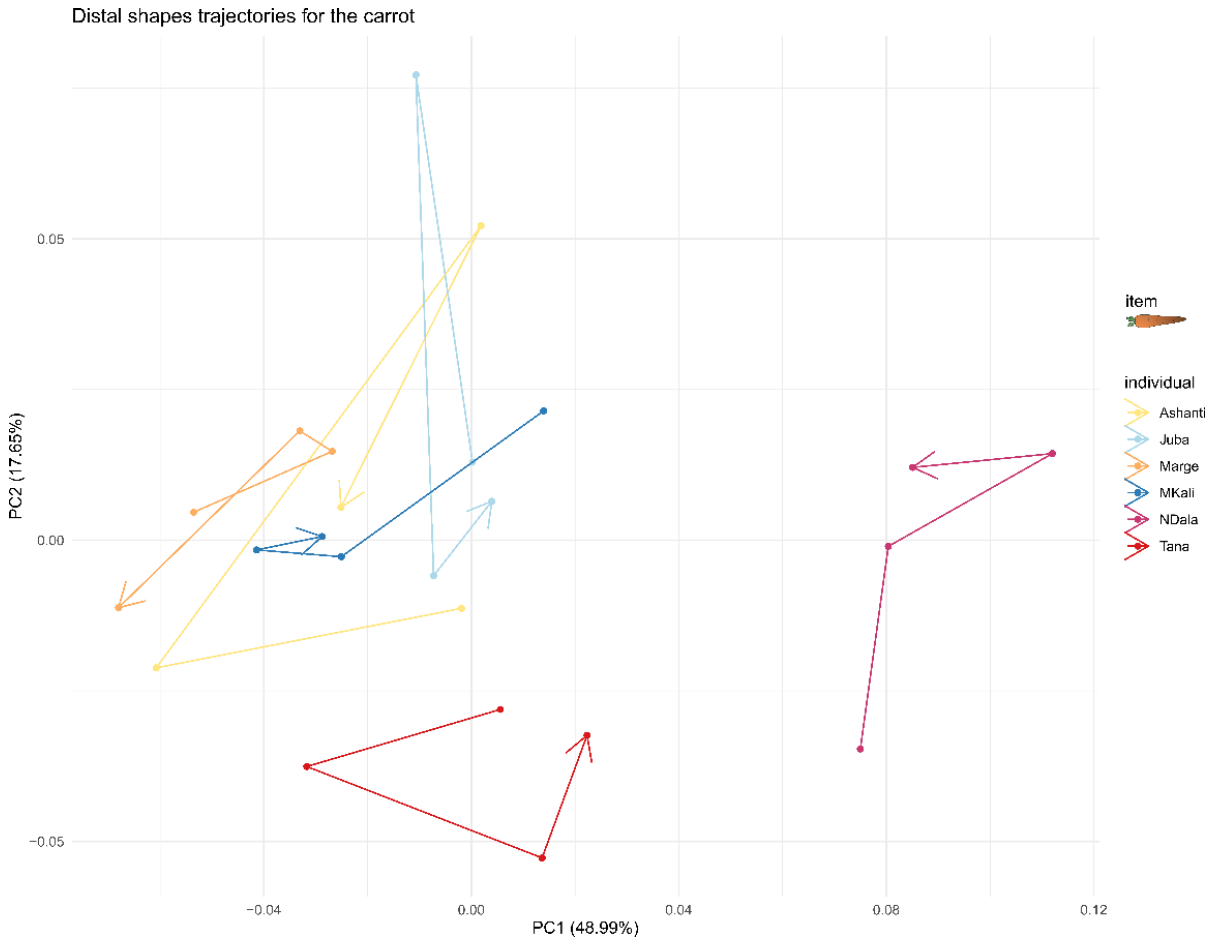
Appendices

DOI: 10.7717/peerj.13108/supp-1

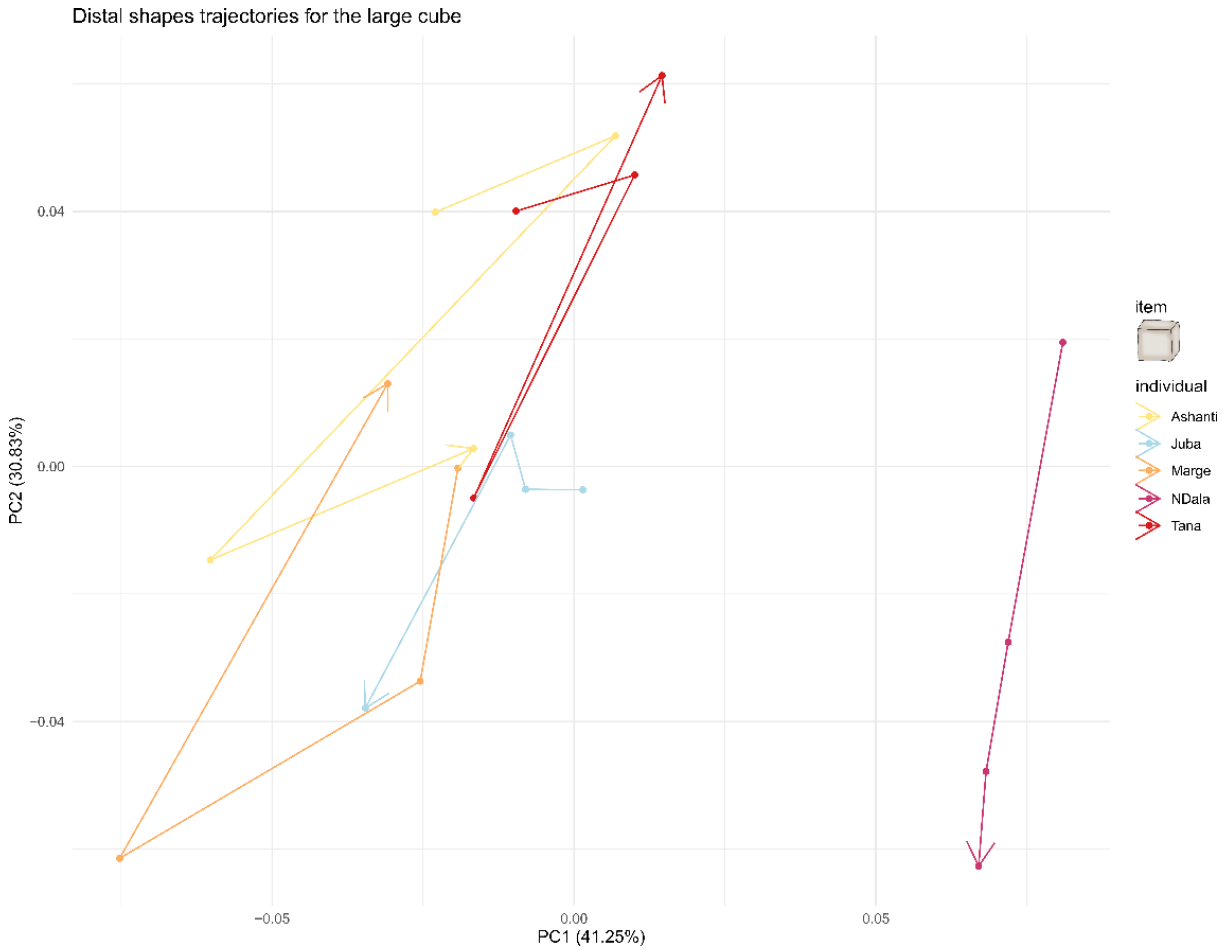
Appendix 4.1 – Experimental design video visualisation (hyperlink). Example film of grasping behaviour obtain during