

Title

Protection service of a leading silverback male from external threats in wild western gorillas

Running head: Male protection services in wild western gorillas

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Abstract

Primate males normally protect reproductive females, genetic offspring, and other relatives from external threats. Nevertheless, male protection of group members other than the above individuals is widely reported. Here, we show qualitative data on a silverback's charging behaviors toward human observers (predator surrogates) to protect group members having various age–sex and kinship traits in a group of wild western gorillas containing one reproductive male. We observed 106 and 33 charging behaviors by the leading silverback in two separate study periods. Two natal infants were often involved in his protective charging. Further, the silverback provided protection services to reproductive females. Surprisingly, immigrant individuals (i.e., unrelated to the silverback), including a wide range of age–sex classes, were also protected multiple times. His protection services for natal infants and adult females can be interpreted as a form of parenting effort and mating effort, respectively. Further, those for some immigrant immatures accompanied by their mothers can be considered part of mating effort, advertising his quality as a mate to the mothers. Finally, his charging behaviors to protect immigrant young males, who could be reproductive threats to him, may be due to group augmentation benefits. That is, the recruitment of additional males in exchange

36 for protection services would improve the ability of group defense. Protection services
37 of the leading silverback in the one-male group of western gorillas, in which members
38 of various age–sex classes and kinship traits coexist, could be interpreted by some
39 existing functional explanations.

40

41 **Keywords**

42 charging behavior; group augmentation; habituation; mating effort; partner choice;
43 parenting effort; protection; western gorilla

Introduction

Male protection services against predation are widespread phenomena in primate taxa (van Schaik et al. 2022). Anti-predator behaviors, especially mobbing and counterattacking, are costly and risky since they may result in injury or even death (Caro 2005). Therefore, males are usually expected to favor providing such services to individuals who have direct fitness benefits for them, such as reproductive females, genetic offspring, and other relatives. On the other hand, however, it is not uncommon for primate males to protect group members other than the above individuals. So far, alternative explanations to interpret such male behaviors have been proposed, such as direct reciprocity, reputation-based partner choice, and group augmentation (reviewed by van Schaik et al. 2022).

In the genus *Gorilla*, a one-male polygynous group is prevalent, especially in populations of western gorillas (*Gorilla gorilla*: Robbins and Robbins 2018). Groups are led by a sole reproductive mature male (referred to as a silverback), who is double the size of the females. Such a leading silverback is thought to be responsible for protecting his group members (Harcourt and Stewart 2007; Robbins and Robbins 2018). Silverbacks that appear to be able to provide better protection from external threats are

able to sustain a group with many females (Breuer et al. 2010). A leading silverback can monopolize mating with these females and can have a high paternity certainty for immatures born in their group (Bradley et al. 2004; Inoue et al. 2013). Thus, providing protection services for group females and immatures from external threats brings fitness benefits to the leading silverback. However, many previous studies have implied that, in multiple populations of western gorillas, there are one-male groups in which a leading silverback and some group members (other than adult females) are unrelated to each other (Stokes et al. 2003; Robbins et al. 2004; Douadi et al. 2007; Arandjelovic et al. 2010; 2014; Hagemann et al. 2018; Forcina et al. 2019; Masi et al. 2021). This type of gorilla group provides a unique and significant opportunity to investigate the functional explanations of male protection services toward group members other than reproductive females and genetic offspring.

The main external threats to wild western gorillas are expected to be infanticidal males (Manguette et al. 2020) and predator leopards (Klailova et al. 2012). However, it is not a straightforward task to obtain quantitative data on a silverback's protection services from these natural threats. As an alternative, behavioral responses to humans could be a valid measure (Isbell 1994). In gorilla groups, a leading silverback rushes toward human observers while barking (henceforth: charging behavior) to protect

his group members (e.g., Schaller 1963). In the process of habituating wild gorillas, such hostile behaviors by silverbacks toward researchers are inevitable (Blom et al. 2004; Doran-Sheehy et al. 2007; Ando et al. 2008; Klailova et al. 2010; Robbins 2020). Taking advantage of this by-product of the process of group habituation, researchers can obtain additional data on male protection services by considering human observers as surrogates for a predator. In this paper, we provide qualitative data on a silverback's charging behaviors toward human observers, focusing on a one-male group of wild western gorillas during its habituation.

