Determinants of vocal usage in the genus *Chlorocebus*

Dissertation

for the award of the degree

"Doctor rerum naturalium" (Dr.rer.nat.)

of the Georg-August-Universität Göttingen

Within the doctoral program of Behavior and Cognition (BeCog)

of the Georg-August University School of Science (GAUSS)

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Göttingen, 2022

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Date of the oral examination:

6th December, 2022

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Summary

The vocal communication of non-human primates has been the center of extensive research efforts that aimed to advance our understanding of the evolution of vocal communication and human speech. The alarm call system of the genus *Chlorocebus* has received particular attention after it was discovered that vervet monkeys (*C. pygerythrus*) produce distinct vocalizations in response to their major predators that appeared to designate the presence of particular threats, which was interpreted as a potential sign of semantic communication.

While the ensuing search for evolutionary precursors to the human language faculty in non-human primates has inspired a productive field of research, basic ethological questions concerned with the biological function of vocal signals that determines their structure and usage have received less attention. This thesis examines variation of vocal usage in the alarm call system of members of the genus *Chlorocebus* and aims to contribute to our understanding of the mechanisms that guide call usage and enable signals to exert their effects on receivers. Further it is examined what inter-individual variation in call usage can teach us about the potential function of vocal signals.

To investigate the mechanisms that guide predator type categorization and the production of specific alarm call types by signalers, an experiment was conducted with West African green monkeys (*C. sabaeus*) and South African vervet monkeys (*C. pygerythrus*). Monkeys were exposed to novel aerial and terrestrial threats, to test if alarm calling behavior is sensitive to positional cues and experience. While the experiment was not able to answer said question since vervet monkeys did not produce any calls in response to the presented stimuli, it demonstrates variation in call usage among different populations which may relate to species differences or population specific differences in anthropogenic disturbance and predation pressure.

To advance our understanding of the inter-individual variation in call usage, a 24-month observational study was conducted on vervet monkeys. The usage of “terrestrial threat barks” or “leopard alarms” by adult male vervet monkeys was quantified and analyzed with regard to male competitive ability, tenure, group specific variation in the degree of male-male competition and the impact of the mating season. Results indicate that high ranking males were more likely to produce barks than lower ranking individuals and that the mating season increases the daily frequency of observed barking events. The findings imply that call usage is gated by male competitive ability or motivation and suggests that barks may function as conventional or quality handicap signals indicating male motivation and potentially stamina. This finding and the frequent usage of barks in contexts other than land predator events show that context specificity in this call type has previously been overestimated and that barks may fulfill a dual function of alarm call and signal of individual quality.

In conclusion, vocal usage in the genus *Chlorocebus* shows considerable population specific and inter-individual variation. This implies that individual experience and social factors may play a central role in guiding individual vocal behavior. The variation in call usage further suggests that signals that have hitherto been primarily viewed as alarm calls may serve more than one function. Potential mechanisms that would render signals effective at exerting their effects on receivers are suggested. Finally, the potential selective forces shaping call structure and usage are discussed and an impact of natural and intra-sexual selection is proposed.

Zusammenfassung

Die akustische Kommunikation nicht-menschlicher Primaten steht im Mittelpunkt umfangreicher Forschungsbemühungen, die darauf abzielen, unser generelles Verständnis der Evolution akustischer Kommunikation und der menschlichen Sprache zu verbessern. Dem Alarmrufsystem der Gattung *Chlorocebus* wurde in diesem Zusammenhang besondere Aufmerksamkeit zuteil, nachdem entdeckt worden war, dass Grüne Meerkatzen (*C. pygerythrus*) in Gegenwart ihrer Hauptraubfeinde Warnrufe produzieren, die auf die Anwesenheit jener Raubtiere hinzuweisen schienen, was als mögliches Zeichen semantischer Kommunikation interpretiert wurde.

Obwohl die darauf folgende Suche nach evolutionären Vorläufern der menschlichen Sprache in nicht-menschlichen Primaten ein produktives Forschungsgebiet inspiriert hat, so haben doch grundlegende ethologische Fragen, die sich mit der biologischen Funktion von Signalen befassen, welche die Struktur und den Gebrauch von Lautmustern bestimmen, weniger Aufmerksamkeit erhalten. In dieser Arbeit wird die Variation des Gebrauchs von Lautmustern im Alarmrufsystem von Vertretern der Gattung *Chlorocebus* untersucht. Ziel ist es, einen Beitrag zum Verständnis jener Mechanismen zu leisten, die den Gebrauch von Rufen steuern und es den Signalen ermöglichen, ihre Wirkung auf die Empfänger auszuüben. Darüber hinaus wird untersucht, was die interindividuellen Unterschiede in der Verwendung von Rufen uns über die potenzielle Funktion von akustischen Signalen lehren können.

Um die Mechanismen zu untersuchen, die für die Kategorisierung von Raubtieren und die Produktion spezifischer Alarmrufe durch Sender verantwortlich sind, wurde ein Experiment durchgeführt, bei dem westafrikanische Grüne Meerkatzen (*C. sabaeus*) und südafrikanische Grüne Meerkatzen (*C. pygerythrus*) neuartigen Bedrohungen aus der Luft und auf dem Boden ausgesetzt wurden. Dies geschah um zu testen, ob das Alarmrufverhalten abhängig von der Position potentieller Bedrohungen und individueller Erfahrung ist. Das Experiment konnte diese Frage zwar nicht beantworten, da südafrikanische Grüne Meerkatzen keinerlei Warnrufe ausstießen, es zeigt jedoch, dass die Verwendung von Rufen in verschiedenen Populationen variiert, was mit Unterschieden zwischen den Arten oder populationsspezifischen anthropogenen Störungen und Raubfeinddichte zusammenhängen könnte.

Um unser Verständnis der interindividuellen Variationen bei der Verwendung von Rufen zu verbessern, wurde eine 24-monatige Beobachtungsstudie an Grünen Meerkatzen durchgeführt. Der Gebrauch von "terrestrischen Barks" oder "Leopard Warnrufen" durch erwachsene männliche Tiere wurde quantifiziert und analysiert im Hinblick auf die Konkurrenzfähigkeit der Männchen, die Präsenszeit in ihrer jeweiligen Gruppe, gruppenspezifische Variationen im Grad der Konkurrenz zwischen den Männchen und die Auswirkungen der Paarungszeit. Die Ergebnisse zeigen, dass Barks häufiger von ranghohen Männchen abgegeben werden als von rangniedrigeren Individuen und dass die Paarungszeit die tägliche Häufigkeit von Barks erhöht. Die Ergebnisse deuten darauf hin, dass die Verwendung von Rufen von der Konkurrenzfähigkeit oder Motivation der Männchen abhängt, und legen nahe, dass Barks als konventionelles oder qualitatives Handicap-Signal fungieren könnten, welche die Motivation oder die Ausdauer der Männchen anzeigen. Dieser Befund und die häufige Verwendung von Barks außerhalb von Landraubtierereignissen zeigen, dass die Kontextspezifität dieses Lautmuster bisher überschätzt wurde und dass Barks möglicherweise eine Doppelfunktion als Alarmruf und individuelles Qualitätssignal erfüllen.

Zusammenfassend lässt sich sagen, dass die Lautmusterverwendung innerhalb der Gattung *Chlorocebus* erhebliche populationsbezogene und interindividuelle Unterschiede aufweist. Dies deutet darauf hin, dass individuelle Erfahrungen und soziale Faktoren eine zentrale Rolle bei der

Steuerung des individuellen Rufverhaltens spielen könnten. Die Variation in der Verwendung von Rufen deutet außerdem darauf hin, dass Signale, die bisher in erster Linie als Alarmrufe angesehen wurden, mehr als nur eine Funktion haben könnten. Es werden potenzielle Mechanismen vorgeschlagen, die es den Signalen ermöglichen, ihre Wirkung auf die Empfänger effektiv auszuüben. Schließlich werden die potenziellen Selektionskräfte, die die Rufstruktur und Verwendung prägen, erörtert, und es wird ein Einfluss von natürlicher und sexueller Selektion vorgeschlagen.

Résumé

La communication vocale des primates non humains a fait l'objet de recherches approfondies visant à mieux comprendre l'évolution de la communication vocale et de la parole humaine. Le système d'appel d'alarme du genre *Chlorocebus* a fait l'objet d'une attention particulière après la découverte que les singes vervet (*C. pygerythrus*) produisent des vocalisations distinctes en réponse à leurs principaux prédateurs qui semblent désigner la présence de menaces particulières, ce qui a été interprété comme un signe potentiel de communication sémantique.

Alors que la recherche des précurseurs évolutifs de la faculté de langage humain chez les primates non humains a inspiré un champ de recherche productif, les questions éthologiques de base concernant la fonction biologique des signaux vocaux qui détermine leur structure et leur utilisation ont reçu moins d'attention. Cette thèse examine la variation de l'usage vocal dans le système d'appel d'alarme des membres du genre *Chlorocebus* et vise à contribuer à notre compréhension des mécanismes qui guident l'usage des appels et permettent aux signaux d'exercer leurs effets sur les receveurs. L'étude vise à contribuer à notre compréhension des mécanismes qui guident l'utilisation des cris et qui permettent aux signaux d'exercer leurs effets sur les receveurs.

Afin d'étudier les mécanismes qui guident la catégorisation des types de prédateurs et la production de types de cris d'alarme spécifiques par les émetteurs de signaux, une expérience a été menée avec des singes verts d'Afrique de l'Ouest (*C. sabaeus*) et des singes vervet d'Afrique du Sud (*C. pygerythrus*). Les singes ont été exposés à de nouvelles menaces aériennes et terrestres, afin de vérifier si le comportement d'appel d'alarme est sensible aux indices de position et à l'expérience. Bien que l'expérience n'ait pas permis de répondre à cette question puisque les singes vervets n'ont pas produit de cris en réponse aux stimuli présentés, elle démontre une variation dans l'utilisation des cris parmi différentes populations, ce qui peut être lié à des différences entre espèces ou à des différences spécifiques à une population en matière de perturbation anthropique et de pression de prédation.

Afin d'améliorer notre compréhension de la variation interindividuelle dans l'utilisation des cris, une étude d'observation de 24 mois a été menée sur des singes vervets. L'utilisation des " aboiements de menace terrestre " ou des " alarmes de léopard " par les singes vervet mâles adultes a été quantifiée et analysée en fonction de la capacité de compétition des mâles, de la tenure, de la variation spécifique au groupe du degré de compétition entre mâles et de l'impact de la saison de reproduction. Les résultats indiquent que les mâles de haut rang sont plus susceptibles de produire des aboiements que les individus de rang inférieur et que la saison de reproduction augmente la fréquence quotidienne des aboiements observés. Ces résultats impliquent que l'utilisation des aboiements est conditionnée par la capacité de compétition ou la motivation des mâles et suggèrent que les aboiements peuvent fonctionner comme des signaux conventionnels ou de handicap de qualité indiquant la motivation et potentiellement l'endurance des mâles. Cette découverte et l'utilisation fréquente des aboiements dans des contextes autres que ceux des prédateurs terrestres montrent que la spécificité contextuelle de ce type d'appel a été surestimée et que les aboiements peuvent remplir une double fonction.

En conclusion, l'utilisation vocale dans le genre *Chlorocebus* montre une variation considérable spécifique à la population et interindividuelle. Ceci implique que l'expérience individuelle et les facteurs sociaux peuvent jouer un rôle central dans l'orientation du comportement vocal individuel. La variation dans l'utilisation des cris suggère également que les signaux qui ont été jusqu'à présent principalement considérés comme des cris d'alarme peuvent avoir plus d'une fonction. Des mécanismes potentiels qui rendraient les signaux efficaces pour exercer leurs effets sur les receveurs sont suggérés. Enfin, les forces sélectives potentielles qui façonnent la structure et l'utilisation des cris sont discutées et un impact de la sélection naturelle et intra-sexuelle est proposé.

Chapter 1 – Introduction

Understanding the evolution of communication is a central problem in the biological sciences and continues to inspire theoretical models and empirical studies. A universal aspect of most attempts to define communication is the idea of an interaction between a signaler who produces a signal, and a receiver who perceives the signal and responds to it on some way (Fischer, 2011; Maynard Smith & Harper, 2003; Owren et al., 2010; Searcy & Nowicki, 2005; Vehrencamp, 2000). From a biological point of view, the structure and usage characteristics of a signal are thus shaped by the function a signal needs to fulfill.

The vocal communication of non-human primates (hereafter primates) has attracted particular interest since their close phylogenetic relationship with humans invites the question whether primate vocal behavior can inform our understanding of the evolutionary origins of human speech. Although initial studies of primate vocal communication were concerned with investigating the relationship between the acoustic structure or form of signals and the function that these signals were assumed to have, this focus changed after the discovery of the vervet monkey alarm call system (Struhsaker, 1967a). Observational studies and field experiments revealed that vervet monkeys responded with acoustically different alarm calls towards different predators and that these vocalizations led to different escape responses in receivers, even if played back in the absence of actual predators (Seyfarth et al., 1980a, 1980b).

Since these escape responses appeared specifically suited to avoid predation by the predators that led to the production of the respective calls, scientists began to investigate the possibility that these calls might have semantic content and conveyed information about the presence of particular threats to receivers. The idea of referential communication systems became immensely popular following the discovery of the vervet monkey alarm calls and research about primate vocal communication became increasingly motivated by attempts to identify evolutionary precursors to human speech in primate vocalizations (Fischer, 2017).

This focus on potential parallels between primate vocal behavior and human speech has generated a productive field of research that advanced our insight into the alarm call systems of primates and many other taxa. Unfortunately, basic ethological questions about how acoustic structure and variation in call usage are related to signal function have been neglected as a consequence of the popularity of this approach (Owren et al., 2010; Rendall & Owren, 2013).

While the information centered views have contributed to the insight that functional responses to vocal signals develop gradually in primates and are hence likely a product of associative learning and experience, little research has attempted to quantify alarm call production across contexts and with regard to signaler demographic and social factors. Since variation in signal structure and usage are a product of the selective forces that shape them, our view of the function of many primate alarm calls and the evolutionary mechanisms that allow calls to reliably exert their effects on receivers may thus be incomplete. In addition, there are comparatively few studies that attempted to identify the predator specific features that are relevant for the classification of a potential threat from the perspective of the signaler. While we thus know that vervet monkeys produce different calls for different threats, we do not know what their assessment is based on.

The following sections of this chapter will begin with a more detailed discussion of described mechanisms by which honest signals can exert their effects on receivers and the implications these mechanisms have for the structure and usage of vocal signals. Thereafter the motivational and affective mechanisms that may guide the production of vocal signals are reviewed. This is followed by an overview of our current understanding of the limitations of vocal communication in non-human primates before the model system, the genus *Chlorocebus*, is introduced. Thereafter, the aims of this project will be outlined with a brief discussion of the individual studies conducted.

1.1| The adaptationist approach

The adaptationist perspective emphasizes that depending on the conflict of interest between signaler and receiver in a given context, signal production needs to be costly to some degree in order to ensure that signals remain honest and evolutionary stable strategies can emerge (Dawkins & Krebs, 1978; Krebs & Dawkins, 1984; Maynard Smith & Harper, 2003). Characterizing the mechanisms that maintain honesty by imposing specific costs or constraints on signal structure and signal usage (Janik & Slater, 2000) is an integral aspect of this framework (Searcy & Nowicki, 2005; Vehrencamp, 2000).

According to Maynard Smith and Harper (2003), a biological signal can be defined as ‘any act or structure which alters the behavior of other organisms, which evolved because of that effect, and which is effective because the receiver´s responses have also evolved’. Evolutionary stable strategies are assumed to emerge when both signaler and receiver benefit on average in such interactions (Maynard Smith, 1978; Maynard Smith & Harper, 1995). This definition builds upon the idea of an evolutionary arms-race between signalers, who seek to manipulate receiver behavior to their own advantage via signals, and skeptical receivers who evolve to become mind-readers and respond to signals in ways that are advantageous to themselves (Dawkins & Krebs, 1978; Krebs & Dawkins, 1984).

An ensuing dilemma of this view is that if signals mainly serve to manipulate receivers, it is unclear why receivers should be selected to respond to them in the first place and instead evolve to ignore them whenever the interests of signaler and receiver diverge (Searcy & Nowicki, 2005).

An early solution to this problem was proposed by Zahavi (1975, 1977), who had suggested that signals in a mating context can be honest predictors of individual quality if their expression is costly and individuals of lower quality are unable to afford them. Although initially met with heavy criticism, it was eventually possible to use game theoretical models to show that costly signals could evolve in aggressive (Enquist, 1985; Grafen, 1990a) or mate choice contexts (Grafen, 1990b), under the assumption that if receivers assess signalers based on signal expression, signalers benefit from higher assessment due to higher signal expression and that the cost of signaling varies among individuals of different quality.

1.1.1| Evolutionary mechanisms of honest signaling

Costs are necessary to ensure signal honesty and several mechanisms have been described that impose costs on signalers (Searcy & Nowicki, 2005; Vehrencamp, 2000). A primary distinction can be made based on whether or not costs depend on receiver behavior (Adams & Mesterton-Gibbons, 1995; Guilford & Dawkins, 1995; Vehrencamp, 2000). Receiver-independent costs may be further subdivided into costs that are incurred during production, development or maintenance of signals (Searcy & Nowicki, 2005). Production costs encompass direct energetic expenses, opportunity costs such as missed foraging time and increased risk of predation, if signal usage also attracts predator attention. Developmental costs relate to the energy invested into the structure that is brought on display during signaling and maintenance costs include energy losses involved in carrying a structure and increased predation risk if structures impede movement (Searcy & Nowicki, 2005).

Quality handicaps are signals that are honest because of energy invested in ornaments or the signaling organs, direct energetic costs during signal production and increased predation risk and opportunity costs (Zahavi, 1975, 1977). If costs vary sufficiently among individuals of different quality, barring low quality individuals from exaggerating their signals, such signaling systems can stabilize (Maynard Smith & Harper, 2003; Vehrencamp, 2000). The intensity or display frequency of a signal is correlated with signaler quality and can be directly related to the underlying signaler quality that is on display. Examples in acoustic communication include higher call rates, which are presumably directly related to signaler stamina, in male red deer (Clutton-Brock & Albon, 1979; McComb, 1991), chacma baboons (Kitchen et al., 2003) crested macaques (Neumann et al., 2010) and geladas (Benítez et al., 2016). General handicaps occur if the potential benefits that signalers gain from receiver behavior vary with signaler need. Signalers with higher need are thus expected to show higher signal intensity. The begging behavior of offspring trying to recruit parental support or provisioning typically falls into this category (Johnstone, 1999; Mondloch, 1995; Vehrencamp, 2000).

Lastly, the structure of signals can be physiologically constrained and directly related to a signaler attribute that is an accurate predictor of individual quality. Such signals have been labeled index signals (Maynard Smith & Harper, 2003) as their structure is causally related to intrinsic signaler characteristics like age, health status or body size and thereby resilient to cheating. A classic example is the relationship between body size and vocal tract length in mammals, which affects formant dispersion in vocalizations (Fitch, 1997). This anatomical constraint renders some aspects of the acoustic structure of vocal signals honest indicators of individual body size and age, both of which are related to fighting ability. Empirical support for this mechanism is found during male-male competition and mate-attraction in ungulates (Reby et al., 2005; Reby & McComb, 2003) and contest competition in male primates (Benítez et al., 2016, 2017; Fischer et al., 2002, 2004; Pfefferle & Fischer, 2006). It has been remarked that the distinction between index and quality handicap may not always be easy, as variation in the size of the signaling organs may not only relate to signaler body size but also to energetic investments committed to a maximal expression of signaling organ size during development (Searcy & Nowicki, 2005).

Receiver-dependent costs are paid only if receivers attack signalers in response to the signal and include so called vulnerability handicaps and conventional signals that have low production costs, but high retaliation costs if receivers choose to escalate a conflict. Vulnerability costs are incurred because the form of the signal itself exposes the signaler to a higher risk of injury (Adams & Mesterton-Gibbons, 1995; Enquist, 1985). Examples are many threat displays that bring signalers into close proximity to receivers (Számadó, 2008; Waas, 1991). Behavior that additionally exposes vulnerable body parts, like the red-white-blue display of vervet monkeys who expose their colored genitals to opponents as a display of dominance may also fall into the vulnerability handicap category (Young et al., 2020).

Honesty of conventional signals is maintained by a receiver retaliation rule, whereby an aggressive signal that has a higher likelihood of assisting to win a conflict also increases the probability of an attack by the receiver (Enquist, 1985; Guilford & Dawkins, 1995). Individuals are assumed to use aggressive signals when in good condition or motivated to escalate a fight and submissive signals when in poor condition or unmotivated. If both opponents use the same signal, ensuing fights will bestow higher costs on signalers who display aggressive behavior while in bad condition (Hurd, 1997; Hurd & Enquist, 1998; Molles & Vehrencamp, 2001).

1.1.2| Strategic and tactical signal design

The discussed evolutionary mechanisms can be complementary and support the same or related signal functions, as was shown in male red deer, where call rate and acoustic structure are both involved in repelling competitors and attracting mates (Clutton-Brock & Albon, 1979;

McComb, 1991; Reby et al., 2005; Reby & McComb, 2003). Structural and usage specific signal characteristics, rendering the signals honest and effective at exerting their effects on receivers are termed strategic design features and the cost associated with these adaptations are known as strategic costs (Guilford & Dawkins, 1991; Maynard Smith & Harper, 2003). Strategic design features and their attached costs can support a handicap argument. However, such strategic costs need to be distinguished from efficacy costs resulting from tactical signal design features (Guilford & Dawkins, 1991) which are required for a signal to overcome a receiver´s receptivity threshold (Johnstone, 1998) or reach a receiver in spite of signal attenuation (Morton, 1975). Habitat structure and the distance that acoustic signals need to propagate impose selection pressure on signals and affect frequency range, signal duration and call rate (Boncoraglio & Saino, 2007; Ey & Fisher, 2009; Maciej et al., 2011; Waser & Brown, 1986). An example is found in many primate loud calls, where the acoustic structure of vocalizations and the daytimes at which they are produced appear to reduce signal attenuation during transmission (Gautier & Gautier, 1977; Mitani & Stuht, 1998; Waser & Waser, 1977). Providing evidence that loud calls are quality handicaps on the basis of signal cost alone can thus be difficult. It may not always be clear whether individuals reduce their call rates after heavy rain (Schel & Zuberbühler, 2012) or at extremer temperatures (Erb et al., 2016) because calling becomes too costly or because sound propagation is simply inhibited in these circumstances.

Another example of tactical design is found in the structure of many alarm calls, which can either be hard to localize in order to avoid higher predation risk for signalers, or at the opposite end, show structural adaptations that make them easier to localize, allowing receivers to estimate predator position from (Marler, 1955; Owren & Rendall, 2001). While costs and constrains associated with signal structure and usage can thus suggest a mechanism that may support that signals are honest indicators of individual quality, tactical design requirements can also impose efficacy costs on signaling behavior and strongly affect the acoustic structure and usage of a vocal signal.

1.2| Motivational and affective determinants of signaling

An alternative influential conception of communication is based on the idea that signals transfer or convey information to receivers (Bradbury & Vehrencamp, 1998; Vehrencamp, 2000). While this notion has been criticized as inaccurate given that signalers are expected to maximize their own fitness by attempting to manipulate receiver behavior (Dawkins & Krebs, 1978; Owren & Rendall, 2001; Rendall et al., 2009; Scott-Phillips, 2008), it has been acknowledged that the approach emphasizes the importance of the receiver's perspective, who exerts selection pressure on the signaler (Krebs & Dawkins, 1984). In this view, skeptical receivers evaluate signals to make inferences regarding the state of the signaler or the environment and may thereby predict imminent events or signaler behavior by assessing to what extent signals change probabilities between different possible scenarios, reducing the uncertainty in a particular context (Fischer, 2011; Skyrms, 2010; Wheeler et al., 2011). Importantly, the stochastic relationship between signals and the events or states they predict sets the focus on the cognitive mechanisms that guide receivers' inferences and subsequent responses to signals. Therefore characterizing a communication system requires to incorporate insights from learning theory, if adaptive responses to signals depend on acquiring associations between signals and the events or behaviors they predict during individual ontogenetic development (Owren et al., 2011; Owren & Rendall, 1997).