the experiment, including a visualisation of the landmark and semilandmarks hanging on the trunk tip.



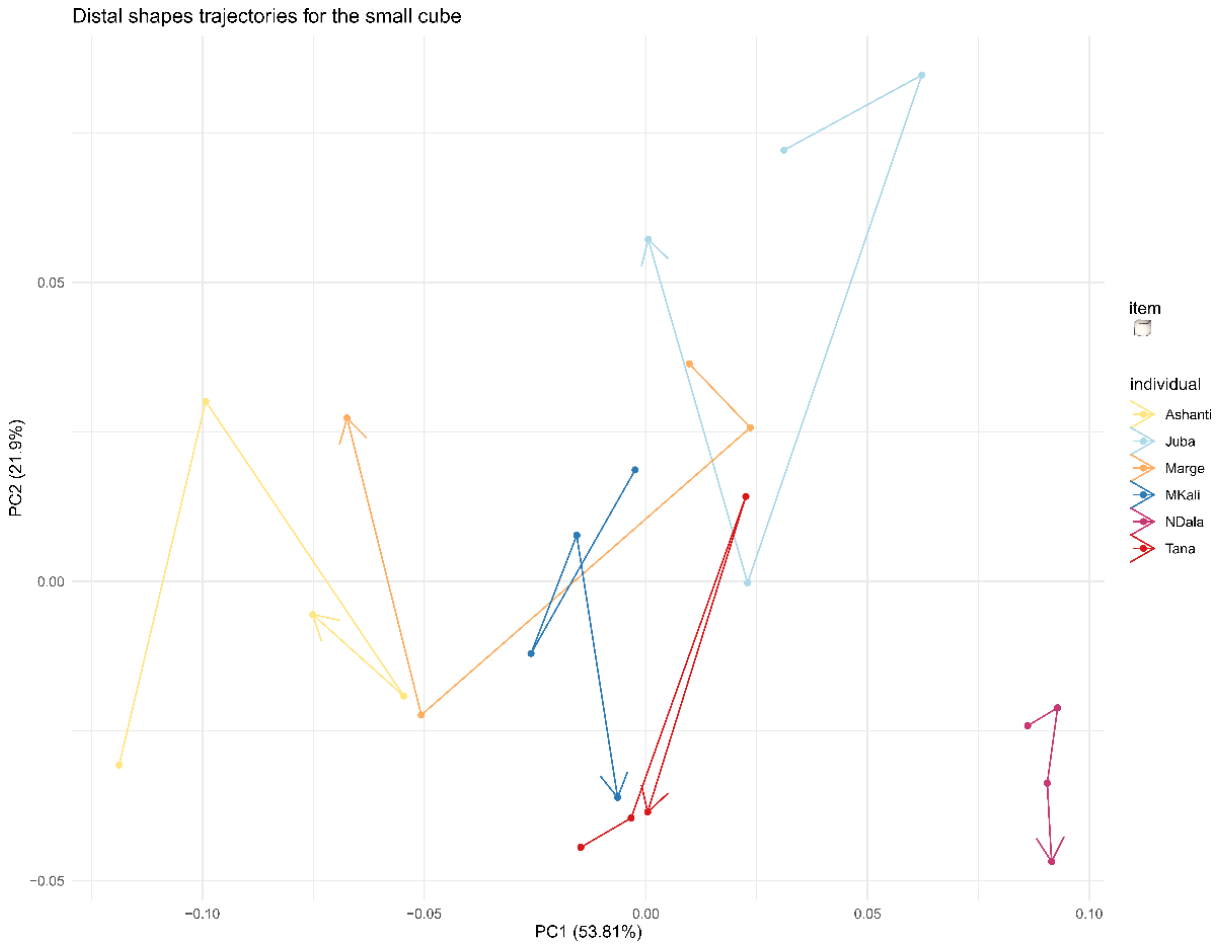
Appendix 4.2 – Distal shape trajectories for the apple. Supplementary figure linked with Figure 7.