We chose our subject group due to its suitability for performing this research, according to two aspects. First, there were many individuals having various age–sex classes and kinship traits, such as related and unrelated individuals to the leading silverback from infants to young males, in the same group due to prior group disintegrations. Second, within this group, the leading silverback was less habituated than many other group members because of a lack of habituation experience (see Materials and methods for details). The latter condition enabled us to investigate the silverback's charging behavior without serious interruptions to the group's daily life. We investigated which group members were protected by the silverback, focusing on their kinship with the silverback, age–sex class, and the presence or absence of the mother.

Based on this information, we discuss a possible functional explanation for the protection services of the western gorilla silverback.

Materials and methods

Study site

Our field survey was conducted in Moukalaba-Doudou National Park, Gabon. A small village is located outside the park across a large river. The local villagers traditionally do not hunt gorillas. However, they say that gorillas were hunted during active selective logging, which began in 1962. In 1988, the logging company left Moukalaba after the Gabonese government prohibited hunting and collecting wildlife in 1986. No poaching of gorillas has been recorded since that time. Moukalaba was then designated a National Park in 2002 (Ando et al. 2008). Long-term socioecological studies of wild western gorillas by group habituation began in 2001. A more detailed description of this area is provided by Takenoshita and Yamagiwa (2008) and Takenoshita et al. (2008).

Study subjects

In this study, we followed the age classification from Breuer et al. (2009):

infants (0–4 years), juveniles (4–7.5 years), subadults (7.5–11 years for males, 7.5–10 years for females), adult females (>10 years), blackback males (11–14 years), young silverback males (14–18 years), and silverback males (>18 years old).

The study subject was a one-male group of wild western gorillas called the Nidai Group (Table 1). This group originally consisted of five individuals: one leading silverback (*Nidai*), two adult females (*Ngou* and *Randa*), and two infants (*Prince* and *Ranguisa*). We identified this group for the first time in March 2018 while monitoring the disintegration of our previous subject group (the Gentil Group). After its disintegration, the remaining 11 members immigrated into the Nidai Group, including two adult females (*Kojiwa* and *Ovono*), one young silverback (*Manbu*), three blackbacks (*Bengos*, *Sanji*, and *Dodo*), two subadults (*Douta* and *Intsi*), one juvenile (*Mituty*), and two infants (*Obnetu* and *Kotama*). In addition, another neighboring, semi-habituated one-male group (the Martial Group) was presumed to have disintegrated. Then, the remaining four members immigrated into the Nidai Group, including one adult female (*Maria*), one subadult (*Okame*), one juvenile (*Tsulime*), and

one infant (*Matase*). Temporal information on their immigration is provided in Table 1, though we lacked detailed monitoring data between May and August 2018. At least, it is certain that all of the above individuals had moved into the Nidai Group by September 2018. Consequently, at the beginning of this study in September 2018, the Nidai Group consisted of 20 individuals (Table 1). The details of this immigration process will be described in Takenoshita et al. *in prep* and Tamura et al. *in prep*.

The above-mentioned mass immigration produced an intriguing situation in the Nidai Group. First, two natal infants and 12 immigrant individuals, from infant to young silverbacks, co-resided in the same group. Genetic analysis found that the two natal infants were sired by *Nidai*, and all immigrants were sired by the leading silverback of the disintegrated groups, that is, they were unrelated to *Nidai* (Inoue et al. 2013; Tamura et al. *in prep*, Table 1). In addition, in the group, there were two types of adult females: the resident females and the immigrant females.

Second, *Nidai*'s level of habituation was much lower than that of the other group members (Table 1). He had no experience of habituation before his first contact with humans from our research team in March 2018. Therefore, he sometimes showed hostile responses, such as barking and charging, to human observers. On the other hand, all immigrants from the Gentil Group were already well-habituated because they had

experienced more than 10 years of habituation or since their neonatal period in the Gentil Group, in which the habituation was conducted from 2003 to 2016. In addition, two resident adult females of the Nidai Group (*Ngou* and *Randa*) and an immigrant adult female from the disintegrated Martial Group (*Maria*) were also previous members of the Gentil Group and had habituation experiences there (*Randa*: from 2005 and 2014; *Ngou* and *Maria*: from 2003 and 2008). Therefore, *Randa* acted fearlessly in the presence of humans, and the others did not show a strong aversion to humans, although they occasionally barked at us. Further, two natal infants (*Prince* and *Ranguisa*) and three immigrant immatures from the Martial Group (*Okame*, *Tsulime*, and *Matase*) did not show much fear of human presence despite their lack of habituation. Under these conditions, *Nidai* showed hostile responses to humans but never fled, likely because the other full- or semi-habituated members remained nearby humans without showing strong fear. In other words, in the Nidai Group, the leading silverback disliked the presence of humans, but the other members cared little about it.