1.2.1| Signals as expressions of internal states

Darwin (1872) had suggested that animal signals are best conceived as expressions of emotions and argued that selection should favor divergence in signal structure to allow receivers to distinguish among different emotional and motivational states of signalers. The idea was widely influential (Gautier & Gautier, 1977; Scherer & Kappas, 1988) and further developed by Morton (1977), who suggested that acoustic signals in birds and mammals that are used in affiliative and agonistic contexts appeared to converge on similar acoustic properties, which were thus suited to convey the motivation of a signaler. Low pitched and harsh sounds appeared to dominate in aggressive signals, whereas higher pitched and more tonal sounds were more frequent in affiliative or submissive signals. Since larger individuals typically vocalize at lower frequency ranges and tend to win fights against smaller individuals, Morton suggested that selection would lead to lower pitch in aggressive vocalizations and higher pitch in submissive or affiliative calls.

The model is compelling as it provides an explanation for how selection could have led to diverging signal structure in contexts that require different responses from receivers and is supported by empirical data (Fichtel et al., 2001; Gouzoules & Gouzoules, 2000). In addition, it has been shown that variation in signaler arousal has effects on acoustic structure and call rate within call types (Borjon et al., 2016; Briefer, 2012; Liao et al., 2018; Manser, 2001; Meise et al., 2011; Scherer & Kappas, 1988). Call type and call intensity together may thus allow a receiver to infer the underlying motivational state of a signaler. These internal states, have been described in terms of several subcomponents which characterize an individual’s affective response to a situation in the form of positive or negative expectations, an arousal level that indicates the perceived urgency of the situation and a motivational component related to an individual’s probability to respond with particular behavior (Fischer, 2011; Fischer & Price, 2017; Todt, 1986). Signals that would allow inferences regarding these different aspects of a signaler's internal state would be well suited to predict whether a signaler's attention was captured by an aversive or appetitive context, how urgent the event is to the signaler and how the signaler will likely behave next. Clearly, receivers would profit from being able to evaluate signals according to this model.

1.2.2| Referential signaling

The traditional view of animal signals as expressions of internal states was challenged after playback experiments revealed that the apparently predator specific alarm calls of vervet monkeys elicited differentiated escape responses even in the absence of said predators (Seyfarth et al., 1980b, 1980a; Struhsaker, 1967a). The authors suggested that these alarm calls were not mere reflections of arousal or motivational states but instead were potentially symbolic and might convey information about ongoing events external to the caller, such as the presence of specific predators.

After surveying mammalian and avian alarm call systems Macedonia and Evans (1993) suggested that species that face predation pressure from multiple predator types, tend to show alarm calls that vary with predator type and lead to different escape responses suited for the respective predators. Similar to Morton (1977), they also argued that incompatibility of contextual, or in this case, predator specific optimal responses to vocalizations led to selection pressure that diversified call structures. However, the signalers in their model were not primarily viewed as responding to an internal state. Instead, signalers were considered to respond to external events that were classified as different threat categories, leading to the idea that the alarm calls were functionally referential (Evans, 1997; Evans et al., 1993; Macedonia & Evans, 1993b; Townsend & Manser, 2013). However, the potentially semantic content of such calls is hard to investigate since probing the receivers evaluation of call meaning is limited to what can be inferred from their behavior during playback experiments (Fischer et al., 2013).

Recent work has emphasized that since call types frequently occur outside of their typical reference context, stimulus specificity in such systems is usually only probabilistic (Scarantino & Clay, 2015; Wheeler et al., 2011; Wheeler & Fischer, 2012, 2015). A statistical relationship between the occurrence of certain call types and external events may still allow receivers to make predictions about ongoing events. However, if the relationship between signals and events they are associated with is not deterministic, the experience receivers have with particular signal types becomes critical for characterizing the meaning that these signals may have to receivers (Fischer & Price, 2017; Owren & Rendall, 1997).

Importantly, the ability to attribute sounds to events, states, subjects or objects is all that is required to render such a signaling system effective. Consequently, calls do not need to be conceptualized as symbolic as long as external events lead to internal states that elicit particular calls in a systematic way. Loose context specificity may render such a system less efficient but also leads back to the question which proximate mechanisms guide call production in signalers. Currently it remains unclear how predator features are connected to internal states and how they in turn are involved in the production of specific call types.

1.2.3| Affect conditioning

Criticizing the impact of functional reference and other linguistically inspired models of primate communication, Owren and Rendall (1997, 2001) expanded upon the traditional ethological view. They proposed an affect-conditioning model that aimed to bring the relationship between signal structure and function back into focus. They argued that the acoustic structure and energy of vocalizations can constitute unconditioned stimuli that are highly salient for receivers and recruit attention, increase arousal and induce negative affective responses based on obnoxious characteristics of sounds alone. Such signals would fulfill the prerequisites to manipulate receiver attention and because of their amplitude and acoustic structure, they could elicit negative affective responses, thus motivating receivers to find a way to make them stop. Examples for such calls are screams produced by juvenile primates that solicit parental care or the screams of subordinate individuals trying to stop an attack by a more dominant aggressor.

Further, they proposed that vocal signals could also become conditioned-stimuli if specific call types are paired with subsequent aggressive or affiliative behavior. Pavlovian conditioning (Rescorla, 1988), leading to associations between calls types and the contexts in which they are delivered could thereby provide a mechanism that elicits affective responses in receivers that are not based on call structure but instead on individual experience (Owren et al., 1997). The authors emphasized that it would be advantageous if such vocal signals were individually distinct, as this would increase their predictive value if animals live in social groups where the same individuals interact frequently with each other. Following this model, signalers are able to induce or reduce fear (Cheney et al., 1995; Silk et al., 1996) in recipients by producing calls that receivers have learned to associate with positive or negative consequences. While the model does provide a good mechanism for how vocal signals exert their effects on receivers, it does not explain which cognitive processes guide the production of specific call types (Fischer & Price, 2017).

1.3| Vocal communication in non-human primates

Primate vocal communication has been studied from a variety of perspectives. A central question is to which degree their vocal behavior is dependent on experience and external factors.

In this regard, it is important to distinguish between the production of vocalizations by signalers, including the structure of vocalizations and the flexibility of usage of vocalizations in specific situations (Seyfarth & Cheney, 2003, 2010).

1.3.1| Vocal production

Compared to the diversity of sounds found in human speech, the vocal repertoires of primates are comparatively small and undergo little acoustic modification during ontogeny. It is by now well established that the acoustic structure of primate vocalizations is mostly hard-wired (Jürgens, 2009; Oller & Griebel, 2008). Infants that are raised under social and acoustic isolation (Hammerschmidt et al., 2001; Winter et al., 1973) or are cross-fostered between species (Owren et al., 1993) acquire the vocal repertoires typical for their species (Hammerschmidt et al., 2001). While primates show ontogenetic changes of call features that can be explained by maturational processes like growth of the vocal folds and an increase in body mass (Ey et al., 2007; Fitch, 1997; Hammerschmidt et al., 2000), they are unable to imitate sounds or modify the basic acoustic structure of their calls, an ability termed vocal production learning (Fischer & Hammerschmidt, 2019; Janik & Slater, 2000). This marks a sharp contrast between nonhuman primate vocal development and human speech acquisition, which relies on experience based production of novel vocal patterns (Egnor & Hauser, 2004).

Recent studies show that a lack of auditory and social feedback during early development can slightly change the acoustic structure of vocalizations (Gultekin & Hage, 2018; Takahashi et al., 2017). Although the change of spectral call features is best explained by maturational processes, the temporal patterning of call types may change with experience (Gultekin et al., 2021; Hage, 2020). Interestingly, changes of call properties due to vocal accommodation effects are also found in adults and can result in group specific vocal signatures (Crockford et al., 2004; Fischer et al., 2020; Snowdon & Elowson, 1999). Context and audience composition were also reported to be associated with subtle structural variation within call types (Crockford et al., 2018; Fischer et al., 1995; Gouzoules et al., 1984; Slocombe & Zuberbühler, 2007). Although the basic structure of primate vocalizations is thus mostly hard-wired, the finer spectral and temporal characteristics can be modified.

The general constraints on vocal production are not caused by the vocal tract anatomy of primates, since the properties of their vocal tracts would likely allow the production of a much wider range of sounds than observed in their calls (Fitch et al., 2016). Instead, the fixed structural characteristics of vocalizations are a consequence of the underlying neural architecture. The neural pathway that enables the voluntary motor control over laryngeal muscles, which is needed for human speech, is comprised of direct projections from the primary motor cortex to the nucleus ambiguous. This pathway is not found in monkeys, explaining the constrained nature of their calls (Jürgens, 1976, 2009). Primates rely on a phylogenetically older neural system that is present in humans as well and controls the production of genetically predetermined vocal patterns like screams and laugher (Ackermann et al., 2014; Hage & Nieder, 2016). This system is composed of circuits connecting the anterior cingulate cortex and parts of the limbic system with the posterior periaqueductal grey which integrates the received input and coordinates the vocal production (Hage, 2018; Hage & Nieder, 2016; Simonyan, 2014).

Primates are no thus vocal learners and show only limited modification of spectral characteristics in their vocalizations (Fischer & Hammerschmidt, 2019; Tyack, 2020). However, constraints in the production of structural variation of signals do not have to limit contextual variation in signal usage.

1.3.2| Vocal usage

Whether primate vocalizations are best described as expressions of affective and motivational internal states, goal directed or even subject to volitional control is a controversial discussion. Proponents of a more flexible control of vocalizations emphasize the presumably strategic usage of vocalizations by primates, observed in their sensitivity to the social context, including the relationships between individuals (Cheney & Seyfarth, 2018; Seyfarth & Cheney, 2018). Variation in call usage during different social contexts has frequently been interpreted as evidence that primates are able to withhold call production (Seyfarth & Cheney, 2010; Zuberbühler, 2008).

Call usage has been reported to depend on the presence or composition of an audience during predator events (Seyfarth & Cheney, 1985; Wich & de Vries, 2006; Wich & Sterck, 2003) and foraging contexts (Di Bitetti, 2005; Pollick et al., 2005). The usage of specific call types for certain predator classes (Berthet et al., 2019; Cäsar et al., 2012, 2013; Coye et al., 2018; Kirchhof & Hammerschmidt, 2006; Macedonia, 1990; Murphy et al., 2013; Ouattara et al., 2009a; Seyfarth et al., 1980a; Struhsaker, 1967a; Zuberbühler, 2000a; Zuberbühler et al., 1997, 1999) or particular food items (Clay et al., 2012; Hauser & Marler, 1993; Kalan et al., 2015; Slocombe & Zuberbühler, 2006) is also often interpreted as sign of control over call usage. Alarm call production outside the typical contexts during aggressive interactions (Price et al., 2014; Struhsaker, 1967a) or feeding contexts (Kean et al., 2017; Wheeler, 2009; Wheeler et al., 2014) also deserves mentioning here. Alarm call frequency may also relate to the perceived urgency of a threat, which may relate to predator distance or movement (Murphy et al., 2013; Wheeler, 2010a). The social relationship between signaler and receiver as well as their recent interactions were also shown to affect call usage (Cheney et al., 1995; Faraut et al., 2019; Silk et al., 2016, 2018).

Developmental studies have suggested a role of individual experience in acquiring adult like alarm call usage (Seyfarth & Cheney, 1986) or species typical temporal patterning of calls (Gultekin et al., 2021). However, critics of this view have argued that the restriction of alarm call usage to stimuli that evoke calling in adults may be better explained by habituation or the gradual refinement of threat categories which lead to specific internal states that elicit call production (Owren et al., 2011; Wheeler & Fischer, 2012).

Laboratory studies suggested that vocal behavior of primates can be brought under some degree of operant control (Hage et al., 2013, 2016; Janik & Slater, 2000; Pomberger et al., 2019), although it has been argued that the vocalizations typically used in such experiments show preexisting affect based connections to the food rewards used as reinforces (Jürgens, 2009; Owren et al., 2011). Withholding of call production to avoid acoustic interference due to noise or conspecific calls has also been demonstrated in the lab (Egnor et al., 2007; Hage, 2013), although this behavior may not necessarily demonstrate volitional control (Luo et al., 2018).

Proponents of a motivational or affect based vocal control maintain that it cannot be excluded that variation in the social context, predator type or food item leads to different internal states, which in turn then determine the vocal behavior. Whatever stance is taken concerning vocal flexibility in primates, there is a consensus that primates have more control over the usage and temporal aspects of vocalizations than the basic acoustic structure of their calls (Seyfarth & Cheney, 2010). This raises the question which proximate factors contribute to the production of specific call types and which cognitive mechanisms mediate this process (Fischer & Price, 2017).

A promising approach to this question is the investigation of alarm call systems that exhibit calls of different structure which are produced in response to different predators (Macedonia & Evans, 1993b). A watershed event in this regard, was the initial discovery of the vervet monkey alarm call system (Seyfarth et al., 1980b, 1980a; Struhsaker, 1967a). Vervet monkeys produce different call types in response to their major predators and respond with different escape strategies to these calls. Comparative analysis showed that the structure of these calls seems highly conserved in the genus (Price et al., 2014; Wegdell et al., 2019). A recent quantitative analysis of this system revealed a graded variation between the different alarm calls and confirmed strong similarity with calls used during agonistic interactions (Price et al., 2015).

Observational studies of vocal development have revealed that young vervets produce alarm calls without any evident need of prior experience (Seyfarth & Cheney, 1986). However, they overshoot with regard to the stimuli that elicit calling behavior and produce alarms towards a range of birds and mammals that do not prey on vervets. Interestingly, these false alarms follow a certain systematic rule, as calls typically produced towards raptors are initially also produced towards a wide range of birds or potential aerial threats but not towards terrestrial predators. It appears that young monkeys categorize potential threats correctly and narrow the range of species they respond to with experience. In this regard, vocal usage learning seems restricted to the refinement of hard-wired categories (Owren et al., 2011). However, adult vervet monkeys reportedly sometimes respond with terrestrial alarms towards stooping eagles or raptors that are situated on the ground. In a congener, the West African green monkey, adult individuals were reported to respond with aerial alarms towards drones, suggesting that they classified these novel potential threats as possible aerial predators (Wegdell et al., 2019). This raises the question whether the monkeys are sensitive towards the positional category of a predator (aerial versus terrestrial). The cognitive mechanisms underlying vocal production thus clearly demand further investigation.

The picture is further complicated by the fact that adult male vervets are also known for producing the same call type during encounters with land predators and during within and between group conflicts (Price et al., 2014, 2015; Struhsaker, 1967a). Not only does this challenge the notion of functional reference since context specificity is no longer guaranteed (Wheeler et al., 2011; Wheeler & Fischer, 2012, 2015) but it also calls into question whether these calls only function as alarm calls. It has been suggested that they may also have a display function during aggressive interactions (Price et al., 2014). This highlights the need for further investigation of inter-individual variation in call usage that may provide insight into the mechanisms that would support such a dual function.

In conclusion, primates show considerable variation in call usage with regard to context. However, it remains unclear which mechanisms guide call usage in signalers at a proximate level. In addition, the use of alarm calls during aggressive interactions invokes the questions whether these calls might also serve as vocal displays and which mechanism might render them effective at fulfilling this function.

1.4 | Model taxon – The genus *Chlorocebus*

The African green monkeys (*Chlorocebus spp.*) are small old world monkeys belonging into the subfamily Cercopithecinae and the tribe Cercopithecini. Until recently, six species were considered to belong into this genus including *C. sabaeus* (West African green monkey), *C. aethiops* (Grivet), *C. djamdjamensis* (Bale Mountains vervet), *C. tantalus* (Tantalus monkey), *C. pygerythrus* (Vervet monkey) and *C. cynosures* (Malbrouck) (Dolotovskaya et al., 2017; Haus et al., 2013). The classification remains under discussion and it has been argued that the Dryas monkey may also constitute a basal member of the genus (Alempijevic et al., 2021; van der Valk et al., 2019). All members of the genus are found in sub-Saharan Africa, where they typically live in multi-male multi-female groups with female philopatry.

The vervet monkeys (*C. pygerythrus*) has by far received most scientific attention, in part because the species has a wide distribution from East to South Africa and is therefore easily accessible. Their ecology and social behavior have been studied excessively (Arseneau-Robar et al., 2018; Baldellou & Henzi, 1992; Borgeaud, Schnider, et al., 2017; Borgeaud, Sosa, et al., 2017; Borgeaud & Bshary, 2015; Cheney & Seyfarth, 1990; García et al., 2022; Henzi et al., 2013; Jarrett et al., 2018; McFarland et al., 2021; Mercier et al., 2017; Struhsaker, 1967a; Young et al., 2019). They have also become an important model organism for studying social learning mechanisms (Bono et al., 2018; van de Waal et al., 2010, 2015; van de Waal, Borgeaud, et al., 2013; van de Waal, Bshary, et al., 2013; van de Waal & Bshary, 2011). While females remain in their natal groups, males disperse shortly before or after reaching sexual maturity and typically migrate into neighboring groups were they stay for an average of two years before migrating again (Henzi & Lucas, 1980).

As vervet groups mostly have multiple adult males, agonistic interactions among males are frequent and usually result in linear dominance hierarchies (Struhsaker, 1967b, 1967c). Females are considered codominant to males and win agonistic interactions either alone or due to coalitions with close bonded females and juveniles (Cheney et al., 1988; Keddy, 1986; Young et al., 2017). Their codominance allows them to resist male sexual coercion attempts, which reduces male monopolization potential and probably contributes to the moderate reproductive skew described in this species (Minkner et al., 2018), although this subject demands further research (Weingrill et al., 2011).

The vocal communication of vervet monkeys has received considerable attention after observational and experimental field work showed that in response to their major predators, monkeys produce structurally distinct vocalizations that lead to specific predator avoidance behavior in monkeys even in the absence of actual predators (Seyfarth et al., 1980b, 1980a; Struhsaker, 1967a). The concept of functional reference was inspired by this discovery (Evans, 1997; Evans et al., 1993; Macedonia & Evans, 1993b). Their vocal behavior outside of predator contexts has also been studied and frequently serves as an example for the flexible use of vocal signals during different social contexts (Cheney & Seyfarth, 1982b, 2018; Fedurek et al., 2019; Kavanagh et al., 2021; Mercier et al., 2017, 2019). By now, their alarm call system has been studied from a variety of different angles including the structural variation among calls produced during different contexts (Owren & Bernacki, 1988; Price et al., 2015; Wegdell et al., 2019), structural variation in relation to phylogeny (Price et al., 2014; Wegdell et al., 2019), responses of receivers to variation in call structure and contexts (Ducheminsky et al., 2014; Owren, 1990; Price et al., 2014; Price & Fischer, 2014) and the ontogenetic development of calls (Seyfarth & Cheney, 1986).

While we currently assume that adaptive responses to calls develop gradually and are the product of associations between call structure and the contexts they predict, we still have no clear understanding of the mechanisms that determine how signalers classify potential threats and produce corresponding alarm call types. While developmental studies and experiments with artificial predator models suggests that threat location could play a decisive role (Seyfarth & Cheney, 1986; Wegdell et al., 2019), it remains unclear to what degree individual experience with particular threats is also affecting call production (Fischer & Price, 2017; Owren et al., 2011). Since the relationship between particular vocalizations and contexts is stochastic and alarm calls also occur outside of predator events during aggressive interactions (Price et al., 2014, 2015; Struhsaker, 1967a), it is possible that some of these call types may also fulfill a display function.

The vervet monkey alarm call system thus continues to be a promising model to investigate proximate mechanisms that guide call production in signalers. In addition, we currently lack any quantitative understanding of inter-individual and contextual variation in call usage, which is not only important for the discussion of vocal flexibility in primates (Cheney & Seyfarth, 2018; Fischer & Price, 2017), but may also inform our understanding of the selective pressures that shape vocal behavior (Snowdon, 2004). Due to the extensive previous work on the social system of this species (Cheney & Seyfarth, 1990), investigating variation in call usage in conjunction with variation in individual social and demographic factors may thus reveal important insight into the drivers off call usage and the function of calls.

1.5| Study aims

The alarm call system of the genus *Chlorocebus* has served as an excellent model to increase our knowledge about the evolution of vocal communication in primates. Unfortunately, the focus on the potential semantic or referential content of primate alarm calls and the potential evolutionary continuity between primate vocal communication and human language has also diverted attention away from classic ethological approaches that seek to understand how signal function is related to variation in signal structure and usage. While previous research suggests that learning contributes to the process that mediates how receivers attribute vocal signals to contexts, our understanding of the cognitive mechanisms that determine the utterance of alarm calls is incomplete.

As structural analyses suggest gradual variation among calls produced in predator and aggressive contexts, it is also apparent that contextual specificity of calls can be overestimated if call usage is not quantified across all possible natural contexts. Since the usage of alarm calls in aggressive contexts suggests that alarm calls may also fulfill a display function in addition to alerting conspecifics and deterring predators, it is necessary to quantify inter-individual variation in call usage with regard to social and demographic factors to test if usage patterns could support such a dual function. Characterizing variation call usage may also enable a better understanding of the mechanisms that render vocal signals effective at fulfilling their function. Since we assume that the meaning that receivers attach to signals is established by the variation that receivers experience among the utterance frequency of certain call types and the contexts in which they occur, quantifying this variation will also contribute to the discussion regarding the referential content of signals. This thesis aims to fill the described empirical gaps in the form of two studies and also contributes a literature review.

Chapter two presents an experimental study that explored how variation in the position (aerial or terrestrial) of a potential threat is affecting alarm call production in members of the genus *Chlorocebus*. Drones and radio controlled cars were presented to groups of free-ranging monkeys as novel potential threats and threat position and threat specific experience were manipulated among different groups. The study aims at clarifying which features of potential threats guide the production of different alarm call types and whether individual experience is affecting the classification of novel threats.

Chapter three is a review paper that examines how drones can be used to study animal behavior and ecology. Drones are increasingly used to survey animal populations and monitor behavior to study the spatial organization and movement dynamics of groups. Since they can affect the behavior and of many species directly, drones are also used to study animal responses to novelty or anti-predator behavior. Drones thus have potential to investigate how group composition, habitat characteristics and population specific predation pressure or anthropogenic disturbance affect individual and collective anti-predator behavior.

Chapter four presents a 24-month observational study that quantified the inter-individual variation in calling activity in one call type, the threat-alarm bark that is produced by adult males in response to mammalian land predators but also during aggressive interactions. The study explored whether this call type serves a dual function of alarm call and signal of male quality, by modeling calling activity in relation to individual and group specific factors that relate to male competitive ability and the degree of male-male competition in groups. In addition, it provides data about the distributions of contexts, duration, numbers of calling males and daily and seasonal frequencies of barking events.

Chapter five summarizes the main findings of the empirical work and discusses them in light of the proximate mechanisms and selective forces that may explain the results. The chapter concludes with an outlook for future work concerned with quantifying vocal usage patterns, predator-prey interactions and group and population specific differences in call usage.

Chapter 2

Responses of *Chlorocebus spp.* to experimental presentations of novel threats

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Manuscript in preparation

Abstract

Many non-human primate species produce acoustically distinct vocalizations in response to different predator species that vary in their hunting strategies. This first such alarm call system was discovered in vervet monkeys, *Chlorocebus pygerythrus*, who produce structurally different calls towards their three main predators: Large mammalian carnivores, pythons and raptors. Previous studies examined to what degree these predator specific calls varied in their spectral structure and how receivers' responses vary depending on the call type and context. However, the physical properties of potential threats that lead to the use of different call types have not been investigated, limiting our understanding of the cognitive mechanisms that determine threat categorization and call usage in signallers. The ontogenetic development of call usage in juvenile vervet monkeys, and the vocalizations produced by adult green monkeys (*C. sabaeus*) towards novel threats, suggest that monkeys may initially categorize potential threats according to an 'aerial' or 'terrestrial' decision rule and then gradually refine these categories with experience. Here, we conducted an experiment with West African green monkeys (*C. sabaeus*) and South African vervet monkeys (*C. pygerythrus*), by presenting subjects with novel aerial and terrestrial threats in the form of drones and small radio controlled cars (RC cars). To investigate whether threat position and threat specific experience affected call usage, we varied the position of drones and the presentation order among groups. We predicted that if call usage depended only on threat position, subjects should utter similar calls towards terrestrial drones and RC cars but different calls towards aerial drones, independent of presentation order. Since vervet monkeys did not respond to drones or RC cars, the small sample size was insufficient for a quantitative analysis. Therefore, we discuss potential species differences and the effects of population specific predation pressure and levels of anthropogenic disturbance on call usage.