Appendix 4.3 – Distal shape trajectories for the carrot. Supplementary figure linked with Figure 7.



Appendix 4.4 – Distal shape trajectories for the large cube. Supplementary figure linked with Figure 7.



Appendix 4.5 – Distal shape trajectories for the small cube. Supplementary figure linked with Figure 7.

Chapter 4 summary

Title: The relationship between distal trunk morphology and object grasping in the African savannah elephant (*Loxodonta africana*)

Background: During reach-to-grasp movements, the human hand is preshaped depending on the properties of the object. Preshaping may result from learning, morphology, or motor control variability and can confer a selective advantage on that individual or species. This preshaping ability is known in several mammals (i.e. primates, carnivores and rodents). However, apart from the tongue preshaping of lizards and chameleons, little is known about preshaping of grasping appendages other than hands and paws. In particular, the elephant trunk, a muscular hydrostat, has impressive grasping skills and thus is commonly called a hand. Data on elephant trunk grasping techniques are scarce, and nothing is known about whether elephants preshape their trunk tip according to the properties of their food.

Methods: To determine the influence of food sizes and shapes on the form of the trunk tip, we investigated the morphology of the distal part of the trunk during grasping movements. The influence of food item form on trunk tip shape was quantified in six female African savannah elephants (*Loxodonta africana*). Three food item types were presented to the elephants (elongated, flat, and cubic), as well as three different sizes of cubic items. A total of 107 ± 10 grips per individual were video recorded, and the related trunk tip shapes were recorded with a 2D geometric morphometric approach.

Results and discussion: Half of the individuals adjusted the shape of the distal part of their trunk according to the object type. Of the three elephants that did not preshape their trunk tip, one was blind and another was subadult. Therefore, we found that elephants preshaped their trunk tip, similar to the preshaping of other species' hands or paws during reach-to-grasp movements. This preshaping may be influenced by visual feedback and individual learning.

General discussion

General discussion

In this thesis, we attempted to address the lack of knowledge on trunk uses and adaptations, and to further explored grasping and manipulation abilities of this muscular hydrostat. The main questions we tried to answer were: 1. When grasping and manipulating with the trunk, what are the main techniques used? 2. Do these techniques vary according to the individual and its sex, age and morphology? 3. Are these techniques linked to habitat? To do so, we combined ethology and functional morphology to characterise trunk grasping and manipulation techniques and the related individual and environmental variation. We quantified trunk use and found that, near water, elephant sex was linked to elephant activity, but not to time spent using the trunk. Main trunk grasping and manipulation techniques were characterised and we highlighted that they could be linked to the task, the item grasped, the social environment, the individual and its tusk profile, the population and the habitat. Finally, we revealed individual techniques of trunk tip preshaping during pinch grasping. This last discussion section of the dissertation aims to connect all these results to the original main questions and the related stakes.

When grasping and manipulating with the trunk, what are the main techniques used?

Trunk uses

To define the main techniques used during grasping and manipulation movements with the trunk, we firstly needed to describe and quantify trunk uses as a whole. Chapter 1 focused on it, as we characterised and quantified the trunk uses near waterholes and rivers (Kruger National Park, South Africa). We highlighted that, in the study context, the elephants used their trunk almost 60% of their time, and especially in drinking, exploring, feeding and self-directed behaviour. This is the first time that trunk uses in the wild are directly specified and quantified. Nevertheless, these results have to be considered in the water context. Although the time spend near water is an essential moment for the elephants (Thaker et al., 2019), the Kruger

elephants spend a majority of their day at relative distance from water (Abraham et al., 2021; de Knegt et al., 2011; Tehou et al., 2019; Thaker et al., 2019). Thus, it is essential for further studies to quantify trunk uses in the Kruger elephants also at distance from water. Moreover, elephant activities differ between water and non-water areas, particularly drinking and feeding activities, as elephants spend most of their daily time foraging at relative distance from water (Soltis et al., 2016; Tehou et al., 2019; Wyatt & Eltringham, 1974). Therefore, we presume that trunk use duration is different in the two environments. Indeed, we observed that if both drinking and feeding activities almost always involve the trunk, feeding activity is more performed in non-water area (68 to 75%, Wyatt & Eltringham, 1974; Soltis et al., 2016) than drinking in water area (37% of their time near water, Chapter 1 of this dissertation thesis). Moreover, the social behaviour probably vary a lot between the two environments, as the water areas are related to more group reunions (Palmer, 2018) and more various playing behaviour (Lee & Moss, 2014). Thus, we suppose that the trunk is used even more in a non-water context. A study has to be realised on the same population to explore this hypothesis.