Behavioral observations

We began collecting data on *Nidai*'s charging behaviors toward human

observers in September 2018, six months after his habituation began in March 2018. The data collection was conducted during two separate periods: September 2018–February 2019 and July–December 2019 (hereafter, 2018 and 2019). We entered the forest at 07:30 h every morning with two to four field assistants to find the Nidai Group. Once the group was found, we normally conducted group follows until 15:00 h, 17:00 h, or the loss of the group location. Furthermore, when *Nidai*'s negative reactions toward human observers were excessive, we stopped the group follow for that day.

We defined charging behaviors as follows: the silverback lunges while emitting barks up to several meters in front of the human observers. Further, as a result of his charge, if he interposes himself between the humans and a member of the group who was closest to the observers immediately before his lunging action, we considered the individual interposed by *Nidai* the “protected individual” (Fig. 1). We recorded the name of protected individuals using ad libitum sampling whenever *Nidai* exhibited charging behaviors at human observers.

Results

In 2018, the leading silverback, *Nidai*, performed 106 charging behaviors over

the course of 601.5 h of observations over 97 days (Table 2). In 65 of these charges, a protected individual was involved in his charges. The protected individuals included a wide range of age–sex classes, encompassing natal infants, immigrants from infants to blackbacks, and resident and immigrant adult females. In 21 of these charges, a natal infant (*Prince* and *Ranguisa*) was protected, and in all but one case, the mother was accompanying the protected infant. Immigrant individuals were also protected in nine cases, including one infant female (*Kotama*), one infant male (*Obnetu*), one subadult female (*Intsi*), two subadult males (*Douata* and *Okame*), and two blackbacks (*Dodo* and *Bengos*). In two of these cases, the mother was accompanying the protected immigrant infant (the cases of *Kotama–Kojiwa* pairs; Table 1). One resident female (*Ngou*) and one immigrant female (*Ovono*), who were not with their infant, were protected 17 and 4 times, respectively. The resident female, *Ngou*, was involved in *Nidai*’s protection services more times than the others because her barking at human observers often triggered his charging.

In 2019, we recorded 33 cases of *Nidai*’s charging behaviors, less than one-third of 2018, in spite of an increase in total observation time (743.7 hours over 115 days). In all but one case, a protected individual was involved in his charges (Table 3). *Nidai* showed his protection service 11 times for the natal infants. In seven of these

cases, the natal infants were away from their mothers. He also protected an immigrant infant female once (*Kotama*). In addition, his protection services were toward three immigrant juvenile males (*Obnetu*, *Matase*, and *Mituty*), one immigrant juvenile female (*Tsulime*), one immigrant subadult female (*Intsi*), and one immigrant male subadult (*Okame*). In all cases except for the *Matase–Maria* pair on two occasions, the protected immigrant individuals were away from their mothers at the moment of *Nidai*'s charges. Blackbacks and young silverbacks were not involved in any charges in 2019. One resident female (*Ngou*) and two immigrant females (*Ovono* and *Maria*), who were not with their offspring, were also protected by *Nidai*.

Discussion

The number of *Nidai*'s charging behaviors drastically decreased from 2018 to 2019. This change may be mainly owing to his increasing habituation. Further, in 2018, he showed charging behaviors without a protected individual in 41 cases. Thus, his charging behaviors can be considered in part of a general aversion towards human presence. On the other hand, however, in 2019, all but one of his charging behaviors (32 cases) included a protected individual. Further, in some cases, immediately after

charging behaviors, *Nidai* put a protected infant under his body, glaring at the human, and then *Nidai* and the infant moved away together (Tamura, *personal observations*). Thus, we thought that *Nidai*'s charging behaviors could be attributed not only to his simple aggressive intentions toward humans but also to his protective intentions toward the members of his group.

For both periods, the two natal infants were often involved in *Nidai*'s protection services. In 2019, in particular, we observed charging behaviors that protected the natal infant away from the mother; thus, his charges can be interpreted as direct actions to protect offspring. Defending vulnerable immatures against external threats is a key role for primate males, including gorilla silverbacks (van Schaik and Paul 1996; Harcourt and Stewart 2007; Fernandez-Duque et al. 2009; Rosenbaum and Silk 2022). Males usually engage in this type of protection only toward immatures with high paternity certainty, as a form of paternal care (Busse and Hamilton 1981; Anderson 1992; Borries et al. 1999). Consistently, genetic paternity between *Nidai* and the natal infants was confirmed by our analyses (Tamura et al. *in prep*). Therefore, protection services for the natal immatures can be attributed to his parenting efforts, which brought fitness benefits to him.