1 | Introduction

Understanding the evolution of human language has long been a driving force for scientists who investigate the vocal communication of non-human primates (from here on, 'primates') (Fedurek & Slocombe, 2011; Fischer, 2017; Fitch, 2010; Hauser et al., 2002; Jackendoff & Pinker, 2005; Seyfarth et al., 2005). However, in contrast to speech, the acoustic structure of primate vocal signals appears essentially hard-wired, likely due to neuroanatomical constraints (Ackermann et al., 2014; Hage & Nieder, 2016; Hammerschmidt & Fischer, 2008; Jürgens, 1976, 2009). In addition, primate infants raised under social or acoustic isolation will still develop largely species-typical vocal repertoires (Gultekin & Hage, 2017; Hammerschmidt et al., 2001; Owren et al., 1993; Winter et al., 1973). Primates thus lack the open-ended vocal learning system (Fischer & Hammerschmidt, 2019; Tyack, 2020) that characterizes human language and instead rely on limited repertoires of vocal signals.

Despite their fixed call structures, primates demonstrate variation in relation to the context in which calls are typically given (Cheney & Seyfarth, 2018; Seyfarth & Cheney, 2010) and their vocal behavior may be brought under a limited degree of operant control in experiments (Hage et al., 2013, 2016). Although most primate call types can, to some degree, still be bound to specific affective or motivational states, primates may be able to use vocalizations in a goal-directed manner (Fischer & Price, 2017; Owren & Rendall, 1997). Variation in primate vocal usage (Janik & Slater, 1997, 2000; Vernes, Sonja C. Kriengwatana et al., 2021) has been described in many contexts (Cheney et al., 1995; Schamberg et al., 2016; Silk et al., 2016). Most of the attention has been directed at the alarm call systems of various primates that were found to produce different alarm calls for different predators, whose hunting strategies vary and thus require different avoidance behavior (Arnold & Zuberbühler, 2006, 2008; Berthet et al., 2018; Cäsar et al., 2013; Coye et al., 2018; Murphy et al., 2013; Ouattara et al., 2009a; Seyfarth et al., 1980b, 1980a; Zuberbühler, 2000b).

Variation in call type usage in relation to external events was first discovered in vervet monkeys (*Chlorocebus pygerythrus*), who produce different alarm calls for their main predators: Large mammalian carnivores (e.g. leopards), eagles and pythons (Struhsaker, 1967a). Other monkeys were described to respond to playbacks of these calls with avoidance behavior that resembles the typical reactions monkeys show in the presence of actual predators that elicit the respective calls (Seyfarth et al., 1980b, 1980a, but see: Ducheminsky et al., 2014). This finding influenced the development of the concept of 'function reference' (Evans, 1997; Macedonia & Evans, 1993a) because the calls appeared to denote specific predator types. However, since context specificity does not imply volitional control (Owren et al., 2011; Wheeler & Fischer, 2012), there is currently no consensus on whether 'functional reference' remains a productive framework (Fischer, 2011; Scarantino, 2013; Scarantino & Clay, 2015; Townsend & Manser, 2013; Wheeler & Fischer, 2012, 2015). Moreover, the underlying cognitive mechanisms that determine call usage in the signaler remain unknown (Fischer & Price, 2017).

Ontogenetic studies of call usage in vervets have shown that learning appears necessary to acquire adult-like usage patterns. While juveniles seem to spontaneously produce 'aerial alarms' in response to a broad array of items in the air (including falling leaves) and 'snake chutters' in response to warthogs and antelopes, their assessment of what constitutes a dangerous predator is refined gradually. Over time, the animals become more selective until only natural predators of vervet monkeys reliably elicit alarm calls (Seyfarth & Cheney, 1986). In turn, this example demonstrates how the usage of specific vocalizations can be used to probe how primates categorize stimuli in their environment (Cheney & Seyfarth, 1990). It also suggests a potential mechanism for call usage in naïve infants: Categorizing potential threats according to an aerial or terrestrial position. Evidence for an effect of position was also found in other primates who responded differentially when predator models or cues predicting predator presence were presented from different positions (Berthet et al., 2019; Cäsar et al., 2013; Murphy et al., 2013).

Although many studies have investigated context-dependent variation in the alarm call structure of the genus *Chlorocebus* (Price et al., 2015; Price & Fischer, 2014; Seyfarth et al., 1980b, 1980a; Struhsaker, 1967a; Wegdell et al., 2019), the relevant stimulus properties that determine the use of these different alarm call types are not well understood (Fischer & Price, 2017). Previous work showed that West African green monkeys (*Chlorocebus sabaeus*) produced alarm calls that resembled aerial alarms of East African vervet monkeys upon encountering drones for the first time, suggesting that naïve adults categorized novel potential threats according to their position (Wegdell et al., 2019). During their study, Wegdell and colleagues once observed that the alarm call structure changed when the monkeys saw that the drone landed (F. Wegdell, personal communication), mirroring earlier reports that vervet monkeys sometimes respond with "land predator alarm barks" towards stooping eagles or eagles on the ground (Cheney & Seyfarth, 1990; Struhsaker, 1967a). These anecdotal observations and the results of the drone experiment with green monkeys suggest that the position of a potential predator could be a decisive feature for monkeys and affect alarm call usage when encountering a potential threat.

This study aimed to examine whether stimulus position (aerial or terrestrial) and experience with a stimulus affect how monkeys categorize novel potential threats and how this affects their vocal behavior. To test whether stimulus position and experience with a stimulus affected the type of alarm call that monkeys produced, we used drones as potentially threatening artificial stimuli and varied their position by presenting them either flying high in the air (aerial) or hovering close to the ground (terrestrial). In addition, we presented a radio-controlled car as a potential terrestrial threat for comparison. By varying the order in which different groups were exposed to the conditions, we manipulated the experience that monkeys had with aerial and terrestrial drones. With this design, we aimed to assess whether the current position of a threat and prior categorization by the subjects due to differential experience affected alarm call usage.

We predicted that if monkeys categorize unfamiliar threats depending on the current position alone, they should always utter a terrestrial alarm call type for low-flying drones and the radio-controlled car while producing aerial alarms to high-flying drones independent of presentation order. In contrast, if the position and previous experience with the stimulus affect alarm call usage, subjects who had first seen the drone flying high should be more likely also to emit aerial alarms when they encounter drones hovering above the ground. Conversely, subjects who first saw the drone flying low should be more likely also to emit terrestrial alarm calls when they subsequently see the drone flying high in the air. Importantly, during their first encounter, monkeys should always produce call types according to the position of the novel threat since they lack any experience with it at that time.

2 | Methods

2.1 | Study sites and groups

The experiment was carried out on two different populations of *Chlorocebus spp.* in Senegal and South Africa. Work on the West African green monkeys (*C. sabaeus*) was conducted between February and July 2019 in the Niokolo Koba National Park, Senegal. The study population consisted of the same three groups Wegdell and colleagues worked on, with group sizes ranging between approximately 30 and 43 individuals. Experiments with vervet monkeys

(*C. pygerythrus*) were conducted between February and July 2020 at the Inkawu Vervet Project, located in the Mawana Game Reserve, KwaZulu-Natal, South Africa. The free-ranging study population was composed of four, with group sizes ranging between 24 and 69 individuals at the time.

Due to the onset of the COVID-19 pandemic during our work on vervet monkeys, the number of groups available for this experiment at the Inkawu Vervet Project was reduced from initially six to four groups. Furthermore, planned work on three more groups of vervet monkeys at a third field site (Samara Private Game Reserve, Eastern Cape, South Africa) could not be conducted as the field site was permanently closed down due to the pandemic. We could thus only work with seven groups instead of the twelve groups we had initially expected.

2.2 | Experimental procedure

We presented three different conditions: An aerial drone flying at approximately 60 m, a terrestrial drone hovering just above the ground and a terrestrial vehicle (see fig. 1). We used a quadcopter drone (DJI Mavic 2 Zoom, SZ DJI Technology Co., Ltd, Shenzhen, China) and a radio-controlled vehicle (Traxxas Summit 1:8 4WD RTR Truck, Traxxas, McKinney, Texas, USA) as experimental stimuli. Every trial consisted of an approximately three-minute-long presentation of one of the three conditions to one of the study groups. The order of conditions was balanced between groups with a time interval of two weeks between presentations. Two to three observers recorded vocalizations with Sennheiser directional microphones (MKH416 and ME66/67 with K6 power modules, all equipped with Rycote softie windscreens). In addition, video recordings were made for documentation.

Since we intended to investigate how experience with the different conditions affected vocal output, we exposed each group only once to each condition. This procedure was also adopted to minimize the effects of habituation.

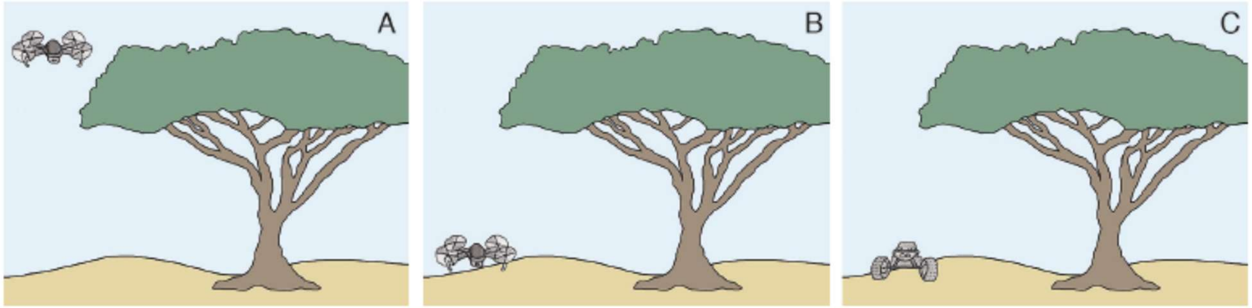

Figure 1: Schematic depiction of the three conditions. **A:** Aerial drone flying at an approximate altitude of 60 m above the group's center. **B:** Terrestrial drone hovering close to the ground (~0.1 m – 0.2 m). **C:** Terrestrial vehicle. During experiments, the vehicle and the terrestrial drone remained at a horizontal distance of approximately 60 m from the subjects.

3 | Results

The two study populations showed substantial differences in their responses. When presented with aerial drones, green monkeys responded by taking cover and producing alarm calls (see fig. 2), much like in our previous study (Wegdell et al., 2019). However, when encountering terrestrial drones and vehicles, only very few vocalizations could be recorded from green monkeys. The quality and number of vocalizations from green monkeys were low, barring any further analysis. In contrast to green monkeys, vervet monkeys did not respond with alarm calls to any of the presented conditions, although they still seemed to avoid the stimuli and scan the sky in response to the aerial drone. Our design restricted us to presenting only a single trial per group in each condition. Since the vervet monkey population did not contribute recordings, we could not acquire the necessary sample size for a structural analysis of the recorded vocalizations. We, therefore, show spectrograms of the alarm calls recorded from green monkeys during aerial drone presentations and typical vervet monkey aerial alarm calls recorded during natural predator encounters, see fig. 2.

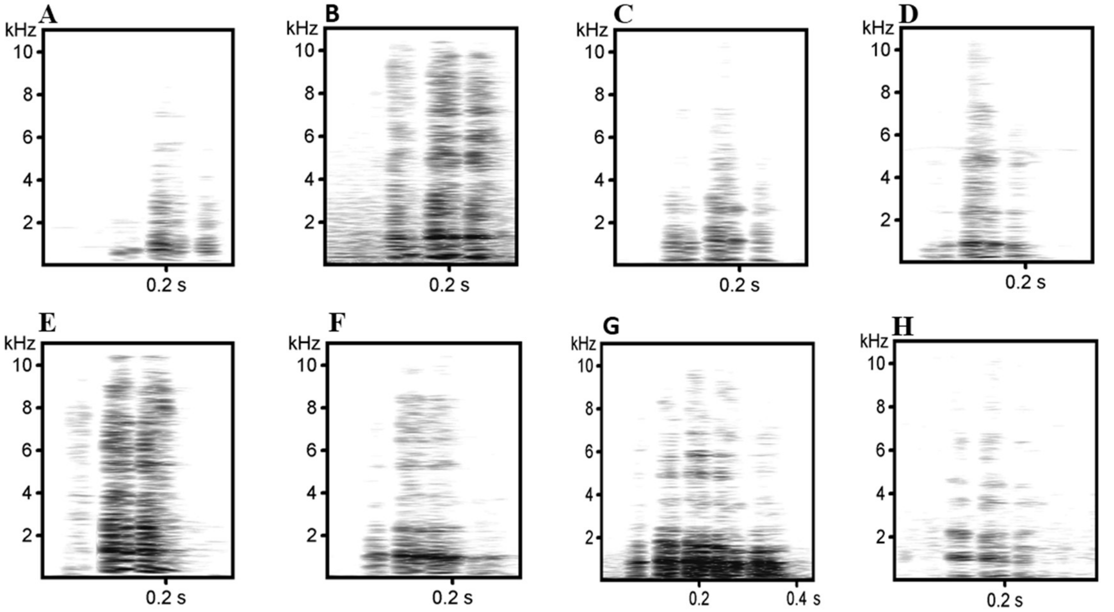

Figure 2: Spectrograms of aerial alarm calls. **A, B, C, D**: Green monkeys aerial alarm calls given in response to drones. **E, F, G, H:** Vervet monkey aerial alarm calls recorded during natural alarm call events. **A, B, E, F**: Adult Females. **C, D, G, H:** Adult males.

As the study was designed to use only call structure as the response variable, we cannot provide data regarding the subjects' behavioral responses or the number of vocalizations produced by each individual. Protocols to reliably record these types of data would have conflicted with attempts to record calls from as many different subjects as possible, given the limited number of observers and the constant need for observers to move into a position that allows making high-quality recordings.

4 | Discussion

Since we could not record a sufficient number of vocalizations, we are currently unable to answer our original research question. However, it appears that both terrestrial conditions were not perceived as very dangerous by any of the subjects since almost no vocalizations could be recorded from green monkeys, while vervet monkeys did not produce any calls at all. To our surprise, green monkeys responded strongly to aerial drones by taking cover and producing alarm calls, whereas vervet monkeys did not. We were puzzled by this observation because our previous work had revealed that the structure of different alarm call types in these two congeners is highly conserved (Price et al., 2014; Wegdell et al., 2019). One of the premises of this study had thus been that it would be unlikely to find any substantial differences between the species.

Why would South African vervet monkeys respond so differently to drones compared to West African green monkeys? At present, we can only provide three hypothetical non-mutually exclusive explanations: First, it is possible that while the acoustic structure of alarm calls in the genus *Chlorocebus* is highly conserved (Price et al., 2014; Wegdell et al., 2019), the context depended usage of these vocalizations is not and the two species categorize potential threats by different rules. While such a species-specific difference cannot be excluded, we can think of no reason why this should be the case given the shared evolutionary history of these two congeners (Dolotovskaya et al., 2017; Haus et al., 2013). Since strong escape responses were absent in vervet monkeys, they appeared to be undisturbed and did not perceive the drones as threats.

Second, the undisturbed reaction of vervet monkeys might be explained by habituation due to previous experience, including the general experimental history of the population. The vervet monkey population had been exposed to various novel objects, predator models and a pilot study with drones in 2018 (A. Deshpande, personal communication). In addition, small airplanes and helicopters were seen flying above the reserve at varying intervals, and it has been shown that animals habituate to drones after repeated exposure (Ditmer et al., 2019). While such disturbances are almost absent from the Senegalese green monkey population, where the very rare airplane flyovers triggered aerial alarm calls (personal observation), it must be noted that the green monkeys probably had similar experience with drones as did the vervets. Despite having seen drones before (Wegdell et al., 2019), the green monkeys showed no signs of habituation when we presented drones again in 2020, and since they regularly spent time at tourist sites during the dry season, they interact at a high frequency with humans too. It is thus difficult to attribute the different responses of vervet and green monkeys to drone-specific experience or differential anthropogenic disturbance rates alone.

Finally, the different reactions might be related to population-specific aerial predation pressure. We noted that green monkeys rarely produced any aerial alarm calls. Experimental attempts to trigger aerial alarms with non-moving predator models shaped to resemble martial eagles were unsuccessful. As aerial alarms thus seemed almost absent in this population, we never attempted to quantify their natural occurrence rate. In South Africa, however, aerial alarm calls could be heard daily. While they were produced in response to several raptor species, monkeys also called in response to non-predatory birds. We interpret the frequent use of aerial alarms as a sign of intense aerial predation pressure. We never observed direct predation by raptors, but several unsuccessful attempts were documented, and we expect that raptors are less likely to prey on vervets in the presence of human observers.

How could predation pressure affect the categorization of novel potential threats? If we assume that green monkeys face almost no aerial predation, then the presence of a novel flying object could, in theory, lead to no response at all since monkeys have no experience with aerial predation and may not perceive any danger from above if they have not previously learned to expect to do so. On the other hand, a population that is unused to threats from the sky might also overreact with extreme responses since the lack of any previous experience in this regard leaves them with no reference background against which they could evaluate this novel perception of an imminent aerial threat. In this latter example, the monkeys would not only perceive a novel threat but also a threat from a previously rarely relevant threat domain and consequently might overshoot in their response to it. The latter interpretation would require them to have a natural propensity to respond to potential threats from the sky without previous experience. This explanation fits with the conserved nature of the alarm calls (Price et al., 2015; Wegdell et al., 2019) and the ontogenetic development of call usage where the context-specific production of the calls appears to precede their understanding (Owren et al., 2011; Seyfarth & Cheney, 1986)

High aerial predation pressure in vervets might, in theory, lead to very strong responses to drones, as one could imagine that it would be adaptive to minimize the rate of occurrence of ‘false negatives’ under such circumstances. After all, missing to call in the case of an actual threat might lead to the death of a relative. However, under high aerial predation pressure, monkeys need to be highly vigilant towards any objects in the sky and frequently have to compare non-predatory birds from actual threats. It is thus feasible that these monkeys get highly proficient in this kind of comparison and consequently very selective in the range of threats that they eventually respond to with calls. Further, since the vervet monkeys can be assumed to have ample experience in discriminating dangerous raptors from non-predatory birds, this experience will, in turn, affect their classification of novel flying objects. Ultimately, it will make them less likely to categorize drones as potential threats, as drones lack many of the physical features they rely on to recognize raptors. Being conservative and avoiding 'false positives' may thus also have the advantage of not losing foraging time whilst hiding or constantly activating their stress response at unnecessarily high rates (Henzi et al., 2021).

The stress response itself could be an additional factor in this puzzle. Monkeys that live in an environment where threats from the sky must be expected at all times will probably not experience the same intensity of arousal as monkeys without this kind of expectation in the event of a potential aerial predator attack. While the arousal level is unlikely to determine the uttered call type alone, it most likely contributes to the frequency at which a given call type is produced and, therefore, whether calls are produced at all (Briefer, 2012; Fischer & Price, 2017). The monkeys' expectations may thus affect their response intensity, and while vervet monkeys might thus still categorize the novel flying object as a potential threat, they might not necessarily be highly aroused in doing so, which would explain the absence of strong escape responses and alarm calls. The green monkeys, on the other hand, presumably having little experience with aerial predation, are prone to overreact following this model. Having experienced no evident aerial predation in their environment, they would have no reference for discriminating dangerous from non-dangerous flying objects. In general, being unused to disturbances from this domain may react strongly if the object fulfills at least the minimal requirements to be categorized as a potential threat.

While our experiment, unfortunately, did not provide any answer regarding the mechanisms that determine the categorization of potential threats and the production of corresponding alarm calls, it highlights the variation in call usage that may be associated with experience and predator-prey relationships. In addition, observations from East and South African vervets have also suggested that males in these populations may use 'threat-alarm-barks' at different rates during agonistic interactions, although aggression rates were not reported to differ (Cheney & Seyfarth, 1990). Therefore, we suggest that future research on primate vocal signals should always aim to characterize the frequency, duration and inter-individual call rate variation of naturally occurring alarm events before experimentally probing these systems.

More than 50 years after Struhsaker (1967) first described vocal behavior in vervet monkeys, we still lack such a descriptive account. This lack of knowledge impairs experimental designs since it is unclear which age and sex classes can be expected to call at all, at what rate they may be calling and for how long. We further suggest that anti-predator behavior, the abundance of predators, and their hunting strategies should best be studied together. If drones are used as predator models, we also recommend identifying which aspects of drone flight behavior, drone silhouette, distance to subjects, and other sources of anthropogenic disturbance can affect the animals' responses to drones.

Acknowledgements

We gratefully acknowledge funding by the Deutsche Forschungsgemeinschaft (DFG FI707/25-1 – Project Number 428036558) and the Leibniz Association through the Leibniz ScienceCampus Primate Cognition (Seed fund: LSC-SF2018-09).

We wish to express our sincere gratitude to all rangers of the Niokolo Koba National Park, with special thanks going to Vieux Biaye, Elijah Dansonkho, Moustapha Faye, Armel Nyafouna, Touradou Sonko, Chérif Kéba Camara, Djibril Coly and Amadou Bamba Diedhiou who supported our work and ensured our safety in the park.

We thank Erica van de Waal for permission to conduct research at the Inkawu Vervet Project and the van der Walt family for permission to work at the Mawana Game Reserve. Finally, we extend our warm thanks to all members of the IVP field team for their assistance with data collection.

Author contributions

LS and JF conceived the study and acquired the funding; LS collected the data, prepared the figures and drafted the first version of the manuscript. Both authors edited the manuscript.

Conflict of interest

None declared.

Chapter 3

Opportunities and risks in the use of drones for studying animal behavior

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Methods in Ecology and Evolution (2022)

https://doi.org/10.1111/2041-210X.13922

Abstract

1. In the last decade, drones have become an affordable technology offering highly mobile aerial platforms that can carry a range of sensory equipment into hitherto uncharted areas. Drones have thus become a widely applicable tool for surveying animal populations and habitats in order to assist conservation efforts or to study the behavioral ecology of species by monitoring individual and group behavior.
2. Here, we review current applications for drone surveys and the potential of recently developed computer algorithms for automatic species detection and individual tracking in drone footage. We further review which factors are reportedly associated with animal disturbance during drone presentations and how drones may be used to study anti-predator behavior.
3. Drone surveys of species and their environments allow scientists to create digital terrain models of habitats, estimate species abundance, monitor individual behavior and study the composition, spatial organization and movement of groups. As drones can influence the behavior of many bird and mammal species directly, they also provide an experimental tool to study animal responses to novel situations, including the drone itself.
4. We conclude that the combined use of drones and automated detection software can assist population estimates and opens new possibilities to study individual and collective behavior. With regard to drone related disturbance and their potential use as predator models we recommend to interpret results against the background of population specific predation pressure and sources of anthropogenic disturbance.

Keywords

Drone, Remotely piloted aircraft system, RPAS, remote sensing, UAV, Unmanned aerial vehicle

1 | Introduction

Unmanned aerial vehicles ('drones') have become a remarkably successful new tool for ecologists, conservationists and behavioral scientists (Anderson & Gaston, 2013; Chabot & Bird, 2015; Koh & Wich, 2012). They provide researchers with remotely controlled airborne platforms that can be equipped with a range of sensors (Jiménez López & Mulero-Pázmány, 2019). Drones can operate in almost any open terrain, enabling scientists to conduct aerial surveys of animals and their habitats without human risk (Christie et al., 2016; Linchant et al., 2015). Among many applications, drones can be employed to study the abundance and distribution of organisms (Corcoran, Winsen, et al., 2021), mapping structure and species specific spatial and temporal usage of habitats (Strandburg-Peshkin et al., 2017), assist in anti-poaching efforts or mitigation of human wildlife conflict (K. R. Adams et al., 2020; Gorkin et al., 2020; Jiménez López & Mulero-Pázmány, 2019; Mulero-Pázmány et al., 2014), estimate morphological and physiological parameters of individuals (Christiansen, Dujon, et al., 2016; Dawson et al., 2017; Horton et al., 2019; Krause et al., 2017; Pirotta et al., 2017) and monitor individual behavior in conjunction with the composition, spatial organization and movement of groups (Torney et al., 2018). The development of machine-learning algorithms for automated detection of target species and individual orientation has further advanced the reliability of drone-based data collection (Corcoran, Winsen, et al., 2021; Graving et al., 2019; Hodgson et al., 2018).