Furthermore, these trunk use duration near water may also differ in an opposing habitat. In arid regions, challenges are higher for elephants because water and food may become scarcer resources during the dry season (Wato et al., 2016). The elephants' foraging behaviour and social interactions are affected (O'Connell-Rodwell et al., 2020; Thornley et al., 2020), and water seeking becomes an essential stage in the elephant's day-to-day life. Therefore, elephant activities and behaviour may differ greatly between habitats, and so their trunk use may be different as well. For example, with water as a limited resource, the elephants cannot immerse themselves in water as grooming behaviour and have to use their trunk to squirt water on their body. The grown males also do not have access to deep water to diversify their play, with behaviour such as swimming and mounting (Lee & Moss, 2014; Webber & Lee, 2020), behaviour that do not involve the trunk. They are thus more engaging in play behaviour that involve the trunk, such as sparring (Chiyo et al., 2011). We can therefore hypothesise that in arid habitat, the trunk is more used than in a habitat with consistent water presence, like the Kruger. We characterised and quantified the use of the trunk in Chapter 1, but to understand the effect of the water presence on these uses, we needed to collect similar data in an arid habitat. Exploring trunk uses duration with respect to habitat was also intended to open the debate on trunk adaptations.

Main trunk grasping and manipulation techniques

In Chapters 2 and 3, we defined the techniques used by elephants during their main feeding grasps. The technique features of food grasping to eat directly, grasping to bundle, grasping to clean and bundle manipulation are detailed in Chapters 2 and 3, in elephants from Kruger Park and Etosha Park. The techniques differed between these grasps and according to the type of object grasped. We also revealed in Chapter 4 a specific grasping technique. Like hands in other species, the elephant trunk can preshape when performing a precise pinch to feed. This preshaping seems to be linked to visual feedback, as it is for other species that do not preshape when there is no visual feedback (Jeannerod, 1981, 1988; Tipper et al., 2006; Uno et al., 1993; Weir, 1994; Winges et al., 2003). Indeed, we compared the preshaping in sighted and blinded elephants to assess the importance of visual input for grasping behaviour. On the contrary of several of its relatives, the blind elephant did not preshape its trunk in accordance with the properties of the object grasped. However, we highlighted that the vision of the elephant is not essential for grasping with the trunk as this blind elephant still performed all the grasping in Chapter 4 experiments. This is concordant with the results of O'Connell-Rodwell (2007), Poole and Granli (2011) and Plotnik and collaborators (2013) that revealed that vision is not the most use sense of elephants.

With this detailed characterisation of the main foraging grasping techniques, we highlighted how the grasps were displayed to, likely, optimise the grasp. Indeed, we revealed, in Chapters 2 and 3, the core combinations of the grasping type (pinch, wrap, torsion) with the side of the grasp (left, right or face), the grasping specific strategy (such as the help of the foot) and the trunk parts involved in the grasp. As the observed grasping follow these different combinations, i.e. the techniques, these grasping are then organised. The foraging grasps are time-consuming tasks during feeding (Nair, 1989). Organise the grasp certainly reduces its duration and increase its movements coordination, and thus lead to more efficient feeding, essential for a large mammal that requires a large amount of food each day (Owen-Smith & Chafota, 2012). Moreover, we revealed that these grasping techniques vary with the object grasped and the grasping task. Elephants likely grasp differently depending on what they are plain to do with the item just after grasping it, like several primates (Pouydebat et al., 2006). The different techniques are therefore certainly optimised for the different objects and tasks. Similar patterns were highlighted in primates: the use of technique for grasping generally provides more optimal grasp (Christel, 1993; Christel et al., 1998; Pouydebat et al., 2009; Spinozzi et al., 2004). In Chapter 4 we also revealed that the preshaping grasping technique probably lead to a more efficient grasp. Indeed, we showed that the preshape of the trunk matched the shape of the food and its difficulty

to grasp. In primates, the preshaping sometimes enable a more appropriate grasp, and we can presume that this is similar for elephants (Christel, 1993; Pellegrino et al., 1989; Pouydebat et al., 2009; Supuk et al., 2005). Therefore, the use of these techniques for grasping food certainly reveal in elephants a tendency toward an optimal grip (Bruineberg & Rietveld, 2014). Such optimisation could be an advantage that improves the animal physical conditions, as it feeds itself with more efficiency.