For both periods, adult females became the protected individuals of *Nidai*'s

charging behaviors. Adult female gorillas rely on silverbacks for protection from predators and other males (Stokes et al. 2003; Robbins et al. 2013; Manguette et al. 2020). The reproductive success of a silverback should depend on the acquisition and retention of reproductive females and providing protection to them from external threats (Breuer et al. 2010; 2012). Thus, leading silverbacks may need to provide protection services for adult females to enhance future reproductive success, i.e., mating efforts. The same explanation can be applied to the protection services provided to the immigrant juvenile (*Tsulime*) and subadult (*Intsi*) females as they are potential future mating partners. In fact, we observed *Nidai* mating with *Intsi* in December 2018 (Tamura, *personal observation*).

It should be noted that *Nidai* showed charging behaviors for protecting a wide range of immigrant individuals. Because they immigrated into the Nidai Group after their birth, *Nidai* did not have paternity certainty for them. In the classical conception, the costly and risky protection services are normally directed toward related offspring, which was seen in Hanuman langurs (*Semnopithecus entellus*) and baboons (*Papio* spp.) (Busse and Hamilton 1981; Anderson 1992; Palombit et al. 1997; Borries et al. 1999). *Nidai*'s behaviors cannot be explained by this conception. On the other hand, the latest review article showed many cases of male protection of probable unrelated immatures

for various primates (van Schaik et al. 2022). The authors indicated that reputation-based partner choice could explain such male behaviors: by performing protection services, males advertise their quality as mates to reproductive females (van Schaik et al. 2022). In gorilla societies, it is hypothesized that males' protective ability influences female mate choice (Caillaud et al. 2008; Breuer et al. 2012). In the case of this study, some immigrant individuals entered the Nidai Group with their mothers (i.e., *Kotama*, *Obnetu*, *Matase*, *Intsi*, *Douta*, and *Sanji*). Thus, *Nidai* might provide costly and risky protection services to them in order to advertise his quality to their mothers. In other words, his protection services toward the immigrant individuals are considered part of his mating efforts, ultimately bringing reproductive success to him.

This explanation may not be sufficient to interpret all of *Nidai's* protection services. Reputation-based partner choice assumes the presence of reproductive females as an important third party who would evaluate a male's quality (van Schaik et al. 2022). Nevertheless, he provided protection services to immigrant individuals whose mothers were not in the group at all, such as a juvenile male, *Mituty*. Further, he showed charging behaviors to protect even two blackbacks (*Bengos* and *Dodo*), who can be reproductive threats to him (Robbins et al. 2004). We presumed group augmentation benefits (van Schaik et al. 2022) to underlie such silverback's protection services toward

these individuals. This idea assumes that male protection may yield a variety of inherent benefits to the protectors; increasing the number of survivors in a group due to protection (i.e., group size augmentation) will provide anti-predation benefits by a greater dilution of risk, improved vigilance, and early detection of predators. In addition, survivors may be able to contribute more to group defense during agonistic encounters against neighboring groups and solitary males. In our case, considering the small size of the Nidai Group before the mass immigration (one silverback, two adult females, and two infants), retaining immigrants within his group may be beneficial. A previous study of western gorillas showed that a larger number of resident subordinate males (subadults and blackbacks) are less likely to be involved in an intergroup encounter (Cooksey et al. 2020). Likewise, the immigrant males of the Nidai Group may deter outsider males. Further, coalitionary attacks of a dominant silverback and subordinate males against an outsider male have been reported in mountain gorillas (*G. beringei beringei*; Mirville et al. 2018; Rosenbaum et al. 2016). Subordinate males in western gorilla groups may also become combatants when encounters develop into physical aggressions. Indeed, there was one case where an immigrant blackback (*Bengos*) faced a solitary silverback approaching the group on the front lines with *Nidai* (Tamura, *personal observation*). The group augmentation may be effective in avoiding encounters with outsider males,

especially in Moukalaba, where gorilla density is relatively high (Takenoshita and Yamagiwa 2008). In other words, the recruitment of additional males in exchange for protection services will bring fitness benefits to the leading silverback.