In the wake of this recent surge of drone usage, however, numerous reports indicate that animals may respond to drone surveillance with avoidance behavior and other signs of disturbance including alarm calling, mobbing and displacement activities (Christie et al., 2016; Mulero-Pázmány et al., 2017) or less overt physiological responses (Ditmer et al., 2015). These reports have led to an increasing number of studies attempting to identify which factors during drone presentations typically lead to behavioral responses in order to minimize disturbance (Mulero-Pázmány et al., 2017; Singh & Frazier, 2018). Although most types of survey methods are associated with some form of animal disturbance, understanding how each method can affect the data collected is necessary to determine the optimal survey method and minimize sampling bias.

Here, we review drone applications that may be of interest for ecologists and behavioral scientists. We discuss how drones can be used for monitoring and as experimental stimuli to study group dynamics during movement, anti-predator behavior, and responses to novelty. Finally, we present a case study from our lab to illustrate how drones may be used to study alarm calling behavior and auditory learning. While drones are generally applicable to investigate anti-predator behavior, various challenges and limitations remain.

2 | Surveying environments and populations

Monitoring environments, assessing the distribution of organisms and estimating fluctuating population sizes are common challenges for ecologists and conservationists. Complementing ground research and satellite imaging with standardized drone transects can quickly cover large areas. Drone-based assessments can be conducted independent of cloud cover with high spatial resolution and thus provide a valuable tool for ecosystem monitoring (Hughey et al., 2018).

The currently most common and commercially available models are fixed-wing and multi-rotor drones. Fixed-wing drones can cover larger areas, fly higher and typically support flight times of one to two hours, but have to circle continuously to remain above an area of interest. Multi-rotor drones can hover stationary above a target area, operate at lower altitudes and can rapidly adjust their position if surveilled animals on the ground start moving, but usually do not exceed flight times of 30-40 minutes. Aerostats, such as balloons or powered airships filled with gas lighter than air (K. R. Adams et al., 2020) have seen comparatively less use, but can provide long time aerial surveillance of designated areas. Flapping-wing drones and other 'avian like' models may be used if drones should resemble raptors (Folkertsma et al., 2017) or need to be capable of specific flight maneuvers (Ajanic et al., 2020). The increasing range of drone models allows scientists to tailor their choice of airframe and carried sensors to the specific needs of their study design, the targeted species or the weather conditions and temperature range of the environment in which the drone is to be operated (Anderson & Gaston, 2013; Linchant et al., 2015), see Fig. 1.

In open savannah and marine habitats, drones were used for population censuses of elephants (Vermeulen et al., 2013), manatees (Martin et al., 2012), dugongs (Hodgson et al., 2013), pinnipeds (Adame et al., 2017; Goebel et al., 2015; J. C. Hodgson et al., 2016; McIntosh et al., 2018), sea turtles (Schofield et al., 2017; Sykora-Bodie et al., 2017), polar bears (A. F. Barnas et al., 2018) and colony breeding bird species (A. Barnas et al., 2018; Chabot et al., 2015; Goebel et al., 2015; Rush et al., 2018). Especially for surveys of species that breed in large aggregations or remote colonies, drones have advantages over conventional aerial, boat or ground surveys as they reportedly cause less disturbance, increase count data accuracy and provide better estimates of the age and sex composition of groups (Adame et al., 2017; J. C. Hodgson et al., 2016, 2018; McIntosh et al., 2018; Schofield et al., 2017). Drones may also assist population censuses of rare or elusive species by searching habitats for indirect signs of species presence, as has been demonstrated by attempts to map sleeping nests of great apes in forest canopies (Bonnin et al., 2018; van Andel et al., 2015; Wich et al., 2016) , or burrows of wombats (Old et al., 2019).

To study nocturnal and elusive species or survey animals in habitats with poor contrast between individuals and background, drones can be equipped with infrared cameras (Burke et al., 2019). Thermal imaging offers the unique possibility to monitor animals in low light conditions and has been used to study forest dwelling ungulates (Chrétien et al., 2016; Witczuk et al., 2018), canopy dwelling mammals (Corcoran et al., 2019; Kays et al., 2019; Spaan et al., 2019; Zhang et al., 2020), marine mammals (Horton et al., 2019; Seymour et al., 2017) and colony breeding birds (McKellar et al., 2021). For many taxa, a combined approach of thermal and visible-spectrum imaging at different daytimes is possible (Chrétien et al., 2016; Kays et al., 2019; McKellar et al., 2021).

Finally, drones can measure detailed structural characteristics of environments to create 3-dimensional reconstructions of habitats (Hughey et al., 2018; Tuia et al., 2021). Such computer models can be used to study animal movement as a function of habitat structure (Strandburg-Peshkin et al., 2017) or help to asses long and short term fluctuations of habitat quality for different species (Olsoy et al., 2018).

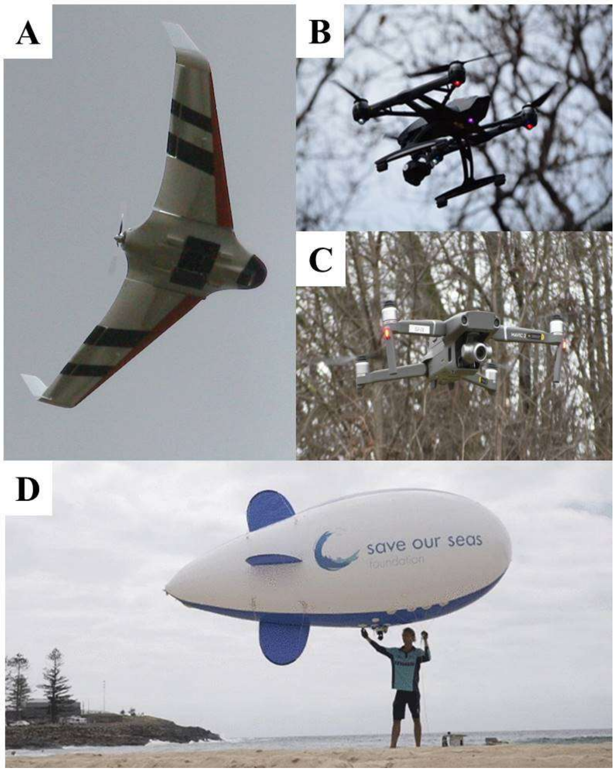

Figure 1: Common UAV types. **A:** Fixed-wing drone used to survey waterfowl, partially reprinted from McEvoy et al., 2016. **B:** Multi-rotor drone used by Wegdell et al., 2019 to elicit alarm calls in non-human primates, image by Davide Montanari. **C:** Multi-rotor drone used by the authors to elicit alarm calls in non-human primates, see below. **D:** Blimp used for monitoring marine megafauna, partially reprinted from Adams et al., 2020.

3 | Algorithms for automated detection of species, individual orientation and body size

While early studies primarily evaluated drone footage manually, recent years have seen an increase in the development of machine-learning algorithms for automated detection of target species from visible-spectrum and thermal video recorded during aerial surveys (Corcoran, Winsen, et al., 2021; Eikelboom et al., 2019; Hollings et al., 2018; Kellenberger et al., 2018; Lyons et al., 2019), see Fig. 2. These tools add to the reliability and replicability of drone surveys and can reduce observer bias, shorten analysis time and process raw material too complex for human observers. Although more systematic comparisons with conventional methods are still needed, automatically detecting and counting species with drones has the potential to increase the accuracy of population estimates in the future (K. R. Adams et al., 2020; Chrétien et al., 2016; Corcoran et al., 2020; Corcoran, Denman, et al., 2021; Dujon et al., 2021; Francis et al., 2020; Gonzalez et al., 2016; Gray et al., 2019; Kellenberger et al., 2021; Seymour et al., 2017). At present, however, these tools remain restricted by how well species can be recognized against their habitat's typical background and to what extent opaque habitats cover parts of a surveyed population. To what degree both of these aspects and issues regarding double counting can be accounted for is therefore critical for the reliability of drone survey based population estimates.

In addition to automated detection of species, software has been developed to track the movement, body orientation and approximate visual fields of individuals from drone footage (Graving et al., 2019; Mathis et al., 2018; Walter & Couzin, 2021), see Fig. 2D. Originally developed for laboratory studies, these methods may now be applicable in field settings. Although body size of targeted species and habitat structure constrain the use of these tools, they possess unprecedented potential for the study of collective movement and behavior (Hughey et al., 2018). Drones may even track and monitor groups independently, as demonstrated by attempts to equip drones with radio-telemetry sensors that automatically find and follow tagged individuals (Cliff et al., 2018; Hui et al., 2021). Finally, video and photogrammetry methods have been developed that use visible-spectrum and thermal drone footage of marine mammals to estimate individual body size or physiological parameters (Dawson et al., 2017; Horton et al., 2019; Krause et al., 2017).

While automated species detection has been shown to be a promising method for population estimates (Corcoran, Winsen, et al., 2021; J. C. Hodgson et al., 2018; Kellenberger et al., 2021), automated tracking of individual pose and movement still requires more empirical testing. Nevertheless, automated evaluation of drone recordings combined with other forms of remote sensing or bio-loggers has tremendous potential for behavioral ecology and conservation research (Hughey et al., 2018; Tuia et al., 2021).

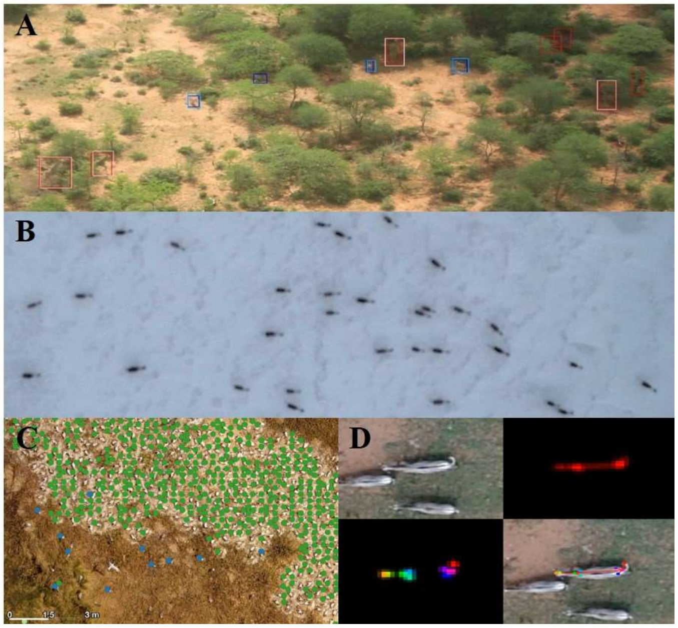

Figure 2: Estimation of species abundance, group movement and individual body position from aerial video footage. **A:** Aerial image with annotated and predicted (lighter colors) bounding boxes showing giraffes (red) and zebras (blue), partially reprinted from (Eikelboom et al., 2019). **B:** Still image from drone video showing a caribou herd being tracked during migration, partially reprinted from (Torney et al., 2018). **C:** Automated detection of gulls (blue) and royal terns (green) in videos recorded during drone surveys of breeding colonies, partially reprinted from (Kellenberger et al., 2021). **D:** Pose estimation of individual zebras from drone footage, partially reprinted from (Graving et al., 2019).

4 | Monitoring group movement, spatial organization and individual behavior

As the methods for tracking orientation and movement of individuals have been developed very recently, few studies have employed such tools so far. Strandburg-Peshkin et al., 2017 used high-resolution drone imagery to create a 3-dimensional landscape reconstruction of the habitat of a troop of olive baboons, *Papio anubis*. Having fitted baboons with GPS-collars to record individual position, they used this data together with their habitat reconstruction to model the influence of structural habitat features on collective group movement. Implementing software for automatic tracking, drones may now also provide the necessary data on individual position. Our own attempts to monitor Guinea baboon, *Papio papio,* movements, were thwarted however, as the baboons mostly remained under tree cover as long as the drone was hovering above (D. Montanari, personal communication).

The first studies that used drones to gather data on movement and inter-individual distances focused on larger herbivores. Using drones to track caribou during their migration, Torney et al., 2018 investigated whether movement choices of individuals belonging to different age classes depended on the movement of neighboring animals and how individual decisions in turn affected group level trends, see Fig. 2B. Drones were also used in conjunction with ground observers to estimate inter-individual distances and individual position relative to the group’s center in feral horses (Inoue et al., 2019, 2020). The authors employed the same approach to create inter-individual proximity networks estimated from drone footage to make inferences about the social organization of the species (Maeda et al., 2021). While they evaluated drone footage manually, future field studies could incorporate tracking tools that have been tested on drone footage from zebras (Graving et al., 2019; Walter & Couzin, 2021), see Fig. 2D.

In marine habitats, drone monitoring was applied to measure individual behavioral events and states in cetaceans or detect and track movements of animals in shallow waters. The results of these studies suggest that drone monitoring increases effective observation time and can provide data on habitat use, social and foraging behaviors that are difficult to collect during conventional boat surveys (Giles et al., 2021; Oleksyn et al., 2021; Torres et al., 2018). For long-term surveillance of coastal waters, blimp-mounted cameras can allow continuous assessment of the abundance and movement patterns of marine megafauna (Ruiz-García et al., 2020) and may even provide non-lethal alternatives to shark meshing (K. R. Adams et al., 2020; Gorkin et al., 2020).

5 | Disturbance and anti-predator behavior

The first descriptions of drone induced disturbance behavior were reported in studies that were primarily concerned with using drones for population estimates. As it was apparent that aversive reactions of animals would have a negative impact on census quality, scientists began to investigate this phenomenon directly. While this led to a vast literature covering many taxa, the methods employed in these studies are very diverse, which hinders systematic comparisons, as has been pointed out in previous reviews on this subject (Christie et al., 2016; Mulero-Pázmány et al., 2017).

Lower flight altitudes or decreasing distance between the drone and the surveyed animals are almost universally associated with disturbance (Bennitt et al., 2019; Fettermann et al., 2019; Headland et al., 2021; McEvoy et al., 2016; Ramos et al., 2018; Rümmler et al., 2021; Schroeder & Panebianco, 2021; Weimerskirch et al., 2018; Weston et al., 2020). While there are exceptions, they appear to be the best general predictors for disturbance and guidelines for the use of drones recommend to always use the highest possible altitude (Duporge et al., 2021; Mulero-Pázmány et al., 2017).

The noise produced by drones and the increase in sound pressure level that is associated with shorter distances between drones and surveyed animals has also been identified as a relevant factor for disturbance (Bennitt et al., 2019; Rümmler et al., 2021; Schroeder et al., 2020; Vas et al., 2015; Weimerskirch et al., 2018). Duporge et al., 2021 reviewed this subject specifically and suggested a method to calculate the minimum drone altitude based on the audiogram of the target species and the noise profile of the drone at different heights. However, even if species specific sensory abilities, prevalent background noise levels and the sound propagation characteristics of the environment are known or can be estimated with reasonable certainty, the potential effects of drone noise should also be evaluated with regard to similar anthropogenic noise that animals may experience and could associate with the noise profile of the drone. Another important aspect in this context is that the flight behavior and approach speed of the drone will affect the noise profile. In marine habitats, drone noise appears to be less problematic since it does not penetrate deep into the water, meaning submerged animals are less likely to be affected than those close to the surface (Christiansen, Rojano-Doñate, et al., 2016). Bird colonies with high levels of background noise may also show higher tolerance for drone sound (Weimerskirch et al., 2018).

Drone silhouette and flight behavior were also identified as potential sources of disturbance (A. Barnas et al., 2018; Bennitt et al., 2019; McEvoy et al., 2016; Rümmler et al., 2021; Schroeder et al., 2020; Vas et al., 2015; Weston et al., 2020). Especially for species facing aerial predation, the shape and movement of novel flying objects might determine whether they categorize them as potential threats or not. Evidently, the more drone behavior and silhouette resemble that of an aerial predator, the more likely it is that drones provokes escape responses (McEvoy et al., 2016). To elicit anti-predator responses experimentally and avoid habituation of subjects, scientists may consider testing flapping-wing drones (Folkertsma et al., 2017) or other more ‘avian like’ models (Ajanic et al., 2020) that resemble aerial predators and are capable of flight maneuvers observed in raptors. Noteworthy, species and population specific predation pressure have been reported to affect the occurrence of disturbance responses in mixed ways. Bennitt et al., (2019) reported that ungulates with higher assumed levels of general predation pressure were less responsive to drones, whereas Brisson-Curadeau et al., (2017) reported that seabird colonies with aerial predators on site responded more strongly than those where aerial predators were absent. We therefore suggest that the extent of population specific predation pressure should be reported and considered when interpreting anti-predator responses.

Variation of response intensity between populations and individuals is another aspect requiring further investigation. Differences between populations could arise due to variation in predation pressure or the extent of anthropogenic disturbance (Ditmer et al., 2019; Schroeder et al., 2020). Inter-individual differences were found to be associated with age categories and the breeding status of individuals (Brisson-Curadeau et al., 2017; Pomeroy et al., 2015; Weimerskirch et al., 2018). Future research should consider social and demographic factors to evaluate how these aspects of group composition affect group level trends during anti-predator behavior (Schroeder & Panebianco, 2021; Torney et al., 2018).

Finally, group size can affect the likelihood, intensity or distance at which responses occur (Giles et al., 2021; Ramos et al., 2018; Schroeder et al., 2020; Schroeder & Panebianco, 2021). Although quantification of group level responses is challenging under field conditions, disturbance or flight behavior can frequently be observed to spread contagiously within groups (Pomeroy et al., 2015; Vas et al., 2015; Weimerskirch et al., 2018). While it has been suggested that larger groups may be able to detect drones faster (Schroeder & Panebianco, 2021), it appears that animals often detect drones acoustically before they can be assumed to be able to spot them visually. Since the predator detection advantage of larger groups is mostly understood as a function of the larger areas they can cover visually by collective vigilance, this mechanism alone would not explain different response characteristics of larger groups if drone detection first occurs acoustically. Simulations and laboratory experiments that investigate collective decisions suggest that the increased sensitivity of groups that can be observed in the form of cascading escape responses is a function of how individuals contribute and respond to the dynamic spatial organization of the group itself (Sosna et al., 2019; Sridhar et al., 2021). Further, increasing group size can reduce the relative proportion of individuals with preferred movement directions that is needed to guide group movement (Couzin et al., 2005). Thus, in the context of drone avoidance, the first individuals to respond likely affect subsequent decisions of other group members who may respond stronger to the reconfiguration of a larger group’s spatial organization than to the drone itself.

So far, tools for automated detection of individual position and movement (Graving et al., 2019; Walter & Couzin, 2021) have not been used to study the dynamics of anti-predator responses in animal groups under field conditions. This will likely change in the near future as these tools could allow experimental investigations of collective behavior in a range of taxa and in the natural conditions in which these behaviors evolved. This could facilitate our understanding of how group size, sociality, demographic composition and other factors affect collective behavior and provide data on population specific differences in anti-predator responses. In particular, the comparison of data coming from different populations could provide valuable insight into the dynamics of predator-prey relationships, the effects of anthropogenic disturbance, and may even shed light on the cognitive mechanisms that guide individuals and groups in their decisions.

6 | Drones as novel aerial threats

In previous work from our group, Wegdell and colleagues used drones as novel, aversive aerial stimuli to investigate the mechanisms that guide predator recognition and alarm call production in free ranging monkeys (Wegdell et al., 2019). They presented drones to West African green monkeys (*Chlorocebus sabaeus*) to test whether the monkeys would categorize the drones as potential aerial predators that would elicit the production of alarm calls. Although researchers at the site had rarely heard aerial alarm calls in this population before (presumably due to the absence of aerial predation), the monkeys responded strongly to the drones and the produced calls closely resembled aerial alarms of a congener, the East African vervet monkey (*Chlorocebus pygerythrus*) (Wegdell et al., 2019).

Wegdell and colleagues followed up the drone presentations by playing back the drone sound to individuals and found that monkeys showed more vigilance during test trials compared to control trials. Since the monkeys did not only show general vigilance behavior but specifically began to look up and scan the sky, this suggested that they had learned to connect the sound with the presence of an aerial threat. This design could be applicable to other taxa as well that produce distinct alarm calls for different threats to probe whether animals categorize novel flying objects as potential aerial predators. As long as the target species has a form of vigilance behavior specifically associated with aerial predation avoidance, playbacks could be used to study whether a species is capable of rapid auditory learning in a predator context.

Future studies that aim to use drones to investigate alarm calling behavior should aim to gather information on the natural frequency and duration of aerial alarms typically produced by their study species. Such data allow for a more efficient planning of the study and the set-up of the recording devices. Given the uncertainty which animals will be calling, it is necessary to have a sufficient number of researchers on the ground. Another problem is the inevitable habituation to the drone and we strongly recommend to keep the presentation of the drone to a minimum. Previous experience with drones may completely derail a study devoted to responses to entirely “novel” stimuli. It is thus necessary to gauge the prior experience before commencing such a study. We also recommend considering to what degree the potential study population is exposed to airplanes, helicopters and other forms of anthropogenic disturbance that have a remote resemblance to drone overflights.

7 | Conclusions

Utilizing the potential of aerial monitoring with automatic detection of species and individual orientation and movement, drones may soon be able to conduct semi-autonomous surveys and collect highly standardized data on habitat structure, species abundance and the demographic composition and movement patterns of groups. This new source of data could improve our estimates of population sizes, the spatial and temporal distribution of species and also allow inferences about the mechanisms that guide individual and collective behavior under natural conditions.

In addition to monitoring, drones can be used as novel aerial threats to probe the cognitive abilities of species. In some cases, they can elicit alarm calling and other anti-predator behavior or may be used in combination with playbacks to investigate the auditory learning capabilities of species. Unless there is a direct need to use drones as predator models, it may therefore in many cases be better to habituate subjects to drones first and subsequently study their responses to more realistic predator models while using drones for monitoring during such experiments. In conclusion, drones are a promising tool for experimental and long-term data collection that can be used alongside other forms of remote sensing and conventional field observations.

Acknowledgements

We gratefully acknowledge funding by the Deutsche Forschungsgemeinschaft (DFG FI707/25-1 – Project Number 428036558) and the Leibniz Association through the Leibniz ScienceCampus Primate Cognition (Seed fund: ‘Drones and RC vehicles for investigating auditory learning in free-ranging primates’–LSC-SF2018-09).

We thank the Diréction des Parcs Nationaux (DPN) and Ministère de l’Environnement et de la Protéction de la Nature (MEPN) de la République du Sénégal for permission to work in the Niokolo Koba National Park. We are grateful to Erica van de Waal and Thibaud Gruber for inviting us to contribute to this special issue.

Conflict of interest

None declared.

Author contributions

Both authors conceived the review; Lukas Schad conducted the literature search and wrote the first draft. Both authors edited the manuscript.