Thereby, this work provides new information on the elephant trunk uses as evolutionary advantage, and, in the broad, add new information on grasping abilities evolution in tetrapods. Indeed, the research displayed in the Biological Journal of the Linnean Society special issue 3 (2019, volume 127: issue 3; Pouydebat & Bardo, 2019) highlighted the importance of exploring grasping in non-primate tetrapods to understand the complex adaptations. As in most primates the manipulative appendage is also used for locomotion, we are mostly unable to distinguish locomotor and manipulative morphological traits (Pouydebat & Bardo, 2019). Since elephant trunks are not involved in locomotion, they are good models to explore the specific grasping/manipulative morphological traits. The manipulative data we collected on elephants can therefore be compared to similar data in primates, to help to distinguish in these species which morphological traits result of manipulation and which are related to locomotion. There is still a long way of research in understanding the evolution of food/object grasping and manipulation in tetrapods. Thus, carry on the studies on elephant trunk grasping and manipulation abilities, but also on other muscular hydrostats and grasping appendages other than the hand, is a significant way to assist in the apprehension of these grasping evolution issues.

Moreover, such grasping optimisation usually leads to precise and specific movements, and thus the realisation of complex tasks (Christel et al., 1998; Spinozzi et al., 2004). In this thesis dissertation, we explored particularly three complex tasks: the precise pinch grasping in Chapter 4 and the bundling grasp in Chapters 2 and 3 with the cleaning grasp in Chapter 2, which require specific movements to prepare the manipulations to come. Understanding how the elephant trunk can optimise grasping and how it can perform these complex tasks is new in the field of grasping research. Most previous research on this question focuses on primate hands (Christel et al., 1998; Spinozzi et al., 2004), on other animal hands (Mendyk & Horn, 2011; Metz & Whishaw, 2000; Whishaw, 1996) and on chameleon tongues (Herrel et al., 2000). Yet, muscular hydrostat grasping and manipulation optimisation is a rising research question, as bio inspired soft robotic is expanding (Cianchetti et al., 2015; Coyle et al., 2018; Manti et al., 2015). Only a few studies recently highlighted several behaviour (Lefeuvre et al., 2020) and biomechanical features of optimised trunk grasps: elementary movement sequences, joint formation, suction, asymmetric stretch, inward

curvature of the trunk tip (Dagenais et al., 2021; Schulz et al., 2021, 2022; Wu et al., 2018). The work we provided in this thesis supplied new information directly in keeping with these previous studies. Indeed, we highlighted how the elephants in natural conditions optimise their main feeding grasps, by revealing the techniques used. These technique precisions can be implemented in the trunk-like soft robotic arms to optimise the efficiency of their grasps. To go further on this robotic grasping optimisation, the elephant optimal performances in terms of grasping and manipulation have to be explored. Indeed, many questions remain open on elephant trunk grasping optimisation. For example, the strength of the trunk tip during pinch grasp is an essential feature to understand, to inspire soft robotic arms. Extend the knowledge for the realisation of bio inspired soft robotic arms from the elephant trunk is essential. Indeed, these new technologies can have many direct applications without the rigid structure constraint of the traditional robots (Xiloyannis et al., 2021).

Do these techniques vary according to the individual and its sex, age and morphology?

The techniques defined in Chapters 2, 3 and 4 were demonstrated to vary with the grasping type and object. There is not a unique technique for trunk grasping and manipulation, but a variety depending on several factors. In Chapters 1, 2 and 4, we highlighted that these techniques vary greatly among individuals.

Trunk uses individual variations

We specified in Chapter 1 several individual trunk-related variations in elephants. Before focusing on grasping and manipulation movements, we explored the trunk uses individual variations in general. We showed how the activities that may involve the trunk and the trunk uses in these activities vary with the sex of the individuals. We concentrated particularly on the variations between the sexes because, in diverse species, the use of the prehensile appendages is intricately linked to the sex of the animal. In chimpanzees, humans and rats, the sex does have an influence on the grasping and manipulation techniques display (Dempsey & Ayoub, 1996; Field & Whishaw, 2005; Hopkins et al., 2009; Koops et al., 2015; Tan et al., 1991). As these sex effects are striking in species with strong sexual dimorphism and segregation (Doran, 1993; Rose, 1994; Ruckstuhl & Neuhaus, 2002), we hypothesised that these sex effects

in elephants are also important, and we therefore explored it. Indeed, male and female elephants live under sexual segregation (Buss & Smith, 1966; de Silva & Wittemyer, 2012; Poole, 1994; Stoeger & Baotic, 2016) and have different head shape, body size and shapes and tusk profiles (Owen-Smith, 1988; Moss, 1996). We highlighted that there are sex variations in the activities that may involve the trunk near water. These variations are probably due to the grown female family constraints, since they live with calves and are therefore more water dependent and more subject to disturbances and risks related to water areas (De Beer & Van Aarde, 2008; Loveridge, 2006; Stokke & du Toit 2002). Thus, the family herds including grown females go to water areas for shorter periods of time for drinking and grooming, whereas the grown males are more engaging in social play related to the water (Lee and Moss, 2014; Shannon et al., 2008; Stokke & Du Toit, 2002; Webber & Lee, 2020). However, we did not find any trunk uses duration differences between the sexes. The behaviour duration did vary with the sex of the elephant, but the sex effects on trunk uses duration generally seem to be more limited. However, the sex may still be linked with the trunk uses variations in terms of type of behaviour display in the activity. For example, when socialising in a water environment context, the grown males are more engaged in play interactions whereas the grown females are more engaging in bonding interactions (Lee & Moss, 2014; Poole & Granli, 2011; Webber & Lee, 2020). Therefore, we can hypothesise that the specific behaviour realised with the trunk during these social interactions also differ. To go further, we could widen this study of the trunk uses sex differences, by exploring the different behaviour display within the elephant activities.