Protection services of the leading silverback in the one-male group of western gorillas in which members of various age–sex and kinship traits coexist, could be interpreted by some existing functional explanations. Future studies of male protective behaviors in different group situations and in response to natural threats will lead to a comprehensive understanding of male protection services in primates.

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Statements

Statement of Ethics

We adhered to the Code of Best Practices for Field Primatology of the International Primatological Society and the Ethical Guidelines for Field Research on Primates of the Primate Society of Japan. This code requires researchers to consider the influence of the presence of human observers and habituation on study animals and make their best efforts to minimize stress on the research subject. We have always respected these statements, and we have never intentionally provoked charges by the

subject silverback at any point in the study period. All data were collected from the behavioral responses of the subject gorillas that occurred while the researchers were doing their best to avoid stressing them. This study complied with the laws of the Gabonese Republic. Research permission was obtained from the Centre National de la Recherche Scientifique et Technologique (permission nos. AR0036/17, AR0041/18, AR0050/19) and the Agence Nationale des Parcs Nationaux (permission no. AE17020) in Gabon.

Conflict of Interest Statement

The authors declare no conflict of interest.

Author Contributions Statement

The first draft of the manuscript was prepared by MT and all authors revised the manuscript. All authors contributed the field observations and MT mainly gathered the data. EFA contributed to the overall field management.

Data Availability Statement

The data that support the findings of this study are available from the

corresponding author upon reasonable request.

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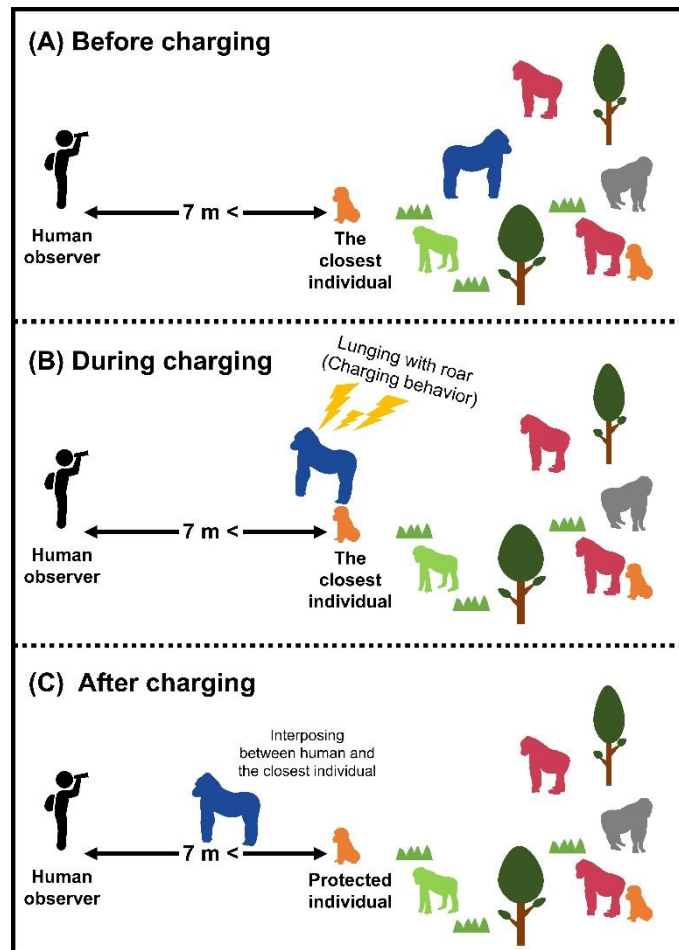
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472 **Figure legend**



473 *Figure 1*

474 Example of a scene of the silverback's charging behavior involving a protected
 475 individual: (A) a human observer watches the subject group, and an infant (orange
 476 silhouette) is the closest individual to the observer; (B) the silverback finds the human
 477 standing close to the infant and lunges with roars (charging behavior) toward the
 478 human; (C) the silverback interposes himself between the human and the closest infant,
 479 where the infant is the protected individual for this charging behavior.

1 Tables

2

Table 1 Membership of the Nidai Group and their traits.