Chapter 4

Alarm barks of male vervet monkeys as vocal displays of male quality

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In preparation for submission

Abstract

Male vervet monkeys (*Chlorocebus pygerythrus*) produce distinct loud calls in response to their major land predators and occasionally during within and between group conflicts. These ‘barks’ or ‘leopard alarms’ are commonly understood to function as alarm calls since they alert group members to potential threats and deter predators, thereby decreasing predation risk for signalers, their offspring and potential mating partners. Since adult males constantly compete for rank and produce barks during agonistic interactions, these loud calls may also function as indicators of male quality. Inter-individual variation in calling frequency could allow receivers to make inferences regarding the signaler’s stamina, competitive ability or motivation to compete. Here, we investigate whether male rank and the degree of male-male competition predict inter-individual differences in loud call usage. We recorded the frequency of naturally occurring bark events over 24 months and sampled individual male participation across events from 45 adult males living in six groups of free-ranging vervet monkeys. We hypothesized that male loud calling activity is under intra-sexual selection and predicted that the probability of producing barks would increase with individual rank and the degree of male-male competition, measured in terms of the number of competitors, adult sex ratio and whether events took place during the mating season. Our results suggest that high-ranking males are more likely to produce barks than lower-ranking ones. We further found an increase in the average number of daily barking events during the mating season. These results corroborate the idea that barks could be under sexual selection, fulfilling the dual function of alarming and indicating male quality.

1 | Introduction

In many primate species, males produce repetitive, high-amplitude calls that are audible over long distances, commonly known as loud calls (Delgado, 2006; Gautier & Gautier, 1977; Mitani & Stuht, 1998; Waser, 1982; Wich & Nunn, 2002). In many forest-dwelling species, these calls exhibit structural features facilitating long-distance transmission (Mitani & Stuht, 1998; Waser & Brown, 1986; Waser & Waser, 1977). The function of these vocal signals has long been understood as promoting group cohesion, advertising the occupation of an area or assisting in the defense of resources by mediating intra- and inter-group spacing (Byrne, 1982; Da Cunha & Byrne, 2006; Gautier & Gautier, 1977; Mitani & Stuht, 1998; Waser, 1975, 1982; Whitehead, 1987). In Addition, loud calls serve an alarm call and predator deterrence function in many primate species (Arnold et al., 2008; Arnold & Zuberbühler, 2006, 2008; Cäsar et al., 2012; Gautier & Gautier, 1977; Isbell & Bidner, 2016; Murphy et al., 2013; Ouattara et al., 2009a; Seyfarth et al., 1980a, 1980b; Struhsaker, 1967a; Zuberbühler, 2000a; Zuberbühler et al., 1997, 1999).

In recent years, primate loud calls have also received attention as potential targets of sexual selection that may fulfill a function in mate attraction or male-male competition (Delgado, 2006; Fischer et al., 2004; Kitchen et al., 2003; Snowdon, 2004; Wich & Nunn, 2002; Zuberbühler, 2002). Since loud calls are produced at high amplitudes and are audible over long distances, physiological constraints affecting signal structure or direct energetic costs related to signal production could impose limitations on individual vocal structure and call rate, rendering loud calls potential honest signals advertising male condition and competitive ability (Ryan, 1988; Vehrencamp, 2000). Support for this function is found in some primate species living in multi-male multi-female groups, where a relationship between loud call structure and call usage with signaler rank has been reported, suggesting a link between individual vocal behavior and competitive ability or motivation to compete (Fischer et al., 2004; Mitani & Nishida, 1993; Neumann et al., 2010; Riede et al., 2007). Furthermore, loud calls propagate over long distances and are thus perceived by a range of receivers, whose responses may vary with the signal's implications for their fitness (McGregor & Peake, 2000). Since loud calls are thus perceived by predators, potential mates and male competitors, some authors have argued that natural and sexual selection may result in more than one function in such signals (Fuller & Cords, 2017, 2020; Zuberbühler, 2002, 2006).

Vervet monkeys (*Chlorocebus pygerythrus*) are an ideal model system for studying inter-individual variation in vocal usage as their alarm call system, and their social ecology have been the subject of intense research for decades (Cheney & Seyfarth, 1990; Price et al., 2015; Seyfarth et al., 1980b, 1980a; Struhsaker, 1967a). They live in multi-male multi-female groups with female philopatry, and males typically depart from their natal groups around the time of sexual maturity and subsequently keep migrating between groups throughout their lives (Henzi & Lucas, 1980). Frequent agonistic interactions characterize relationships among adult males, resulting in a linear dominance hierarchy (Struhsaker, 1967b, 1967c). While there is moderate sexual dimorphism (Turner et al., 1997), females were described as codominant and frequently win conflicts against males, allowing them to resist copulation attempts (Cheney et al., 1988; Keddy, 1986; Young et al., 2017). While male monopolization potential is thus low, recent genetic studies still indicate moderate male reproductive skew in free-ranging (Minkner et al., 2018) and high male reproductive skew in captive vervets (Weingrill et al., 2011). A moderate male reproductive skew despite low monopolization potential thus suggests that dominance presumably increases male fitness due to higher-ranked males´ ability to restrict the reproductive success of competitors by displacing them from limited resources and directly interrupting their copulation attempts.

In response to their main predator categories, vervet monkeys respond with different vocalizations that were found to elicit broadly different escapes responses that appeared to be suited to avoid predation by the respective predator type provoking the calls (Seyfarth et al., 1980b, 1980a; Struhsaker, 1967a). These alarm calls were among the first animal signals described as designating particular threats or events external to the signaler. They thus played a fundamental role in the development of the concept of functional reference, which remains widely influential (Evans, 1997; Evans et al., 1993; Macedonia & Evans, 1993a; Marler et al., 1992; Scarantino & Clay, 2015; Townsend & Manser, 2013).

One of these alarm call types, which is typically produced in response to mammalian land predators (e.g. leopards and caracals), is commonly referred to as 'leopard alarm' or 'threat-alarm-bark' (from here on 'bark') and has been classified as a loud call (Gautier & Gautier, 1977). Barks are only produced by adult males, beginning with the age of sexual maturity (Seyfarth & Cheney, 1986) and are high amplitude calls (Struhsaker, 1967a) that are audible over long distances (≥ 300 m, personal observation). Barks reportedly affect the movement patterns of leopards, suggesting that in addition to alerting group members, they act as a deterrent for predators by advertising to them that their presence has been noticed by their prey (Isbell & Bidner, 2016; Zuberbühler et al., 1999).

Although the alarm and predator deterrence function of barks is thus well understood, their utterance is by no means restricted to the context of mammalian land predators since they also occur during within and inter-group aggressive interactions (Price et al., 2014; Struhsaker, 1967a). A recent structural analysis of barks produced in predator and aggressive contexts revealed graded variation, suggesting that signal structure alone may not allow receivers to make precise inferences regarding the stimulus that provoked calling (Price et al., 2015). The finding that in playback experiments, subjects do not always react with stereotypical escape responses like ‘climbing into a tree’ but show considerable variation in their responses supports this interpretation (Ducheminsky et al., 2014; Price et al., 2014; Seyfarth et al., 1980b). Adult males were even found to frequently approach barks and pay more attention to barks of unknown males in playback experiments, leading the authors to suggest that barks may also function as intra-sexual displays (Price et al., 2014). This interpretation is in accordance with a proposal from Zuberbühler (2002), who suggested that specific predation pressure may have initially led to the evolution of loud alarm calls due to their predator deterrence effect, which could then have served as substrates for sexual selection.

Despite the extensive body of previous research on bark structure and receivers' responses to them, the degree of variation in bark usage has received comparatively little attention (but see: Cheney & Seyfarth, 1981; Seyfarth & Cheney, 1985). However, a complete understanding of the function of vocal signals requires that variation in signal usage is examined among individuals with regard to all aspects of a species’ social ecology (Byrne, 1982). Due to their high amplitudes, barks are audible for many different receivers simultaneously (Isbell & Bidner, 2016; McGregor & Peake, 2000), and signalers may incur energetic costs in their production, in addition to potential opportunity costs (Henzi et al., 2021). Since barks not only occur in predator contexts but also during agonistic interactions, costs related to call production could result in a ‘quality handicap’ where barks become honest signals of individual competitive ability (Vehrencamp, 2000), as has been suggested for the contest barks produced by chacma baboons and geladas during male-male conflicts (Benítez et al., 2016; Fischer et al., 2004; Kitchen et al., 2003).

In this study, we tested the following two non-mutually exclusive hypotheses: (1) Barks are honest signals of individual competitive ability and under intra-sexual selection. (2) Males adjust their bark production according to their number of potential offspring in the group, which should correlate with their tenure. In the first part of this study, we examined how frequently individual males produced barks in group-level events in relation to individual quality, tenure and the degree of male-male competition. We used rank as a proxy for individual quality, as this construct reflects male competitive ability. We gauged male-male within group competition by considering the number of adult males in the group and the adult sex ratio, measured as the number of adult females per male. Finally, we assumed increased male-male competition during the mating season, which is approximately between April and July, based on previous work in this species (Young et al., 2020) and the distribution of births in our study time, assuming a 157-168 day gestation period (Minkner et al., 2018). We calculated male tenure as the number of mating seasons an adult male was present in a group, since only presence during the mating season can result in reproductive success, which could not be measured directly.

If barks were honest signals of individual competitive ability, the likelihood of participating in a barking event should increase with individual quality and the degree of male-male competition. Therefore, we predicted a three-way interaction of rank, mating season and the number of adult males in the group as well as a three-way interaction of rank, mating season, and adult sex ratio. Male calling probability was expected to increase with male rank, with the steepness of the increase depending on the number of male competitors, the adult sex ratio and whether events took place during the mating season or not (fig 1A-1D). However, if barks were primarily adaptive due to their alarm function, we would expect that males gain differential fitness benefits from alarm calling depending on the number of potential offspring they had in the group. Males with more offspring would be expected to profit more from alarm calling and should thus show higher barking activity. Due to moderate reproductive skew among male vervets (Minkner et al., 2018), we assumed male offspring number to correlate positively with tenure and predicted that individual likelihood to participate in barking events should increase with individual tenure.

In the second part of the study, we investigated whether the daily number of barking events was related to group composition and the mating season. We predicted that if barks functioned primarily as alarm calls, the number of daily events would only increase with increasing group size. However, if barks were honest signals of male competitive ability, we predicted that the daily number of alarm events would increase with increasing male-male competition, whereby mating season and the number of adult males should interact as well as mating season and the adult sex ratio (fig. 2).

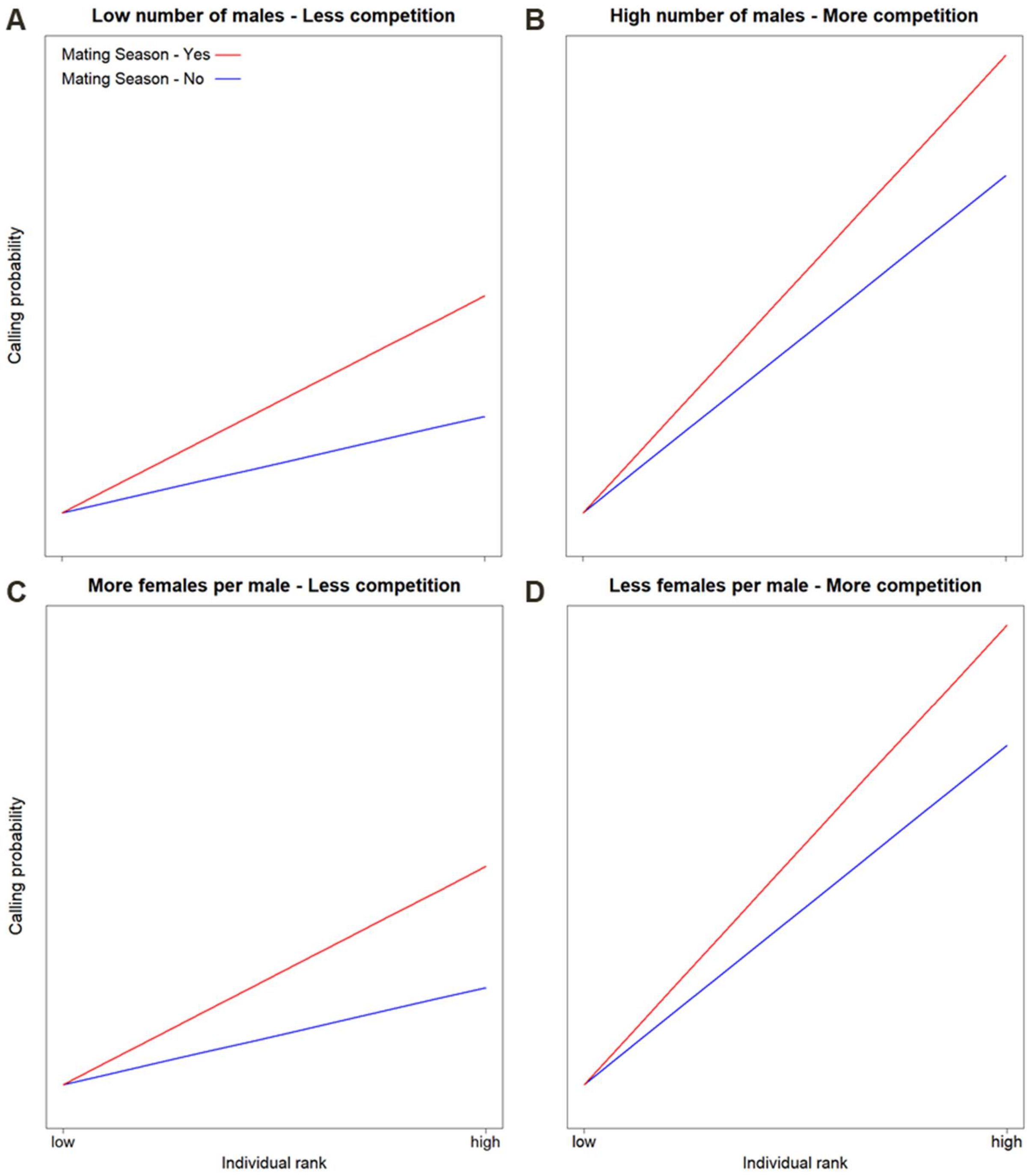

Figure 1: Predictions for barks as vocal displays of male quality. Male calling probability is predicted to increase with male rank (**A**, **B**, **C**, **D**), with the steepness of the increase depending on the number of male competitors (**A**, **B**), the adult sex ratio (**C**,**B**) and whether events occur inside or outside the mating season (**A**, **B**, **C**, **D**).

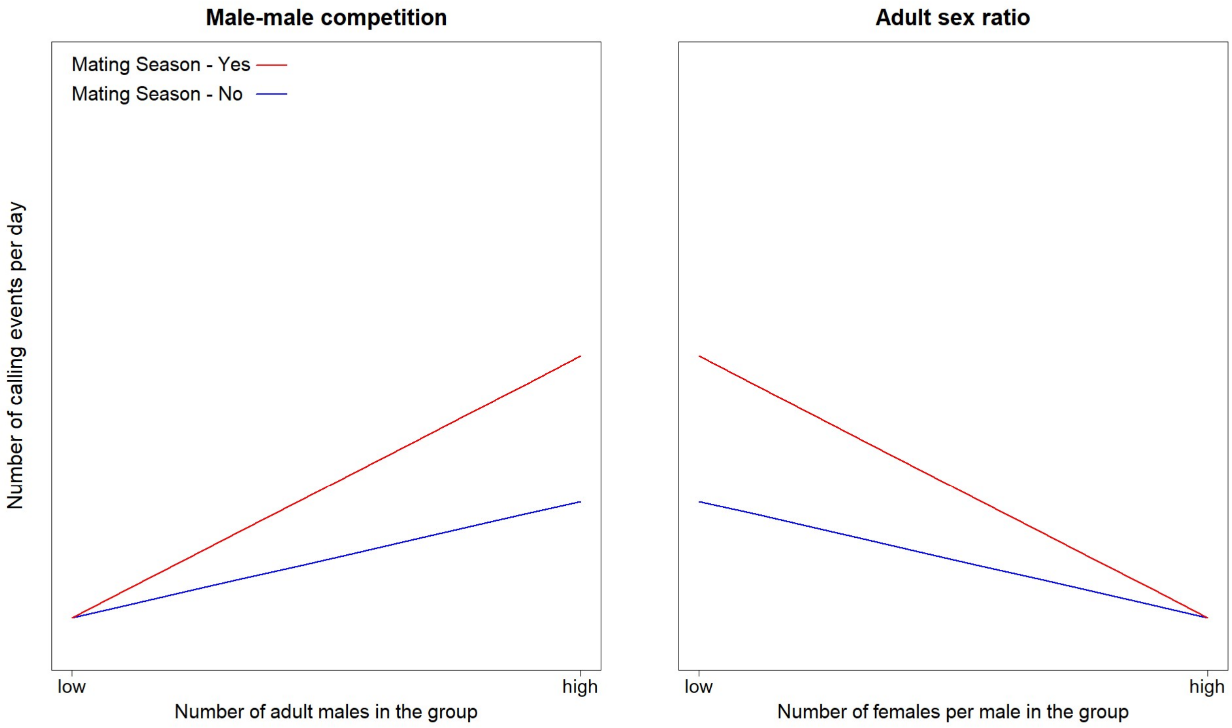

Figure 2: Predictions for barks as vocal displays of male quality. The daily number of alarm events is expected to increase with increased male-male competition in the group, measured in the number of adult males per group (**A**) and the adult sex ratio (**B**). The steepness of the slope for both predictors is further expected to depend on whether an observation day falls into the mating season (**A**, **B**)

2 | Methods

2.1 | Study site, subjects, data collection and data set composition

Between Mai 2020 and April 2022, we collected data on six groups of free-ranging vervet monkeys at the Inkawu Vervet Project in the Mawana Game Reserve, KwaZulu-Natal, South Africa. We recorded individual presence or absence from a group in a logbook dataset for every observation day and used *ad libitum* sampling (Altmann, 1974) to record data on agonistic interactions and individual participation in group-level barking events. All subjects could be recognized by researchers using individual facial and body features. Unfortunately, since the number of researchers working at the field site was reduced from 20 to six at the beginning of 2020 due to the Covid-19 pandemic, we could only work with four groups for the majority of 2020. We re-added two more groups (KB and CR) in 2021 that had already been under observation in the past as soon as the number of researchers allowed us to monitor these groups again regularly.

Individuals could be missing from their respective groups because of injury, whilst exploring other groups (especially during the mating season from April to the end of July), for unknown reasons or due to temporary group splits that could last from days to several weeks. Due to this fluctuation in group composition, we used data on individual presence in logbook recordings to calculate the total group size, the number of adult females and adult males, and the adult sex ratio of a group for every observation day. In addition, using logbook entries, we also accounted for unknown adult males in the above-listed group composition variables whenever their presence was recorded in the field.

We recorded data on individual participation in barking events *ad libitum* whenever one or more males produced barks. Since barks are audible over several hundred meters ($\geq$ 300 m, pers. observation), exceeding regular group spread in this species by far ($\leq$ 150 m, pers. observation), we deem it unlikely that we missed a barking event while observers were with a group. For every barking event, human observers spread out to approach the directions the barks were heard from in order to track down and identify individual callers one after the other. An event was determined to be over when calling ceased for more than five minutes. In each of these group-level events, we recorded the date, time, group, the identity of every adult male producing barks, the number of unknown male callers that could not be identified in time, the duration of the event (estimated in

5-minute intervals from the first to the last call) and the larger context of the calling bout (table 1S).

We used decided dyadic conflicts to calculate dominance hierarchies based on Elo-ratings (Neumann et al., 2011). After each conflict, we updated every individual's position in the hierarchy and calculated group hierarchies for every day in our dataset. We used all available conflict data from 2012 onward to calculate individual positions in the hierarchy and added new individuals joining a group as soon as observers could reliably identify them. Thereby, we estimated group hierarchies for the entire 23-month study time with individual Elo-ratings for every day in our data set. We proceeded to rank individual adult males according to their Elo-scores to express the number of other adult males that an individual dominates on any given day in their respective group. The lowest-ranked male on a day was assigned a zero (dominating no other males), while the highest-ranked male was assigned a value of N – 1, where N is the number of males present on that day (dominating everyone but himself). Subsequently, we divided this numeric rank by N – 1 to express the proportion of other males dominated (range: 0 – 1). We excluded unknown adult males from the ranking as they had no Elo-scores. As a result, the relative male ranks for every observation day were comparable between groups with different numbers of adult males.

We then used the logbook data, male ranks and the data on individual male participation in barking events to compile two datasets. The 'individual participation dataset' provides the following information for every barking event: The identity of every male present, whether a male produced barks (Yes/No), the relative male rank (range: 0 – 1), male tenure (number of mating seasons present in a group), the number of adult males, the adult sex ratio (number of females per male), whether the event took place during the mating season (Yes/No), as well as group identity and the date of the event. In the second 'event count dataset', we calculated the total number of group-level barking events for every group on every observation day in addition to the group size (total number of individuals), number of adult males, the adult sex ratio, the observation time for the respective day and whether the day fell into the mating season (Yes/No).

2.2 | Statistical analysis – General procedure

All statistical analysis was conducted in R (v. 4.2.1) using the 'lme4' package (v. 1.1-30) (Bates et al., 2015; R Core Team, 2021) and the glmmTMB package (v. 1.1.4) (Brooks et al., 2017). We fitted a binomial and a zero-inflated Poisson model and included all theoretically identifiable random slopes into the models to minimize type I error rate (Barr et al., 2013). The assumption that the best linear unbiased predictors for each random effect were normally distributed was confirmed by visually inspecting histograms for every random intercept and slope component (Baayen, 2008). To assist model conversion and ease comparability of model estimates, we used the optimizer 'bobyqa' in the binomial model, z-transformed all covariates to a mean of zero and a standard deviation of one and dummy coded and centered the factor mating season, using 'outside mating season' as reference category (Schielzeth, 2010). We excluded all correlations among random intercepts and slopes as they appeared unidentifiable (absolute correlation parameters $\geq .9$) (Matuschek et al., 2017). To rule out collinearity among predictors, we checked variance inflation factors using the R package 'car' (v. 3.1.0) (Fox & Weisberg, 2019) on reduced general linear mixed models excluding only the random effect structure.

For the zero-inflated Poisson model, we checked the dispersion parameter to avoid potential type I errors due to overdispersion. To prevent 'cryptic multiple testing' (Forstmeier & Schielzeth, 2011), we compared the full models to null models that only included control predictors and offset terms and the same random effect structure as the full models by using a likelihood ratio test

(Dobson & Barnett, 2018). We assessed the model stability with a custom function (provided by R. Mundry), in which we compared the estimates of the full model with those obtained from reduced models that excluded one random effect at a time (Nieuwenhuis et al., 2012). Confidence intervals were calculated with the ‘bootMER’ function of the ‘lme4’ package using 1000 parametric bootstraps. P-values for individual fixed effects and all interactions were derived from likelihood ratio tests using the R function ‘drop1’ with a Chi-square test argument (Barr et al., 2013). If interactions were not significant according to likelihood ratio tests, we constructed reduced models and removed the respective interactions as main effects without changing the random effect structure of the models.

2.3 | Binomial model – Individual participation

We used a Generalized Linear Mixed Model (Baayen, 2008) with binomial error structure and logit link function to investigate which factors influenced male probability to participate vocally in a barking event. As fixed effects, we incorporated the covariates male rank, number of adult males, adult sex ratio, male tenure, and mating season (yes/no). We also included two 3-way interactions, namely of male rank, mating season, and number of adult males, and of male rank, mating season, and adult sex ratio. As random factors, we included individual ID, group ID, event ID and the combination of date and group since we assumed that the effect of date varies among the different groups.

We excluded all events where unknown males produced barks from the analysis since the barking activity of unknown callers would introduce uncertainty into the binomial response ‘male produced barks (yes/no)’. We also excluded events from groups that temporarily just had a single resident adult male since males in single-male groups could not be ranked with regard to the position of other male competitors inside the group. Lastly, we excluded events that only contained subadult male callers.

2.4 | Poisson model – Event count

To assess whether group composition and the mating season affected the number of barking events recorded per day, we used a Generalized Linear Mixed Model with a Poisson error structure and a log-link function (Brooks et al., 2017; McCullagh & Nelder, 1989), accounting for zero inflation. We included the covariates number of adult males, adult sex ratio and the factor mating season as main fixed effects. In addition, we added the interactions of mating season and number of adult males, and of mating season and adult sex ratio. In addition, we included the covariate group size as a control predictor and a log-transformed offset term reflecting the observation effort (hours spent with the group) on a respective day. As a random factor, we included group ID. An initial Poisson model revealed that the observed number of zeros was higher than expected given the model. To account for zero-inflation we incorporated a random intercept in the zero-inflation part of the model, but none of the predictors from the count part of the model. We had to exclude all days with missing observation time entries from the dataset since it is impossible to calculate an offset for observation effort on such days.