Thus, this work increases the knowledge of behavioural differences and similarity between the sexes on a highly dimorphic species (Owen-Smith, 1988; Moss, 1996). As in zoos the male and female elephants are usually housing separately (Hartley et al., 2019), improving the information on their natural behaviour differences could help to understand their different needs and adapt their different enclosures consequently. Indeed, several studies helped to improve zoo animals living conditions by highlighting the different needs depending on the sex (Hartley et al., 2019; Liu et al., 2003). The previous results demonstrated the interest for zoos to provide male elephants with a deep-water hole, to let them perform the variety of play behaviour they usually display in natural and optimal conditions (Lee & Moss, 2014; Webber & Lee, 2020).

Although these differences between male and female elephants, the sex is not a major trunk uses individual variable, on the contrary of other species prehensile appendages, as describe above (Dempsey & Ayoub, 1996; Field & Whishaw, 2005; Hopkins et al., 2009; Koops et al., 2015; Tan et al., 1991). However, other individual

features do affect its uses more than the sex, particularly its grasping and manipulation movements.

Individual variations in trunk grasping and manipulation techniques

Lefeuvre and collaborators (2020) highlighted a high inter-individual variability of trunk uses for the main feeding behaviour in elephants. In this thesis dissertation, we explored further this variability in natural conditions and with a different characterisation of the trunk techniques. Indeed, we revealed that the main foraging grasp and manipulation techniques and the specific preshaping of the trunk tip technique are highly related to the individuals. Specifically, the preshaping technique was performed with different shapes depending on the individual, and not every individual performed it. These results are consistent with the literature on other species with grasping appendages. Previous research shows inter-individual variations in techniques with hand use in bonobos (Bardo et al., 2016), capuchins (Byrne & Suomi, 1996), orangutans and humans (Bardo et al., 2017), and on the pecking movement in pigeons (Siemann & Delius, 1992). However, this is the first study to describe these individual trunk uses techniques in wild elephants. Similar to the previous part of this dissertation, this work adds knowledge on grasping and manipulation evolutionary questions, with an individual variation focus.

Thus, these individual variations in behavioural and functional techniques may be explained by learning. Racine already suggested in 1980 that the individual variations in behaviour he observed in African savannah and Asian elephants can be explained by learning skills and practising. Indeed, elephants have much to learn, but they are highly social mammals with extended parental care, high social learning opportunities with the allomothering system and slow reproduction (Hedwig et al., 2021; Lee, 1987). Therefore the young elephants have access to a uniquely long learning period to develop and improve their trunk skills, which develop gradually with age (Revathe et al., 2020) and can be practising all along the elephant life. However, the only difference in trunk techniques we found between calves and older elephants concern the lateralisation of the trunk, and this is certainly related directly to the individual, as the lateralisation is developed very early in elephants (Giljov et al., 2018; Keerthipriya et al., 2015; Revathe et al., 2020). Nevertheless, the differences in the techniques we found per individual and probably per herd are consistent with the learning hypothesis. Similar hypotheses were suggested for other species with individual-level variability in grasping and manipulation techniques and abilities (pigeons: Siemann & Delius, 1992, humans: Cutts & Bollen, 1993, bonobos: Bardo et al., 2016). Indeed, we presumed that the slice-with-foot strategy we observed during

bundling grasp task was performed only by the members of a herd, as well as the break and strip strategies during eating grasp task for another herd. Therefore, we hypothesise that some techniques features are inherent to herds, as a result of transmission throughout the herds. Besides learning, the individual intrinsic preferences may explain the different grasping and manipulation techniques. Particularly for the preshaping technique we showed in Chapter 4, we suggested that its uses are not only dependent on the elephant learning, but also on its food taste preferences. Next studies should focus on testing these hypotheses to increase the understanding of these individual variation in links with the transmission of the trunk techniques. Specifically, we could run a study on the techniques variations between different herds from the same population, but also from diverse populations to investigate the population effect in learning.

Moreover, we highlighted in the different chapters that grasping techniques can be directly related to the inherent morphology of the individual. Indeed, during grasp to eat directly, the grasping way differs with the tusk profile of the Kruger elephants: only the elephants that had their right tusk likely small, directed toward the trunk and high, performed a left side grasping. We presumed that this tusk profile certainly obstructs trunk movements toward the right. Thus, diverse tusk profiles can have an effect on the trunk uses for grasping, especially the tusk size and orientation, as they may obstruct several movements. This effect of tusk morphology on the grasping techniques was not highlighted in the Etosha elephants as their tusks were much smaller and breaks. Moreover, in Chapter 4, we revealed that the inherent morphology of the individual also probably affected the preshaping technique. Indeed, the trunk tip preshaping technique may differ with the individual as we revealed that each individual has a unique trunk tip shape. The different morphologies are therefore a strong assumption to explain the individual preferences in techniques. Racine (1980) also suggests the impact of morphology in individual elephant behaviour. Thus, this work shows new insights into the morphological features correlated with behavioural and functional grasping and manipulation abilities of the elephant trunk. To our knowledge, although elephant tusks were much studied (Campbell-Staton et al., 2021; Elder, 1970; Kurt et al., 1995; Whyte & Hall-Martin, 2018), this is the first study to characterise a link between the use of the trunk and the tusks morphology. It opens new concerns about how the tusks are specifically used in foraging techniques. As an example, tusk laterality when used for feeding could be explored in relation to the foraging trunk laterality (Giljov et al., 2018; Keerthipriya et al., 2015; Lefeuvre et al., 2021; Revathe et al., 2020). We could also explore the differences in tusk uses depending on their sizes. Tusks are fundamental in elephant lives as they are used for foraging, water seeking and social interactions (Bielert et al., 2018; Racine, 1980; Whyte & Hall-Martin, 2018). With this highlighting of the relation between tusks