ID	Age class	Sex ^a	Kinship with <i>Nidai</i> ^b	Mother ^{b, c}	Time of immigration ^d	Habituation experience
The original members of the group						
<i>Nidai</i>	SB	male	–	–		Mar. 2018–
<i>Ngou</i>	AF	female	–	–		2003–2008/Mar. 2018–
<i>Randa</i>	AF (13–14*)	female	–	–		2005–2014/Mar. 2018–
<i>Prince</i>	IF (3–4*)	male	related	<i>Ngou</i>		Mar. 2018–
<i>Ranguisa</i>	IF (1–2*)	female	related	<i>Randa</i>		Mar. 2018–
The immigrant members of the group						
<i>Kojiwa</i>	AF	female	–	–	May–August 2018	2003–
<i>Ovono</i>	AF	female	–	–	May–August 2018	2003–
<i>Maria</i>	AF	female	–	–	May–August 2018	2003–2008/Mar. 2018–
<i>Manbu</i>	YS (15–16*)	male	unrelated	–	March 2018	2003–
<i>Bengos</i>	BB (13–14*)	male	unrelated	–	March 2018	Birth–
<i>Dodo</i>	BB (13–14*)	male	unrelated	<i>Ngou</i>	March 2018	Birth–
<i>Sanji</i>	BB (12–13*)	male	unrelated	<i>Kojiwa</i>	May–August 2018	Birth–
<i>Douta</i>	SA (8–9)	male	unrelated	<i>Ovono</i>	May–August 2018	Birth–
<i>Okame</i>	SA (8–9*)	male	unrelated	<i>Ngou</i>	May–August 2018	Mar. 2018–
<i>Intsi</i>	SA (7–8)	female	unrelated	<i>Kojiwa</i>	May–August 2018	Birth–
<i>Mituty</i>	JV (6–7)	male	unrelated	–	March 2018	Birth–
<i>Tsulime</i>	JV (5–6*)	female	unrelated	–	May–August 2018	Mar. 2018–
<i>Matase</i>	IF–JV (4–5*)	male	unrelated	<i>Maria</i>	May–August 2018	Mar. 2018–
<i>Obnetu</i>	IF–JV (4–5*)	male	unrelated	<i>Ovono</i>	May–August 2018	Birth–
<i>Kotama</i>	IF (2–3)	female	unrelated	<i>Kojiwa</i>	May–August 2018	Birth–

Numbers in parentheses and abbreviations indicate individual ages and age classes in 2018–2019, respectively.

Abbreviations and symbols: SB, silverback; AF, adult female; YS, young silverback; BB, blackback; SA, subadult; JV, juvenile; IF, infant; asterisk, estimated age.

^a The sex of group members (other than the silverback and adult females) was determined by amplification of the X–Y homologous amelogenin gene.

^b The genetic paternity and maternity is confirmed by Inoue et al. (2013) and Tamura et al. *in prep.*

^c Only mothers who were present in the Nidai Group appear in the Table.

^d The detailed monitoring information between May and August 2018 is unavailable.

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Table 2 The number of *Nidai*'s charging behaviors and its protected individual in 2018 and 2019.

Protected individual	2018	2019
Natal infant		
<i>Prince</i> (m/IF)	1	4
<i>Prince</i> + <i>Ngou</i> (m/IF+MO)	10	3
<i>Ranguisa</i> (f/IF)	0	3
<i>Ranguisa</i> + <i>Randa</i> (f/IF+MO)	10	1
Immigrant individual		
<i>Bengos</i> (BB)	1	0
<i>Dodo</i> (BB)	1	0
<i>Douta</i> (m/SA)	1	0
<i>Okame</i> (m/SA)	1	2
<i>Intsi</i> (f/SA)	2	1
<i>Mituty</i> (m/JV)	0	1
<i>Tsulime</i> (f/JV)	0	2
<i>Matase</i> (m/IF–JV) ^a	0	1
<i>Matase</i> + <i>Maria</i> (m/IF–JV+MO) ^a	0	2
<i>Obnetu</i> (m/IF–JV) ^a	1	4
<i>Kotama</i> (f/IF)	0	1
<i>Kotama</i> + <i>Kojiwa</i> (f/IF+MO)	2	0
Adult female		
<i>Ngou</i> (AF)	17	4
<i>Ovono</i> (AF)	4	1
<i>Maria</i> (AF)	0	2
Individual unknown^b	14	0
No protected individual^c	41	1
Total	106	33

Abbreviations and symbols: IF, infant; JV, juvenile; SA, subadult; BB, blackback; AF, adult female; IF+MO, infant with mother; m/, male; f/, female.

^a The age-class of *Matase* and *Obnetu* changed from the infant in 2018 to the juvenile in 2019.

^b A protected individual was presented, but researchers could not identify it.

^c *Nidai*'s charging behaviors involving no protected individual.