3 | Results

In 23 months, we recorded a total of 886 barking events. The context of most events could not be determined (fig. 3). The distribution of the number of adult males that produced barks in calling events revealed that in the vast majority of events, only a single male was calling (fig. 4). We also found that event durations showed considerable variation, with the majority of events not lasting longer than about five minutes, while in rare cases, durations of up to one hour were recorded (fig. 5). Barking events occurred at all times of the day, with no apparent increase in activity around sunrise or sunset (fig. 1S).

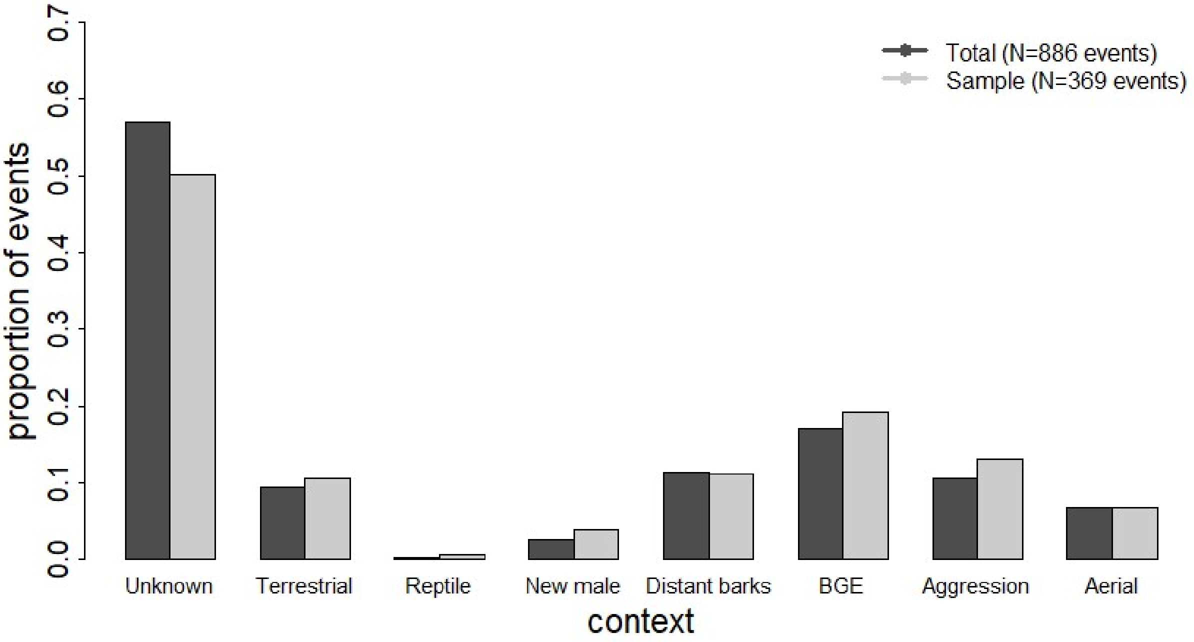

Figure 3: Relative proportions of contexts across all barking events (N=886, dark grey) and in the sample (N=369, light grey) used in the individual participation analysis. Note that barking events can be assigned to multiple contexts simultaneously.

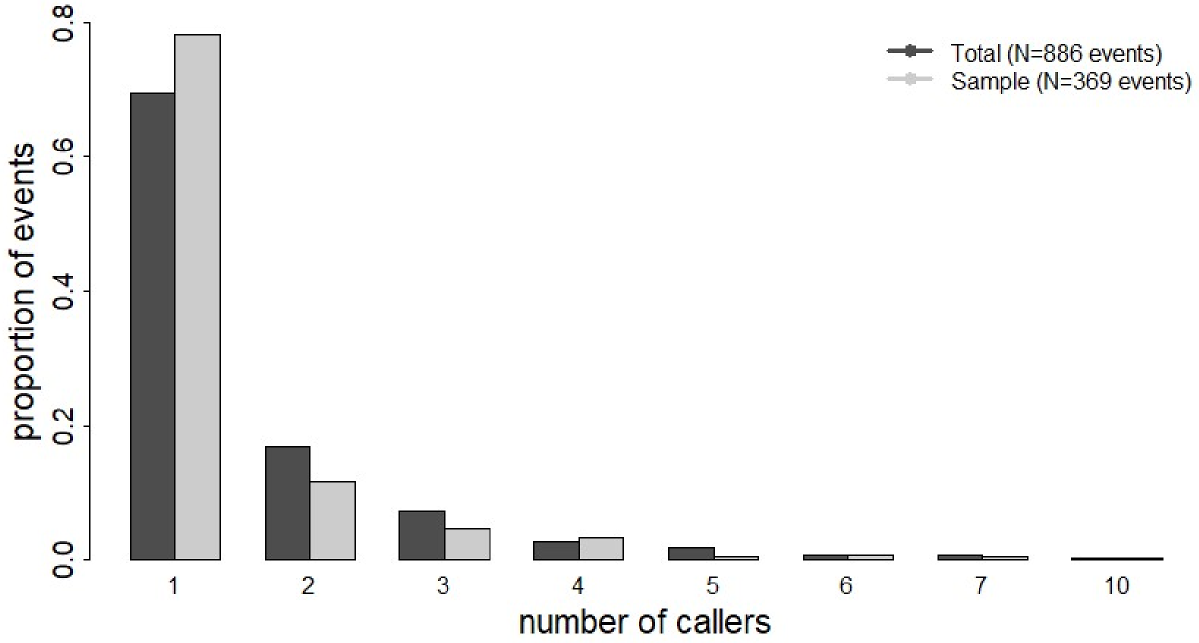

Figure 4: Distribution of the number of callers across all events (N=886, dark grey) and in the sample used for analysis (N=369, light grey). In the majority of events, only a single adult male produced barks.

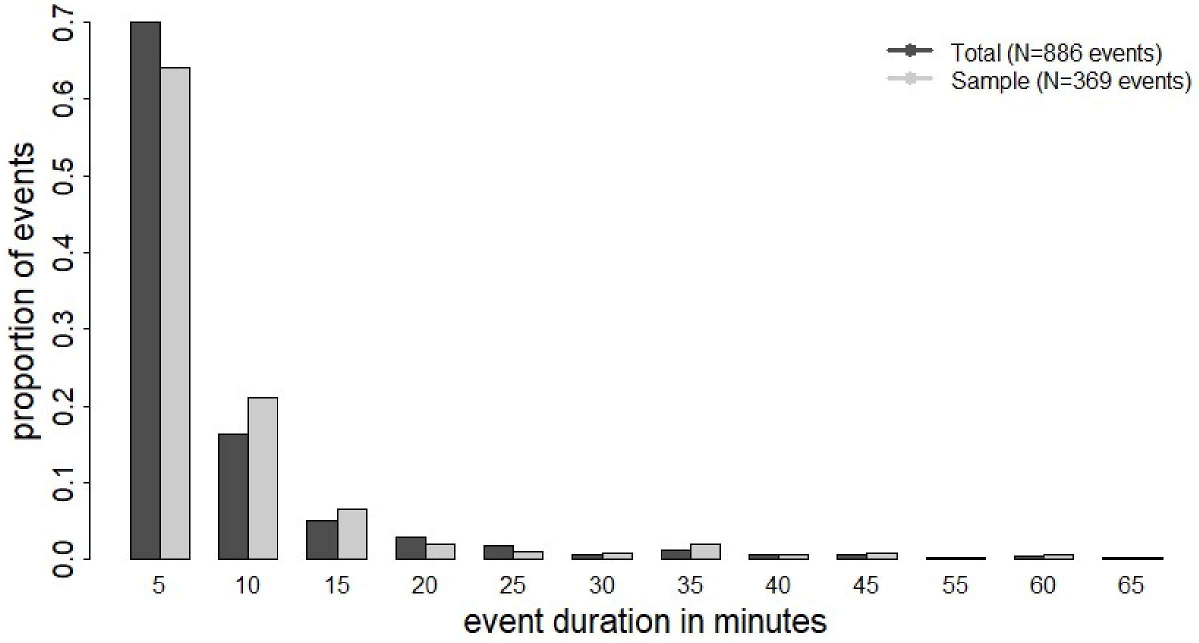

Figure 5: Distribution of event durations in 5 min intervals for all events (N=886, dark grey) and the sample used to analyze individual participation (N=369, light grey). Most events last about 5 minutes.

3.1 | Binomial model – Individual participation in barking events

After excluding unknown male callers, single male groups and events only containing subadult male callers, the sample for the model comprised 369 events yielding 2055 individual data points (524 barking participations) from 45 adult males in six groups over 291 days (table 1). Participation rates of individual males appeared to vary substantially, with some males being active in a large proportion of events they were present in, while most males rarely engaged in call production (table 2S). Male rank and tenure also varied among and within individuals, with 23 of 45 individuals at least temporarily holding the highest rank in their respective groups and males being present in their groups from zero to seven cumulative mating seasons (table 2S).

Table 1: Individual participation dataset, showing the number of events and the mean and standard deviation of the group composition predictor variables for all six groups.

Group	AK	BD	NH	LT	KB	CR
Events inside the mating season	68	49	23	28	16	6
Events outside the mating season	47	46	33	35	12	6
N adult males mean ± s.d.	3.7 ± 1.2	10.5 ± 1.3	6.9 ± 1.4	4.1 ± 1	2.6 ± 0.6	3.7 ± 0.6
Adult sex ratio mean ± s.d.	2.2 ± 1	1.9 ± 0.4	1.8 ± 0.5	2.5 ± 0.8	2 ± 0.5	2 ± 0.9

Collinearity among predictor variables could be ruled out with all variance inflation factors < 1.8. The fixed effects of the model had an overall impact on the probability of individual participation in barking events, as shown by comparing the full and null models ($\chi2$ = 25.326, *df* =

12, *P* = 0.013). Since likelihood ratio tests indicated that none of the interactions were significant, we removed them and fitted a reduced model in the following (see table 3S and 4S for full model results and the results of likelihood ratio test on three-way and two-way interactions). The model revealed that higher-ranking individuals had a higher probability of engaging in barking activity (fig. 6 and table 2). The positive effect of rank on calling probability appeared moderate overall, except for the highest-ranked individuals, who showed a high average calling probability compared to all other ranks (fig. 6).

Table 2: Model results showing the impact of the fixed effects on the probability of participating in a barking event. Shown are model estimates, standard errors, confidence intervals (CI) and the test results obtained from likelihood ratio tests.

Term	**Estimate**	**SE**	**Lower CI**	**Upper CI**	***χ2***	***df***	***P***
Intercept	-1.767	0.266	-2.263	-1.165			*
Rank	0.667	0.144	0.363	0.941	9.589	1	0.002
N males	-0.919	0.238	-1.399	-0.421	10.479	1	0.001
MatingSeasonY	-0.133	0.238	-0.617	0.341	0.325	1	0.568
SexRatio	0.022	0.139	-0.272	0.315	0.024	1	0.876
Tenure	0.268	0.184	-0.110	0.685	2.021	1	0.155

* Not shown due to limited interpretability.

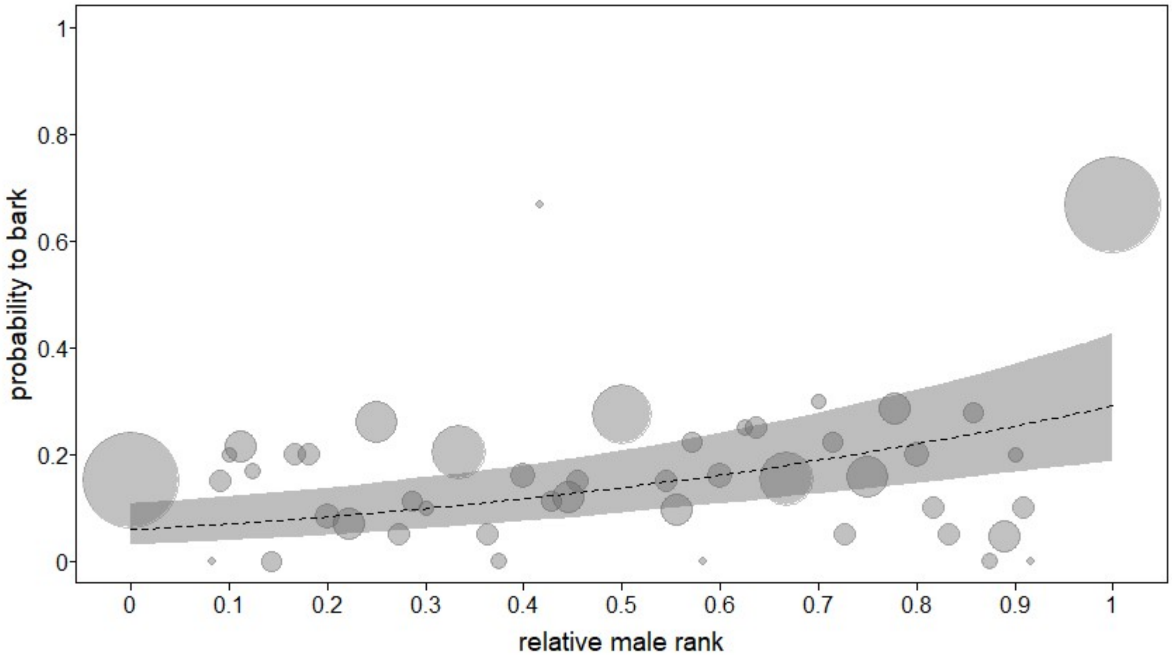

Figure 6: The effect of male rank (relative to other males in the group) on the probability of producing barks in a group-level calling event. The plot shows the average barking probability for every rank value in the data set, with the circles´ area proportional to the frequency that a given rank value occurred. The dashed line depicts the fitted model, and the grey shaded area the bootstrapped 95% confidence intervals, with all other predictors being at their mean for covariates and centered reference category for the factor mating season. Higher-ranked individuals are likelier to participate in a barking event (GLMM: n = 2055, *p* = 0.002).

In addition to a positive effect of rank on calling probability, the model revealed that a higher number of adult males in the group was associated with decreased individual probability to produce barks in an event (fig. 7 and table 2). The distribution of the number of calling males showed that in most events, only a single male was calling (fig. 8 and fig. 4). Notably, the highest-ranked males were responsible for more than half of the single male calling events and also participated in a large proportion of all other events (fig. 8). We found no obvious effects of the adult sex ratio, mating season and male tenure on individual probability to produce barks in a calling event (table 2).

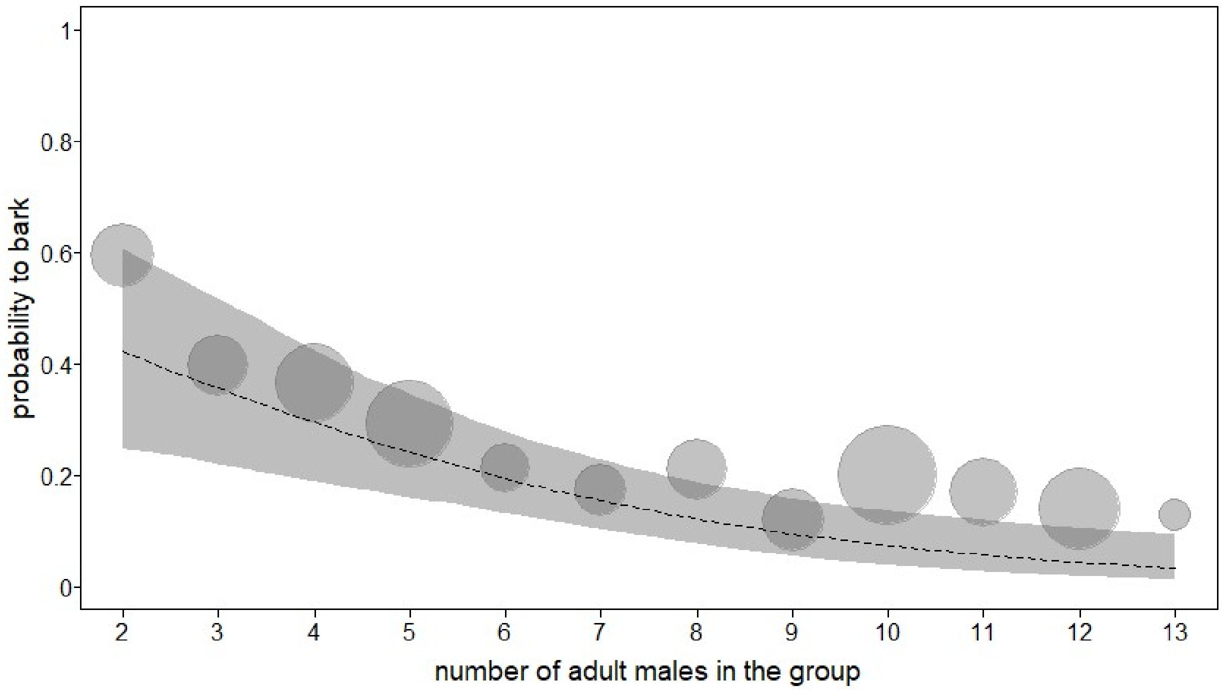

Figure 7: The effect of the number of males in the group on the probability of producing barks in an event. The plot shows average barking probability, with the circle area proportional to the frequency at which a given number of males occurred. The dashed line depicts the fitted model, and the grey shaded area the bootstrapped 95% confidence intervals, with all other predictors at their mean or centered reference category, respectively. Higher numbers of males decrease barking probability (GLMM: n = 2055, *p* = 0.001).

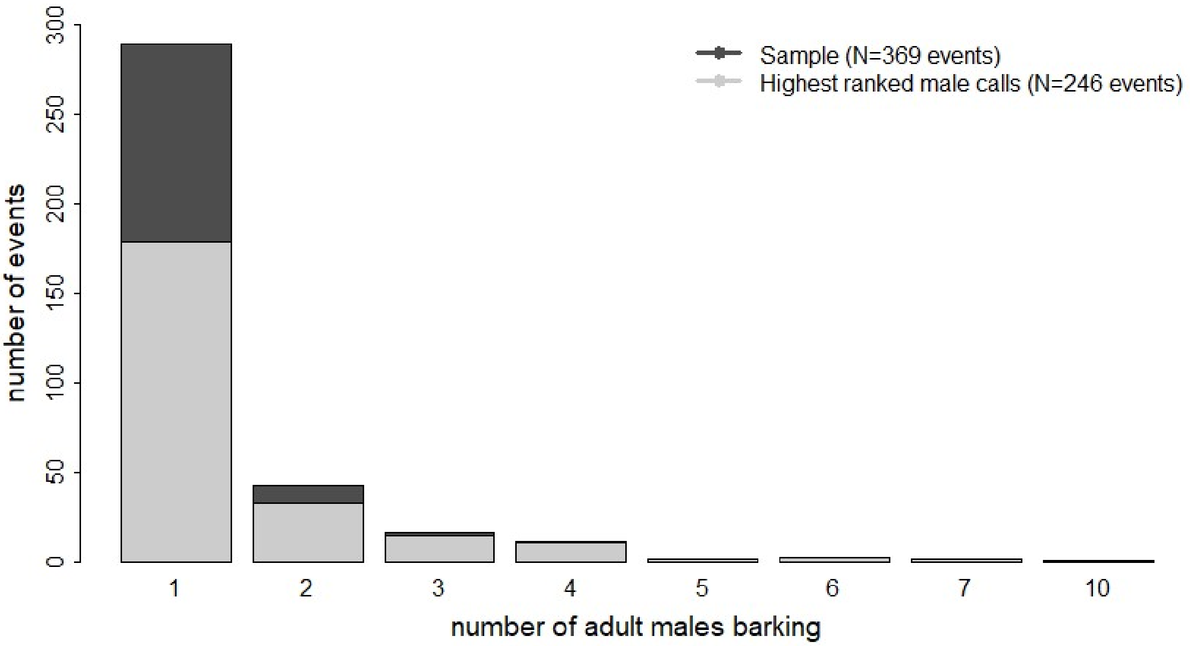

Figure 8: Distribution of the total number of callers in the sample (N = 369, dark grey). The light grey area shows the proportion of events where the highest-ranked male present produced barks in the event (N = 246). In most events, only a single adult male called. The highest-ranked males were active in the majority of events.

3.2 | Poisson model – Event count

After excluding days with missing observation times, the sample for analysis comprised 1915 group observation days (mean ± s.d. 6.9 ± 2.1 hours) with 821 barking events (table 3). Collinearity among predictor variables could not be entirely excluded with variance inflation factors for 'mating season' and 'sex ratio' < 1.9, but 'number of adult males' and 'group size' < 6.8. Overdispersion could be ruled out (dispersion parameter = 1.08). The fixed effects appeared to affect the number of group-level barking events per day, as shown by comparing full and null model ($\chi 2 = 20.387$, $df = 5$, $P = 0.001$). Subsequent likelihood ratio tests indicated that none of the interactions were significant (see table S5 for full model results and the likelihood ratio test on interactions).

Table 3: Event count dataset, showing the number of observation days and the mean and standard deviation of the predictor and control variables for all six groups.

Group	AK	BD	NH	LT	KB	CR
Sample days inside the mating season	135	163	147	123	58	30
Sample days outside the mating season	239	319	305	223	115	58
N adult males mean ± s.d.	3.3 ± 1.3	9.8 ± 1.9	6.4 ± 1.3	3.4 ± 1.1	2.4 ± 0.7	3.6 ± 0.7
Adult sex ratio mean ± s.d.	2.8 ± 1.3	2.1 ± 0.6	1.8 ± 0.5	3.1 ± 1.4	2.4 ± 1	2.2 ± 0.9
Group size mean ± s.d.	24 ± 3	60 ± 8	38.8 ± 4.1	26.9 ± 3.2	17.8 ± 2.1	25.8 ± 4

Table 4: Model results show the impact of the fixed effects on the number of barking events per day. Shown are model estimates, standard errors, confidence intervals (CI) and the test results from likelihood ratio tests.

Term	Estimate	SE	Lower CI	Upper CI	*χ2*	*df*	*P*
Intercept	-2.658	0.095	-2.876	-2.490			*
MatingSeasonY	0.742	0.098	0.532	0.930	14.798	1	0.000
SexRatio	0.042	0.084	-0.139	0.186	0.274	1	0.601
N males	0.187	0.117	-0.068	0.402	2.353	1	0.125
Group Size	-0.109	0.105	-0.325	0.108	1.087	1	0.297
Zero-infl-Intercept	-0.555	0.145	-0.886	-0.303			*

* Not shown due to limited interpretability.

The reduced model revealed that during the mating season, the number of barking events per day increased (fig. 9 and table 4). However, the group size, adult sex ratio and the number of adult males in the group did not obviously affect the number of bark events per day (table 4). The distribution of the number of barking events per month also indicated an increase in monthly event frequencies during the mating season (fig. 10). The distribution of births in the 23 months of the study period shows that our estimate of the mating season from April to July was accurate, as most conceptions occurred in May in June, and only one apparently outside the mating season (fig. 11).