morphology and the grasping and manipulation techniques, we added value to this essential role of the tusks. Yet, elephant tusks tend to shorten and disappear with the poaching pressure (genetic variable, Campbell-Staton et al., 2021; Kurt et al., 1995). Preserve the elephants with great tusks is then even more important for the preservation of the diversity of the elephant's morphologies, behaviour and techniques. Moreover, this new observation reveals the importance for further studies to consider the tusks when examined the trunk abilities, especially if the elephants display a large variety of tusks profiles like the Kruger elephants.

Are these techniques linked to habitat?

To continue with grasping and manipulation evolutionary questions, we explored in Chapter 3 the link between the techniques, populations and habitats. We highlighted that, for similar task and grasp object, the techniques are different within the elephant population of the study site from the Kruger National Park (South Africa) that live in gallery forests and the elephant population of the study site from the Etosha National Park (Namibia) that live in an arid environment. In particular, we found that for the most common feeding task, the grasp to eat directly, the Etosha elephants preferred the pinch whereas the Kruger elephants preferred the wrap. However, the techniques in both populations vary too with the object and the task. Several studies demonstrated that behavioural variability at population-level is common in elephants and in vertebrates in general (Cronin et al., 2014; Johnston & Fenton, 2001; Srinivasaiah et al., 2012; Sueur et al., 2011). It was proposed that these behavioural population-level variations are a result of population-level social learning and traditions, population genetics and local environmental conditions (Cronin et al., 2014; Gaechter et al., 2010; Lamba & Mace, 2011; Langergraber et al., 2011). The grasping and manipulation movements, as they are directly related to the animal behaviour, can therefore be affected by these population-level variations. Thus, our findings on elephant population-level grasping and manipulation techniques are in agreement with the literature. This new information could open up the debate specifically about the effects elephant morphology and habitats on the trunk techniques.

Indeed, we presume that elephant morphology differences per population have an effect on the trunk techniques. We noted that the tusks profiles in the two populations we examined were drastically different in terms of size, breaking and curvature, certainly due to their unalike habitats. In the arid habitat of the Etosha

study site, we supposed that high fluoride ingestion levels related to the aridity lead to crumbly and small tusks, on the contrary of the Kruger elephants (Auer, 1997; Raubenheimer, 1999; Raubenheimer et al., 1998; Steenkamp et al., 2007; Whyte & Hall-Martin, 2018). Yet, we previously introduced the importance of the tusks in the grasping and manipulation techniques, especially the tusks sizes and orientations as they may obstruct several trunk movements. With their crumbly and small tusks, the Etosha elephants grasping and manipulation techniques seem to have not been affected by their tusks profiles, on the contrary of several Kruger elephants with their large tusk size and orientation profiles. Thereby, these differences in tusk profiles in the two populations, in relation to their habitats, may explain these population-level variations in trunk techniques. We can extend Chapter 3 study to explore this hypothesis, by enlarging the number of elephant populations studied in relation to the fluoride concentration in their habitats. Many studies highlighted the morphology and performances induced by ecological context in a large variety of species (Luger et al., 2020; Tulli et al., 2011). In particular, the adaptive significance of grasping with the habitat was highlighted in tetrapods (Nyakatura, 2019; Toussaint et al., 2013). We know that trunk uses are directly related to the elephant environment (foraging, manipulation of objects from the environment, interaction with congeners depending on the resources availability). Therefore, the habitats and especially the food availability certainly have a direct and strong effect on the techniques used by the elephants with their trunk depending on their population. With current climate change leading to greater aridification of elephant habitats, it could be assumed that elephants living in wetter environments such as Kruger elephants would have to use more the Etosha elephants grasping behaviours, in order to adapt to these changes. Indeed, understanding how elephants adapt to different environments lead to understanding how they might adapt to rapid environmental change linked to climate change. However, it seems essential to explore further this potential habitat-related pattern of techniques, starting with the link between the techniques used and the resource availability (how elephants can or cannot adapt their techniques to the resources access). Indeed, access to resources is actually a striking issue in elephant management.

Furthermore, Campbell-Staton and collaborators demonstrated in 2021 that poaching elephants for their tusks leads to an increase of tuskless elephants in the poached populations. As our results showed a link between tusks and trunk, it would be interesting to see how the loss of tusks in these populations might affect their use of the trunk.

Finally, we presumed that the social learning in elephants is also related to the trunk techniques within a population. As explained before, young elephants have access to a long social learning period to develop and improve their trunk skills, skills that are then practised all along the elephant life (Hedwig et al., 2021; Nair, 1989). Particularly, if trunk motor control takes a year to mature, the foraging behaviour and related trunk use take more time to be perfectly controlled (Revathe et al., 2020). After three-month-olds, the calve elephants start to display adult-like feeding patterns, but the feeding efficiency is still not reached by one year old and take more practising time, especially concerning the food item diversity (Nair 1989; Revathe et al., 2020). This learning is essential for the development of elephant grasping and manipulative skills, and can differ with the population. Indeed, the elephants in the two populations probably have different life history, habitats and traditions that have an effect on their learning and practice of feeding grasping and manipulation. Regarding the life history and habitat, Kruger and Etosha elephant populations differ in their survival rates, with low juvenile survival in the Etosha population (Shrader et al., 2010). These survival rates are directly impacted by the high annual rainfall in Kruger and low annual rainfall in Etosha that have an effect on the food availability, combined with the presence of fences around the two parks that restrict the elephant migrations (Shrader et al., 2010). Thus, these differences in life history, directly related to the two population food availability differences, probably affect the learning and practising of food grasping and manipulative skills. We can hypothesise therefore a learning effect at population-level on trunk grasping and manipulation techniques, directly related to the food availability and the elephant survival. These learning differences at population-level may also be linked with different populations traditions, as Whiten (2021) demonstrated that foraging techniques in animals are affected by traditions. However, to test the learning effect on trunk grasping and manipulation techniques, in relation to the food availability, survival rates and traditions of the two populations, it appears essential to firstly characterise the behaviour, and particularly the social learning differences between the two elephant populations.

General conclusion

General conclusion

In this thesis, we characterised the main feeding grasp techniques used by the trunk of African savannah elephants, including the trunk tip preshaping technique. We highlighted that these techniques vary with a panel of factors, including the population, the habitat, the individual and its tusks morphology.

This work is the first to quantify trunk uses in the wild. It also shed light on the functioning of optimal foraging grasp with the trunk, which probably improve the animal physical conditions. We developed afterward on the individual and population levels of the trunk grasping and manipulation techniques. We hypothesised the links of habitat and inherent morphology with the techniques on both levels, and we draw attention on the importance to consider the tusks when exploring elephant trunk abilities. The following work will be to develop on the use of the tusks in the grasping techniques.

Thus, this work adds fairly more knowledge on trunk uses adaptations and evolution. This thesis is a promising example of the use of an interdisciplinary approach to address evolutionary questions. Yet, to truly comprehend the evolution of grasping and manipulation in tetrapods, and as most studies in the field were realised in captivity, more research have to be carried out in natural conditions. Carry on the studies on elephant trunk grasping and manipulation abilities could then contribute to the distinction of the manipulation morphological traits and locomotion morphological traits of tetrapod prehensile appendages. As we highlighted that individuals have unique distal trunk shapes that preshape differently, the work planned for the continuity of this thesis will focus on inter-individual trunk tip strength in relation to the inherent morphology. Besides, to bring new information on the morphology and habitat effects, it appears important to develop the same interdisciplinary approach on the two other elephant species trunk uses.

Moreover, extant some part of this thesis work can have direct applications for zoo elephant well-being, the soft robotic field and wild elephant preservation. Indeed, develop on the trunk uses sex differences may assist the improvement of zoo elephant enclosures. Likewise, the new information we brought on elephant trunk grasping abilities and further studies on trunk optimal performances can open bio-inspired project in the soft robotic field. Finally, investigate the effect of the habitat on elephant trunk uses will help to understand how elephants may adapt to rapid changing environments.

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Brief abstract

The trunk is a fundamental organ for the elephants that can perform both powerful and delicate functions. However, its evolution remains an enigma. To address the adaptations of this prehensile organ, we can study extant proboscideans, whose populations vary in terms of behaviour and habitats. To understand specifically the links between ecology, form and function during trunk grasping and manipulation behaviour in extant African savannah elephants, we explored with an interdisciplinary approach the variability of these behaviour between individuals and populations. The results obtained enable us to apprehend the effects of learning, habitat and morphology on elephant grasping and manipulation. Furthermore, this work perspectives are to approach how elephants adapt to rapid environmental changes to help with the great challenge of their conservation, but also to obtain data useful for the design of new bio-inspired robotic arms, flexible, powerful and precise like elephant trunks.

Court résumé

La trompe est un organe fondamental pour les éléphants, capable d'accomplir des fonctions puissantes et délicates. Cependant, on sait peu de choses sur cet organe préhensile et son évolution. Pour appréhender ses adaptations, il est possible d'étudier les Proboscidés actuels. L'enjeu de cette thèse est donc de comprendre spécifiquement quels sont les liens existants entre le milieu, la variabilité morpho-fonctionnelle et la variabilité comportementale associés à la trompe, lors de mouvements de saisie et manipulation. Avec une approche pluridisciplinaire, nous avons exploré, chez les éléphants de savane d'Afrique, la variabilité de ces saisies et manipulations entre individus et entre populations. Les résultats obtenus permettent d'en apprendre davantage sur l'utilisation et les adaptations de la trompe des éléphants, et notamment les effets de l'apprentissage, de l'environnement et de la morphologie sur ces utilisations. Ce travail pourra alors avoir des applications directes en robotique avec un transfert de données pour la conception de bras robotiques bio-inspirés, mais aussi en conservation des éléphants en comprenant mieux comment ils s'adaptent aux changements rapides d'environnement.