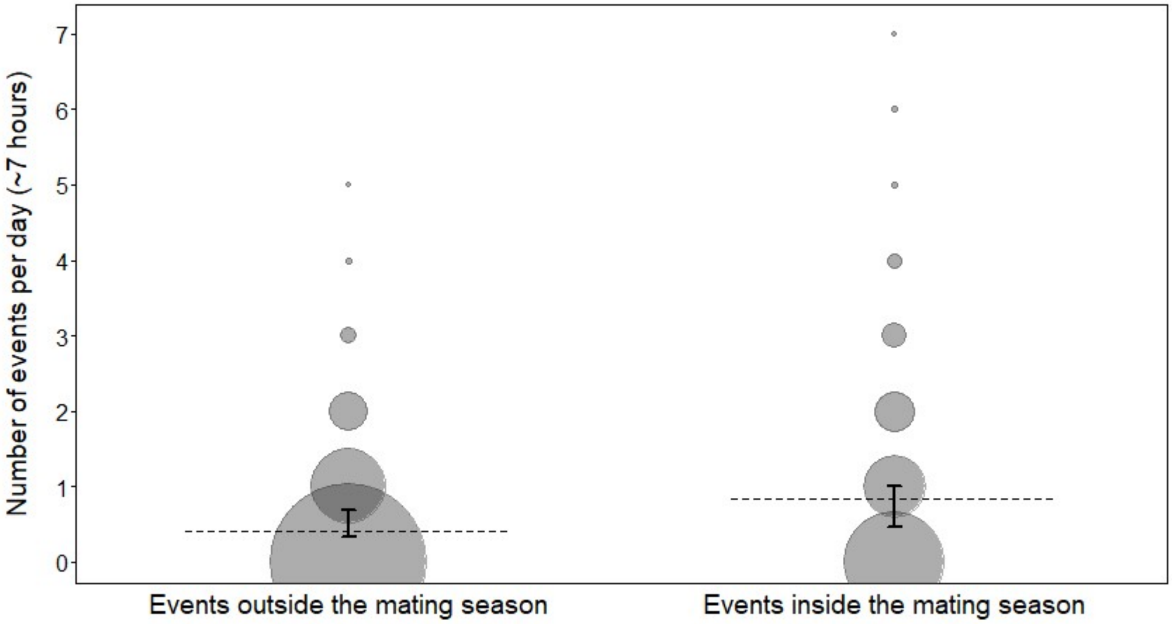

Figure 9: The effect of the mating season on the number of barking events recorded per observation day, with an average observation time of approximately seven hours. The plot shows the daily number of barking events, with the circle area proportional to the frequency that a certain number of events was recorded per day. The dashed grey line depicts the fitted model, and black error bars indicate the bootstrapped 95% confidence intervals, with all other predictors being at their average. Barking events occurred more frequently during the mating season (GLMM: n = 1915, $p < 0.001$, see table 4).

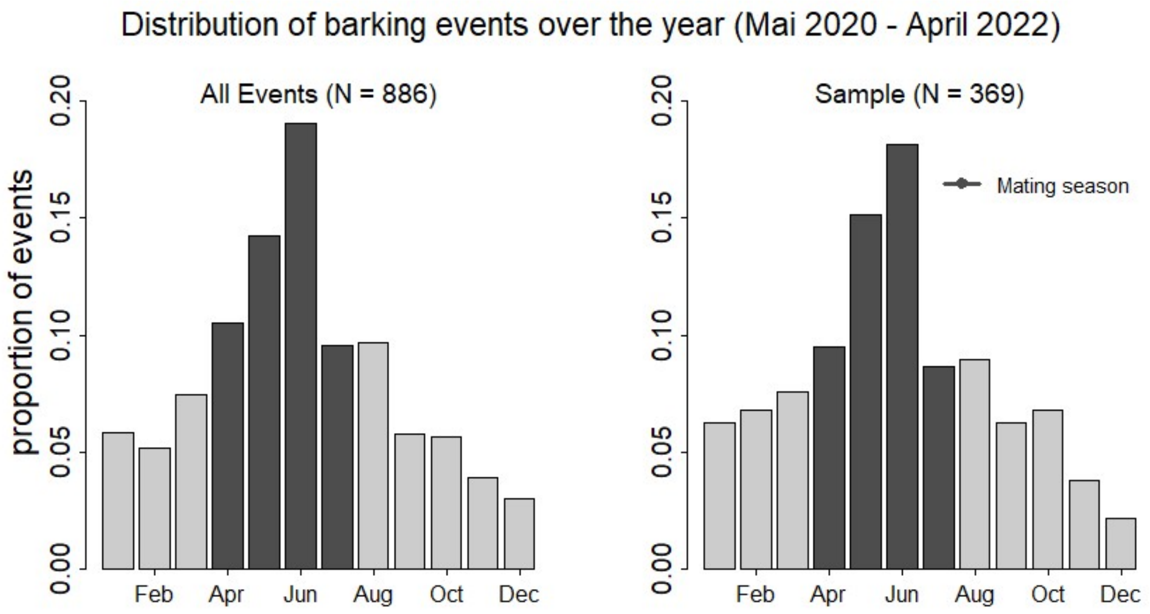

Figure 10: Proportion of calling events per month with mating season indicated.

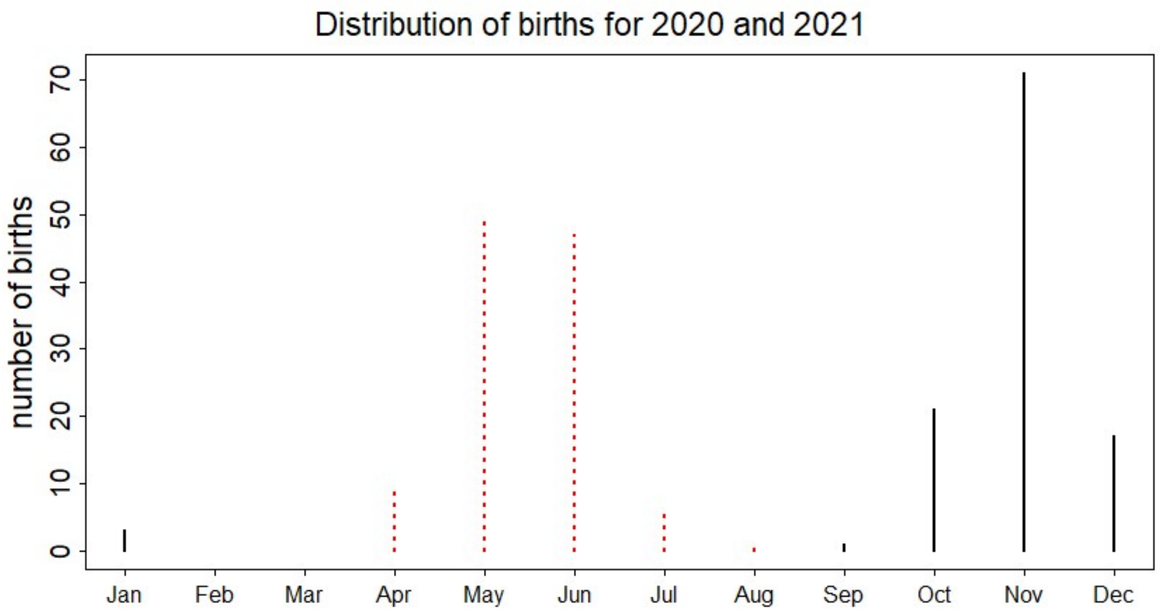

Figure 11: Monthly frequency of births (solid lines) and dated back times of conception (dashed lines) in all six groups for the years 2020 and 2021 (N=107 births). The majority of births occur in November. With a gestation period of 165 days, most conceptions occur in Mai and June.

4 | Discussion

In line with our predictions, the probability of adult males engaging in barking varied with the rank that an individual male held at the time of the event. While our data showed sizeable inter-individual variation in participation rates, the highest-ranked males in a group showed much higher calling probabilities than all other ranks. Furthermore, the individual barking probability decreased with increasing numbers of adult males in a group. This result contradicted our predictions but is most likely due to the surprisingly low number of callers across events. Since, in most events, only a single male engaged in the barking activity, the individual baseline calling rate decreased when more males were present. Taken together, the model results and the distribution of the number of callers across events indicate that, independent of the number of adult males present in a group, in most events, only a single male will produce barks, with the highest-ranked males being the most likely individuals to do so.

The fact that barking seems primarily restricted to the highest-ranking male at the time may also explain why we found no effect of the adult sex ratio or the mating season on calling probabilities. An alternative explanation is that barks are not reserved for within-group conflicts but are also used in between-group encounters and against new males trying to join the group (Price et al., 2014). In contrast to our predictions, which were within-group focused, resident males in groups with a low number of males and many females per male might be incentivized to engage in frequent barking activity to repel new rival males before they join the group and thereby maintain a low number of competitors (Sekulic & Sekulic, 1982). An increasing number of males in the group may thus result in a 'diffusion of responsibility' and a volunteer dilemma (Diekmann, 1985) if males are less motivated to repel new competitors when in-group competition is high, and they are already unable to monopolize females under such conditions. Males may thus be incentivised to bark frequently because of high within group competition, but also to keep out new rivals to maintain low within group competition and thus favourable access to females. Due to this dilemma, the potential effects of group composition will require further investigation.

Our analysis of daily event frequency also showed that group composition variables were again without any noticeable effect. However, the results revealed that during the mating season, when males face increased competition for access to females, the average number of daily barking events is increased compared to the rest of the year. Taking the results of both models into account, we thus found an increase in daily event frequency during the mating season but no substantial changes in individual probability to participate in barking events in and outside the mating season.

While the increase in daily event frequency appeared moderate, we wish to highlight that the distribution of barking events suggested a peak in barking activity between Mai and June. Our estimate of the mating season ranging from April to the end of July is, however, a conservative estimate based on previous work in the species (Young et al., 2020) and our observations regarding the presence or absence of mating behavior in the respective month. Furthermore, the distribution of births in the 24 months of our dataset showed that the vast majority of individuals are born in November, meaning that with an average gestation period of 157-168 days (Cho et al., 2002; Hess et al., 1979; Seier, 1986; Seier et al., 2000), most females conceive between Mai and June, which is precisely the time of year when barking events are most frequent. Although it is currently assumed that female vervet monkeys conceal the time of ovulation from males (Andelman, 1987), the increase in barking activity when most females conceive still suggests that males may respond to female receptive status by altering their barking frequency.

Future studies could use male focal data to explore whether males potentially respond to increased copulation rates and interrupt copulations by using barks. Taken together, male vervet monkeys demonstrate call usage variation that appears to be driven by rank, with the frequency of call usage increasing during the mating season. Previous studies also suggest that barks are sexually dimorphic (Price et al., 2014, 2015; Seyfarth & Cheney, 1986; Struhsaker, 1967a). Barks of vervet monkeys thus potentially fulfill two of Snowdon´s (2004) criteria for demonstrating sexual selection in a signal: Sexual dimorphism and inter-individual variation in signal usage. The increased frequency of barking events during the mating season and the higher calling probabilities of high-ranking males further support the idea that this variation in call usage is likely to have implications for male reproductive success. Neither of these results would be assumed under the conventional assumption that barks only serve as alarm calls.

Since barks are used in aggressive interactions, they have the potential to play a role in the resolution of conflicts without costly fights by displaying male competitive ability or motivation. Given that barking is associated with some costs, either by direct energy expenditure or opportunity costs such as missed foraging time (Henzi et al., 2021), alpha males can be assumed to face higher theoretical costs than other males in the group, especially during the mating season. It is thus possible that barks are ‘quality handicaps’ (Vehrencamp, 2000) and an honest signal of male competitive ability if lower-ranked individuals were also of lower condition and could not afford to engage in barking activity as frequently due to the cost incurred during signal production. Studies on chacma baboons, geladas and crested macaques have shown that call usage is predicted by individual rank, and the authors suggested that a quality handicap could explain this pattern (Benítez et al., 2016; Kitchen et al., 2003; Neumann et al., 2010). However, male vervet monkeys do not appear to engage in direct signaling contests, and since we do not present an analysis of call rates here, our support for this idea is limited.

An alternative mechanism that may explain our results is that in aggressive contexts, barks could be conventional signals that relate to male motivation to escalate a fight (Enquist, 1985; Vehrencamp, 2000). Conventional signals are thought to remain honest even when the costs of signal production are low due to a receiver retaliation rule, whereby if both parties in a conflict choose an aggressive signal, fights become highly likely, which effectively punishes individuals who signal aggressively but are not in good enough condition for a fight (see: Molles & Vehrencamp, 2001). Most barking events lasted under five minutes and only had a single caller, with alpha males accounting for most of these events. This pattern is in line with the idea that barks are an aggressive signal used by high-ranking individuals to intimidate other individuals who would likely predict that they are about to face an imminent attack unless they submit or retreat immediately. Unfortunately, our results indicate that the precise context of a barking event cannot be determined in most cases, preventing an in-depth analysis of this matter. It further needs to be acknowledged that short barking events with just one caller could also be explained by occasional 'false alarms', although it is questionable why high-ranking males would have higher false alarm rates than lower-ranking individuals.

We contend that the mechanisms for a reliable signal of male competitive ability or motivation that we suggest here are complementary. A conventional signal could explain the high proportion of short one-male calling events. In longer barking events with more than one caller that may even be triggered by an actual predator, prolonged male barking could not only deter predators (Isbell & Bidner, 2016; Zuberbühler et al., 1999). These barking events may simultaneously allow males to display stamina to each other, which would speak for a quality handicap that may affect the dynamics of male dominance relationships. This hypothesis could be supported if rank predicts call rate during events with more than one caller, an analysis that is currently in preparation. If barking was costly and reliably predicted individual competitive ability, receivers could also consider changes in individual barking activity over a longer time frame and evaluate signalers based on a cumulative assessment rule (Enquist & Leimar, 1983; Payne & Pagel, 1996, 1997). Should males evaluate each other's stamina or motivation this way, one might expect that individuals who exhibit a decrease in their probability to participate or a decrease in their call rates in relation to competitors during events will likely lose rank in the future. Follow-up studies should aim to clarify whether the structural aspects of barks are also related to dominance or caller age, as has been found in baboons, geladas and crested macaques (Benítez et al., 2016; Fischer et al., 2002, 2004; Neumann et al., 2010), which would imply that barks may even have index-like properties concerning a signaler´s competitive ability.

In summary, our study shows that barks occur in a variety of contexts, increase in frequency during the mating season and are most likely to be produced by high-ranking individuals. While we presently do not see strong evidence for a specific mechanism that would make barks reliable signals of male competitive ability, future analysis of call rate and call structure may substantiate the interpretation that barks are under intra-sexual selection. Although we do not call into question that one of the main functions of barks is to alert group members and deter predators, the notion that barks 'refer' to the presence of specific predators is not supported by our results. As receivers experience the contextual and inter-individual variation in bark usage described here, they can be assumed to account for these patterns in their responses (Fischer & Price, 2017; Owren & Rendall, 1997). The relatively moderate reactions of free-ranging vervets to naturally occurring alarm events (Henzi et al., 2021) and variable responses in playback experiments (Ducheminsky et al., 2014; Price et al., 2014; Seyfarth et al., 1980b) support this idea further. We suggest that future studies should address long-term ontogenetic changes in bark usage with age, rank, tenure, health status and an individual's social position within a group. Comparing bark usage among captive, urban living, and free-ranging populations inhabiting different environments may further reveal whether ecological factors like population-specific predation pressure affect vocal behavior in this species.

Acknowledgements

We gratefully acknowledge funding by the Deutsche Forschungsgemeinschaft (DFG FI707/25-1 – Project Number 428036558) and the Leibniz Association through the Leibniz ScienceCampus Primate Cognition (Seed fund: LSC-SF2018-09).

We thank Erica van de Waal for permission to conduct research at the Inkawu Vervet Project and to the van der Walt family for permission to work at Mawana Game Reserve. Finally, we thank Michael Henshall and all members of the IVP field team for their help and invaluable commitment to keeping the IVP field site alive throughout the COVID-19 pandemic.

Conflict of interest

None declared.

Author contributions

LS and JF conceived the study and acquired the funding; LS collected the data, conducted the statistical analyses, prepared the figures and drafted the first version of the manuscript. PD provided the male hierarchy data and assisted with data collection. LS and JF edited the manuscript. PD and EW will be invited to comment on the manuscript.

Supplementary material

Table 1S: Descriptions of context categories assigned as the most likely event that adult males responded to by producing barks. Researchers could assign multiple contexts for the same event if applicable.

Context	Description
Aerial	Any aerial object, including bird species (predominantly raptors) and occasionally helicopters and small airplanes.
Aggression	Within group male-male or male-female conflicts.
Between group encounter (BGE)	Encounters of one or more vervet monkey groups ranging within 100 meter of each another.
Distant barks	Barks from other groups faintly audible in the distance and outside of encounters. Note that events were only scored in the presented data sets if males in the observed group responded to distant barks by producing barks themselves.
Snake	Encounters with snake species including pythons, black mambas, spitting cobras, puff adders and unidentified snakes.
Terrestrial	Potential terrestrial threat, including mammalian land predators but also running antelopes and warthogs as predators are typically very hard to see. Confirmed predators include leopards and caracals. Potential but unlikely predators include jackals and poaching dogs. All predator types listed here are present on site. Note that predators are notoriously hard to confirm, meaning that if researchers could not identify any clear stimulus responsible for the calls, such events had to be classified as unknown (see below).
New male	Sighting of and conflict with unknown adult male in the group.
Unknown	Any barking events whose context could not be clearly determined. Note that this may include all the above categories and potential displays of males. Although male behavior on occasion appears to suggest a display context, where a male barks, runs around, jumps into a tree and shakes branches while most monkeys do not seem particularly concerned, it can unfortunately never be excluded that the individual saw a predator that was not visible to human observers (Consider that monkeys tend to have a better overview being able to climb into trees). Unfortunately such behavior may also occur in confirmed predator cases. We therefore did not include 'male display' as a category since we are not confident that it could be scored reliably and without high uncertainty.

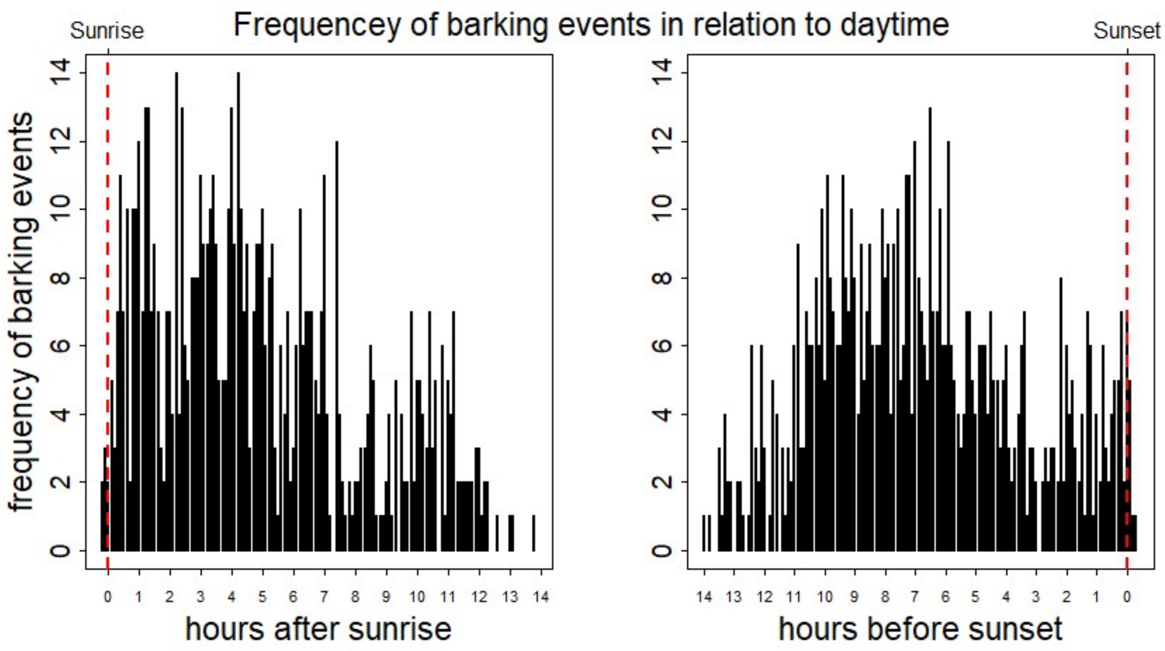

Figure S1: Frequency of barking events in relation to daytime. Onset of barking events is shown in relation to the sunrise (left) and sunset (right) of the respective day. No increased barking activity around sunrise or sunset.

Table 2S: Individual participation dataset, showing the number of events present, the mean, standard deviation and range of the predictor rank and the range of the predictor tenure (number of mating seasons present) for each individual. Table sorted by 'Proportion of events barking'.

Individual	N events present	N events barking	Proportion events barking	Rank mean	Rank s.d.	Rank range	Tenure range
oua	17	16	0.94	1.00	0.00	1-1	2-2
yan	107	97	0.91	0.83	0.33	0-1	1-2
hei	12	9	0.75	1.00	0.00	1-1	2-2
obe	9	6	0.67	0.59	0.15	0.33-0.67	2-2
xiu	12	8	0.67	0.19	0.22	0-0.67	6-6
geo	63	40	0.63	0.82	0.31	0-1	2-3
eto	8	5	0.62	1.00	0.00	1-1	1-1
tev	23	13	0.57	0.48	0.44	0-1	1-2

pro	90	48	0.53	0.96	0.14	0.3-1	2-4
ass	10	5	0.50	0.18	0.25	0-0.67	3-3
twe	16	7	0.44	0.00	0.00	0-0	1-1
oke	28	11	0.39	0.25	0.40	0-1	1-2
bas	34	13	0.38	0.57	0.13	0.22-0.8	4-4
tas	48	18	0.38	0.55	0.38	0-1	1-2
vla	61	23	0.38	0.56	0.38	0-1	1-2
vul	54	20	0.37	0.77	0.26	0.2-1	1-3
lif	28	10	0.36	0.87	0.12	0.67-1	1-7
utr	41	14	0.34	0.47	0.20	0.12-1	1-3
sio	28	8	0.29	0.38	0.35	0-1	0-1
flu	93	25	0.27	0.57	0.15	0.17-0.83	2-4
bab	17	4	0.24	0.78	0.27	0.33-1	2-2
ubu	5	1	0.20	0.92	0.10	0.75-1	5-5
dok	95	18	0.19	0.15	0.13	0-0.67	2-4
kom	90	17	0.19	0.38	0.21	0-0.9	1-3
mom	39	7	0.18	0.17	0.13	0-0.33	1-1
pal	88	16	0.18	0.77	0.16	0.44-1	4-5
mat	78	9	0.12	0.23	0.12	0.09-0.73	1-2
nge	8	1	0.12	0.18	0.10	0-0.29	0-1
apa	39	4	0.10	0.49	0.16	0-0.75	1-1
buk	58	6	0.10	0.56	0.18	0-0.75	1-2
rat	34	3	0.09	0.08	0.21	0-0.67	1-1
tam	43	4	0.09	0.10	0.16	0-0.56	1-3
can	24	2	0.08	0.66	0.08	0.5-0.8	7-7
sho	99	8	0.08	0.24	0.37	0-1	0-2
rhe	75	5	0.07	0.75	0.16	0.4-1	3-4
sey	94	7	0.07	0.50	0.24	0.08-1	2-4
tch	60	4	0.07	0.24	0.19	0-1	1-1
war	29	2	0.07	0.28	0.15	0-0.6	0-1
cus	17	1	0.06	0.83	0.04	0.75-0.88	3-3
neu	31	2	0.06	0.78	0.11	0.64-1	7-7
umb	95	4	0.04	0.56	0.19	0.25-0.89	2-4
fle	32	1	0.03	0.63	0.29	0-1	1-3
ted	93	2	0.02	0.04	0.10	0-0.43	2-4

kek	17	0	0.00	0.01	0.06	0-0.25	1-1
lip	13	0	0.00	0.45	0.09	0.25-0.57	2-2

Table 3S: Model 1 – Individual calling probability in barking events – Full model

Model formula:

```
glmer(Bark ~ z.Rank*z.Males*MatingSeason + z.Rank*z.SexRatio*MatingSeason +z.TenureMS+
    (1+ z.Rank*z.Males*MatingSeason.1 + z.Rank*z.SexRatio*MatingSeason.1 +z.TenureMS ||Individual)+
    (1+ z.Rank*z.Males*MatingSeason.1 + z.Rank*z.SexRatio*MatingSeason.1 +z.TenureMS ||Group)+
                (1 + z.Rank |Event_ID)+
                (1 + z.Rank ||Date.in.group),
data = t.data, family=binomial, control=glmerControl(optimizer="bobyqa", optCtrl = list(maxfun=1000000)))
```

Results of binomial model on barking probability. Shown are model estimates, standard errors, confidence intervals (CI), the test results obtained from likelihood ratio tests (*χ2*, *df*, *P*) and the range of estimates obtained when dropping levels of grouping factors one at a time (Min, Max). All covariates (Rank, Males, SexRatio and TenureMS) were z-transformed to a mean of 0 and a standard deviation of 1. The factor MatingSeason was dummy coded and centred with the reference category set to outside MatingSeason.

Term	Estimate	Std. Error	2.5% CI	97.5% CI	*χ2*	*df*	*P*	Min	Max
Intercept	-1.818	0.261	-2.28	-1.325	(-)	(-)	(-)	-1.934	-1.5
z.Rank	0.75	0.234	0.306	1.166	(-)	(-)	(-)	0.453	1.61
z.Males	-1.063	0.268	-1.576	-0.504	(-)	(-)	(-)	-1.285	-0.945
MatingSeasonY	-0.047	0.207	-0.463	0.367	(-)	(-)	(-)	-1.082	0.037
z.SexRatio	0.028	0.17	-0.312	0.343	(-)	(-)	(-)	-0.07	0.109
z.tenureMS	0.267	0.188	-0.108	0.639	1.91	1	0.167	0.101	0.711
z.Rank * z.Males	0.064	0.236	-0.4	0.508	(-)	(-)	(-)	-0.094	0.979
z.Rank * MatingSeasonY	-0.168	0.329	-0.711	0.466	(-)	(-)	(-)	-0.5	0.024
z.Males * MatingSeasonY	0.286	0.227	-0.192	0.768	(-)	(-)	(-)	-0.743	0.424
z.Rank * z.SexRatio	0.1	0.145	-0.161	0.396	(-)	(-)	(-)	-0.084	0.295
MatingSeasonY * z.SexRatio	-0.098	0.237	-0.546	0.403	(-)	(-)	(-)	-0.332	0.042
z.Rank * MatingSeasonY * z.Males	-0.073	0.332	-0.657	0.515	0.048	1	0.827	-0.475	0.101
z.Rank * MatingSeasonY * z.SexRatio	-0.11	0.222	-0.552	0.29	0.25	1	0.616	-0.267	0.05

Model sample: N = 2055, Distribution of response: Bark (Yes) = 524, Bark (No) = 1531

Grouping factors: Individual (N=45), Group (N=6), Event ID (N=369), Date in Group (N=291)

(-) Not shown due to limited interpretability

Table 4S: Model 1 – Individual calling probability in barking events – Results of likelihood ratio tests assessing the two-way interactions

Term	*χ2*	*df*	*P*
z.TenureMS	1.871	(-)	(-)
z.Rank * z.Males	0.025	1	0.171
z.Rank * MatingSeason	0.21	1	0.874
z.Males * MatingSeason	1.101	1	0.647
z.Rank * z.F_M_ratio	0.244	1	0.294
MatingSeason * z.F_M_ratio	0.223	1	0.622

(-) Not shown due to limited interpretability

Table 5S: Model 2 – Bark events per day – Full model

Model formula:

glmmTMB(BarkEvents ~ MatingSeason * (z.Males + z.SexRatio) + z.TotalMonkeys +
offset(log.TimeSpent) +
(1 + MatingSeason.1 * (z.Males + z.F_M_ratio) + z.TotalMonkeys ||Group),
data = t.data, family=poisson, ziformula = ~1)

Results of the Poisson model on the number of barking events per day. Shown are model estimates, standard errors, confidence intervals (CI), the test results obtained from likelihood ratio tests (*χ2*, *df*, *P*) and the range of estimates obtained when dropping levels of grouping factors one at a time (Min, Max). All covariates (Males, SexRatio, TotalMonkeys) were z-transformed to a mean of 0 and a standard deviation of 1. The factor MatingSeason was dummy coded and centred with the reference category set to outside MatingSeason.

Term	Estimate	Std. Error	2.5% CI	97.5% CI	*χ2*	*df*	*P*	Min	Max
Intercept	-2.647	0.089	-2.843	-2.489	(-)	(-)	(-)	-2.814	-2.572
MatingSeasonY	0.712	0.090	0.531	0.886	(-)	(-)	(-)	0.65	0.884
z.Males	0.255	0.145	-0.002	0.503	(-)	(-)	(-)	-0.121	0.309
z.SexRatio	0.169	0.138	-0.032	0.369	(-)	(-)	(-)	0.053	0.268
z.TotalMonkeys	-0.126	0.11	-0.341	0.083	1.342	1	0.247	-0.185	-0.042
MatingSeasonY * z.Males	-0.091	0.097	-0.283	0.096	0.957	1	0.328	-0.161	0.173
MatingSeasonY * z.SexRatio	-0.243	0.146	-0.493	0	2.4	1	0.121	-0.36	-0.105
Zi@Intercept	-0.55	0.145	-0.881	-0.325	(-)	(-)	(-)	-0.644	-0.480

Model sample: N = 1915, Grouping factors: Group (N=6), Dispersion parameter: 1.08

(-) Not shown due to limited interpretability

Chapter 5 – Discussion

The general discussion will summarize the results of the empirical contributions of the thesis in light of our current understanding of the proximate mechanisms that determine call usage and the ultimate function that vocal signals are assumed to fulfill. In the first part, the discussion of proximate mechanisms will center on what the presented studies contribute to our understanding of the factors that affect call usage in signalers, with a particular focus on individual experience and social factors as well as potential group and population specific differences. Furthermore, the observed variation in call usage will be discussed with regard to the implications of this variation for the meaning that vocal signals may develop for receivers.

The second part will discuss how natural and sexual selection may have contributed to a dual function in alarm barks and how the results relate to the evolution of primate loud calls in general. The chapter closes with an outlook that suggests which methods future research projects may employ to substantiate the presented findings and expand upon them.

5.1| Mechanisms affecting call usage and call meaning

5.1.1| Population specific differences in call usage

The experiment presented in **chapter two** was unfortunately not able to clarify whether vervet monkeys categorize novel potential threats according to positional cues as had been suggested by previous work on primate alarm call systems (Berthet et al., 2019; Cäsar et al., 2013; Murphy et al., 2013; Wegdell et al., 2019). Surprisingly, South African vervet monkeys did not produce any alarm calls towards drones and only responded by scanning the sky and occasionally taking cover. On the contrary, West African green monkeys fled and produced alarm calls that resembled vocalizations vervet monkeys produced towards raptors. While it cannot be excluded that this is related to a species specific difference in how monkeys categorized novel threats, it is here suggested that this difference is most likely related to differential experience these populations have in terms of anthropogenic disturbance and especially predation pressure. Assuming that species differences were not responsible for the different responses of subjects implies that individual experience affects call usage. While it is unclear whether differential exposure to humans or predation pressure account for the different reactions, it is clear that the general assumption of alarm calls being routinely produced in response to aerial threats may oversimplify the variation in call usage observed in our study groups.

The study presented in **chapter four** did not find any effects of group composition or group size on barking activity. However, anecdotal descriptions in earlier studies suggested that barks during intra- and inter-group aggressive interactions occur more frequently in South African compared to East African vervet monkeys (Cheney & Seyfarth, 1990; Price, 2013). Although the authors suggested that rates of aggressive interactions within and between groups did not differ between South and East African vervets, a population difference in the use of barks during aggressive interactions was still observed. Quantifying predation pressure, population structure and call usage on a larger scale will thus be necessary to confirm that population differences in call usage exist and which factors may be responsible for these different call usage patterns.

The only study that has assessed the development of alarm call usage in vervet monkeys reported that juveniles initially followed positional cues and gradually learned to restrict their calling behavior to the exclusive range of stimuli adults responded to (Seyfarth & Cheney, 1986). Diminished calling propensity over time has been interpreted as a sign of habituation (Owren et al., 2011), which would also explain the results in **chapter two** partially. However, it is difficult to argue that vervet monkeys habituated to drones due to their limited previous exposure. Instead we may assume that they frequently experience aerial predation attempts by raptors or aerial disturbances by planes and helicopters and thus did not categorize drones as threats anymore. Since drones lack the features of actual threats and similar disturbances occasionally occur, vervet monkey most likely did not respond with high arousal levels to drones anymore which is known to affect call production (Briefer, 2012). In addition, experience with actual aerial predators, which we assume to be rare in green monkeys, should lead to different expectations regarding the shape and behavior of potential threats and thus affect whether drones are perceived as potentially dangerous or not. Both of these aspects may result in different alarm call usage in response to novel flying objects, since monkeys would evaluate the situation with respect to how frequent threats from a particular domain are in general and which features typically characterize such threats. Presumably, individuals that experience higher predation pressure from raptors would be less prone to overreact to novel aerial objects as such behavior would be associated with opportunity costs (Henzi et al., 2021). The more conservative call production in adults also suggests such a mechanism (Seyfarth & Cheney, 1986).

While the structure of alarm calls is thus highly conserved in the genus (Price et al., 2014; Wegdell et al., 2019), the frequency of call usage may be subject to individual experience. Differential predation pressure among populations might thus lead to different call rates in response to different threats, a notion that requires further investigation. The assumption that green monkeys face little aerial predation is based upon the fact the aerial alarm calls were rarely recorded in this population. As a consequence, it is worth exploring whether populations do not only differ with regard to their calling frequency but also in their responses to their own calls.

There is ample evidence that most contingencies in the auditory domain must be learned in primates. Learning is assumed to mediate individual recognition of group members by voice (Cheney & Seyfarth, 1980, 1982a, 1988; Fischer, 2004; Owren et al., 1993; Rendall et al., 1996), associations between alarm calls and predators (Fischer et al., 2000; Seyfarth & Cheney, 1986) and the integration of acoustic and contextual information (Price & Fischer, 2014; Rendall et al., 1999). If we assume that primates attach meaning to sounds by integrating the experienced variation in contexts and the respective utterance of particular calls, then individuals that are used to hearing alarm calls of a certain type may respond differently from individuals who rarely perceive such calls. However, it requires clarification whether predation pressure is truly different in our study populations. Quantifying the daily occurrence and inter-individual variation in the usage is also necessary, which was attempted in South African vervet monkeys (unpublished data) but not in West African green monkeys, since the focus of the thesis lay entirely on experimental studies before it became clear that the methods were not suited to acquire the needed data.

5.1.2| Inter-individual differences in call usage

The study presented in **chapter four** demonstrates that the usage of calls varies strongly among individuals. By quantifying inter-individual variation in the use of a male loud call, the terrestrial threat bark (Struhsaker, 1967a) or leopard alarm (Seyfarth et al., 1980b, 1980a), we found that high ranking males had a higher probability to engage in barking activity, which is in line with findings from other old-world monkeys where more dominant individuals show higher loud call activity (Benítez et al., 2016; Harris et al., 2006; Kitchen et al., 2003; Neumann et al., 2010; Teichroeb & Sicotte, 2010). In addition, most events only had a single caller and lasted no longer than five minutes. While group composition and individual tenure had no effects on barking activity, we also found that the number of daily events increased during the mating season. It was not possible to analyze barking events by context, since the majority of contexts could not be clearly determined, but the variation in contexts observed was even higher than originally reported by Struhsaker (1967).

The results provide a substantial challenge for the notion that barks are primarily used in land predator events as they occur with high frequency in other contexts. Context specificity, an important criterion for functional references, is thus quite low for barks (Scarantino, 2013; Scarantino & Clay, 2015; Wheeler & Fischer, 2012, 2015). Furthermore, most events were short with only a single caller, but experimental presentation of a caracal taxidermy (a confirmed predator at the study site) typically led to call bouts that lasted twenty to forty minutes and led to participation from many males (unpublished data). While it cannot be excluded that false alarms are highly common and account for the majority of short events with a single caller, it may also suggest that males respond to a much wider range of contexts and with much higher frequency than previously known.

Fischer and Price (2017) suggested a model for the potential relationships among vocalizations, underlying internal states and the external contexts they depend on. They proposed that different contexts could either lead to different or identical internal states. Independent of whether the monkeys would have different or similar internal representations of external contexts, the internal states would map onto the same pattern generators, leading to the production of specific calls. Following this model, predators or aggressive contexts could thus lead to the generation of barks independent of whether they resulted from identical or different underlying internal states. The results of this study can expand this model in two ways. Firstly, the variation in external events that can trigger barks is even more diverse, meaning that the underlying internal states may also be more complex. Second, the results clearly demonstrate a relationship between male rank and calling probability, which implies that an individual´s evaluation of its own position within the social group and the hierarchy may be an important gating factor that determines whether an individual produces calls or not.

Although an analysis of individual and contextual variation in bark structure cannot be presented here, the rapid onset and high amplitude of barks (Struhsaker, 1967a), may be assumed to render them obnoxious unconditioned stimuli that lead to affective responses in receivers based on the energy and structure of the call alone (Owren & Rendall, 1997, 2001). Barks thus show tactical design features that support an aggressive signal that may repel competitors and predators.

By triggering startle responses in receivers, capturing their attention, presumably inducing high arousal and eliciting negative affective responses (Herzog & Hopf, 1984; Hollén & Radford, 2009; Rendall et al., 2009), barks may also facilitate subsequent learning (Owren & Rendall, 1997; Todt, 1986). Learning would not only allow receivers to associate barks with the presence of predators (Seyfarth & Cheney, 1986), but may also lead to the expectation of an imminent attack by another individual since barking occurs in conflicts. The fact that high ranking individuals show higher barking probability supports this notion since high ranking males frequently reinforce their dominance with aggressive behavior (Cheney & Seyfarth, 1990).

At present, there are only two studies that attempted to quantify variation in “alarm call” usage in vervet monkeys (Cheney & Seyfarth, 1981; Seyfarth & Cheney, 1985), but the authors did not separate calls into their different categories in these studies. The authors also strongly emphasized that the calls were exclusively alarm calls and did not report any contexts other than predation. In fact, although it was already known that these calls can occur outside of predation events (Struhsaker, 1967a), this fact is entirely missing in these two studies. While the results of

chapter four show that it is mostly not possible to confirm the precise context of a calling event, this should not lead to the assumption that any calling event must be associated with a predator (Henzi et al., 2021).

Using ad libitum data, Cheney and Seyfarth (1981, 1985) recorded which individuals were the very first callers during an assumed alarm event, irrespective of the type of predator and the kind of call produced. They reported that higher ranking males were more frequently the first individuals to produce a call compared to lower ranking males, which is in line with our results regarding individual barking probability. However, the data are not directly comparable to our data since the authors pooled all ‘alarm’ call types in their studies. In addition, the authors could not estimate the overall frequency of calling events outside of the sample they used for analysis. Due to the very low sample size of alarm events from adult males, with 32 events (Cheney & Seyfarth, 1981) and 35 events (Seyfarth & Cheney, 1985) respectively, it is therefore difficult to assess whether the observed patterns in the sample are representative. .

By presenting a leopard model in two groups and measuring individual call duration, the authors also found that high ranking males called longer than lower ranking males (Cheney & Seyfarth, 1981). This result in in line with reports in other old-world monkeys where high ranking males show higher loud call rates than low ranking males (Benítez et al., 2016; Harris, 2006; Kitchen et al., 2003; Neumann et al., 2010). However, the methods of the experimental design of the leopard model presentations (Cheney & Seyfarth, 1981) do not provide a clear description of how call duration was actually measured. The presented data strongly suggests that the authors were restricted to estimating the time elapsed between the first and last call of an individual. This measurement would unfortunately not describe actual calling effort, because individuals may produce only few calls at the beginning and end of a call bout and thus acquire a high calling duration although the actual number of calls produced can be low. Further, the authors claim to have recorded such durations for 98 % of all individuals in the group (Cheney & Seyfarth, 1981). How such measurements can be reliably achieved simultaneously for almost all individuals in a group is entirely unclear to the author of this thesis who found that a single observer is rarely able to register call rates via audio recordings for more than a single individual at the same time (unpublished data).

In a second experiment on captive green monkeys (Seyfarth & Cheney, 1985) the authors also reported that higher ranking males showed higher call rates. However, they only measured calling activity within the first ten seconds of their experiment and the stimulus they used was a human dressed as a veterinarian. Not only is the time frame that they choose to assesses call rates in this experiment quite short, but in addition, vervet monkeys commonly produce “chutters” towards disturbance by humans, which is a call type that is also uttered in response to snakes but not mammalian land predators like leopards or caracals (Cheney & Seyfarth, 1990; Struhsaker, 1967a). The results of these studies are hence difficult to compare with the data presented in **chapter four**.

In conclusion, we still lack an actual comparison of within event call rates for males of different ranks under natural and experimental conditions. Although most barking events are short and only have a single caller, an analysis of call rate is needed to confirm that the increased probability of males to participate in barking events that is reported in **chapter four** also corresponds to an increased calling effort during events with more than one caller. Although it is important to note that in the present data set, the probability of a male to be registered as calling by a human observer is most likely positively correlated with the time that male spends calling, it is still necessary to quantify actual calling effort to substantiate the findings.

Finally, the contextual variation and rank driven call usage in male barking activity may be expected to have implications for receivers who will make inferences about ongoing events based on the variation in call usage they experience (Fischer, 2011; Fischer & Price, 2017; Owren & Rendall, 1997; Wheeler et al., 2011). As the data clearly shows, high ranking individuals almost always participated in events but were also responsible for a high proportion of short barking events with only a single caller. Receivers can be assumed to be sensitive to this variation and thus may evaluate barking from a high ranking male differently than the very rare barks of low ranking individuals. It may be assumed that high ranking males use barks more frequently in aggressive contexts than lower ranking individuals, which might result in calling activity from low rankers to be more strongly associated with predator events. If barks were increasingly used as displays by high ranking males, barks from low ranking males may be interpreted as a more reliable signal for the presence of predators (Cheney & Seyfarth, 1988; Wheeler, 2010a, 2010b), which might be tested with playback experiments (Fischer et al., 2013).

Such an experiment would require that it can be safely excluded that the acoustic structure of barks does not strongly predict the context they are uttered in. Gradual variation in bark acoustic structure produced during aggressive and predator contexts does support such an assumption (Besson, 2017; Price et al., 2015). Unfortunately, isolated playbacks of male barks would not reflect the typical group level calling that is observed during actual predator events. Most predator events tend to begin with very soft calls, not barks and multiple individuals will be calling at most times (personal observation). Playing back bark vocalizations from a single individual for a very short time (as is typical for playback experiments) may thus lack the acoustic features that receivers associate with actual predator events. It may thus be difficult to interpret such a playback experiment. A more detailed analysis of the sequence and latency of different call types during predator model presentations may help in this regard. A better understanding of which features characterize the natural group level vocal patterns during actual predator events would improve our choice of stimuli in playback experiments in general and help explain why responses can be very subtle (Ducheminsky et al., 2014; Price et al., 2014; Seyfarth et al., 1980b). Lastly, the effect of predator distance and behavior on call rates needs to be examined (Manser et al., 2002).

5.2| Signal function and loud call evolution

5.2.1| Mechanisms that ensure signal honesty

The data presented in **chapter four** may suggest that barks serve a dual function of alarm call and signal of male dominance, since high ranking males have a higher probability to produce barks compared to low ranking individuals. As a signal of individual quality requires a mechanism that ensures that signals remain honest (Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005), two mechanisms were suggested. In aggressive interactions, barks could indicate individual motivation to escalate a fight in the form of a conventional signal (Enquist, 1985; Vehrencamp, 2000). The costs would be imposed in the form of receiver retaliation, whereby bark production will likely provoke physical attacks from receivers who consider themselves dominant over the signaler. Producing barks in a conflict would thus be associated with high risk and individuals who are not motivated to escalate a fight should abstain from call production to avoid costly fights (Molles & Vehrencamp, 2001).

During longer lasting calling events with multiple signalers, barks could also function as quality handicaps if individual stamina is limiting the rate and total amount of calls an individual can produce. Such a relationship has been described in primates (Benítez et al., 2016; Kitchen et al., 2003; Neumann et al., 2010) and red deer (Clutton-Brock & Albon, 1979). Importantly, such events would not need to occur in the form of direct signaling contests as has been described in baboons and geladas, but could also happen during predator events. Prolonged barking activity in vervet monkeys likely serves as a deterrent for mammalian land predators (Isbell & Bidner, 2016).

Although the author acknowledges the highly speculative nature of this thought, it is possible that males, who bark to repel a caracal or leopard, may at the same time use such an opportunity to display their own stamina and assess the stamina of potential rivals, which may help to avoid costly fights in the future. Reserving such battles of endurance for assumed predator contexts provide additional individual benefits for all participants if increased calling activity is more effective at repelling predators (Zuberbühler et al., 1999). In addition, if dominant males tend to respond with physical attacks towards subordinates who produce barks outside of predator contexts, an attempt to start a barking contest outside of a predator event might be associated with the risk of an ensuing fight for anyone except the alpha male.

Unfortunately an analysis of call rates during barking events is still lacking. Following the assumption that barks are quality handicaps during such events, it would be likely that males adjust their own call rate in relation to the call rate of other individuals in the group by taking the rank differences among each other into account (Kitchen et al., 2003). High ranking males could thus be expected to be more likely to respond to calls from other individuals within a shorter time than low ranking individuals. The rank difference among individuals could be of particular interest here since males may preferably respond to individuals that they perceive as closest competitors in an attempt to “out-call” them.

5.2.2| A dual function in the evolution of loud calls

Alarm calls are typically viewed as evolving via natural selection by increasing the survival rate of closely related kin (Hamilton, 1971; Sherman, 1977; Smith, 1965) and by deterring or mobbing a predator via advertising that ambush is no longer possible (Curio, 1978; Hasson, 1991; Shelley & Blumstein, 2005; Zuberbühler, 2006). Barks of male vervet monkeys are likely effective at both of these aspects (Isbell & Bidner, 2016; Seyfarth et al., 1980b, 1980a; Struhsaker, 1967a). However, an exclusive alarm call function would not explain why dominant individuals would be more likely to produce calls than lower ranking individuals. It is thus proposed that barks may also be signals of male dominance that are effective via a conventional receiver retaliation rule and as quality handicaps that indicate individual stamina (Searcy & Nowicki, 2005; Vehrencamp, 2000). Such a dual function could be the product of intra-sexual selection.

Importantly, barks are loud calls which are only produced by adult males starting around the time of sexual maturity (Struhsaker, 1967a). Loud calls are found in many primate species and apparently fulfill a variety of different functions including, group cohesion, mediating inter-group spacing, defending resources and deterring predators (Byrne, 1982; Da Cunha & Byrne, 2006; Delgado, 2006; Gautier & Gautier, 1977; Mitani & Stuht, 1998; Waser, 1975, 1982; Whitehead, 1987; Zuberbühler, 2002) and dual functions in the same call type have been described by some authors (Fuller & Cords, 2017, 2020). Zuberbühler (2002, 2006) suggested that loud calls in forest guenons may have originally evolved due to predation pressure and subsequently acquired additional functions due to sexual selection. In primate species living in one male groups or pairs, parameters of loud call structure or usage were found to be related to male pairing status, tenure, body mass, age, hormonal status or group composition and have been suggested to indicate an individual´s ability to defend occupied resources, including access to mates (Barelli et al., 2013; Benítez et al., 2016; Delgado, 2006; Erb et al., 2013; Fuller & Cords, 2017, 2020; Harris, 2006, 2010; Harris et al., 2006; Mitani, 1988; Steenbeek et al., 1999; Wich et al., 2003).

In primates living in multi-male multi-female groups like vervet monkeys, the structural features of loud calls, call rates, call bout duration and frequency to engage in call bouts were reported to be related to signaler age and rank, corroborating the idea that loud calls indicate individual stamina and competitive ability (Fischer et al., 2002, 2004; Kitchen et al., 2003; Neumann et al., 2010). Some authors consider these findings as evidence that sexual selection may affect the structure and usage patterns of male loud calling behavior in primates (Delgado, 2006). Wich and Nunn (2002) argued that loud calls can be considered an ancestral trait in many primates and there is no consistent relationship between their occurrence and the degree of male-male competition.

If future studies could show that individual call rates during events also predicted by male dominance rank this would substantiate a role of intra-sexual selection. A recent study suggests that the acoustic structure of barks in male vervet monkeys likely carries individually specific signatures and that the pitch of male calls is disproportionately lower than that of female calls relative to what would be expected by differences in body mass between the sexes (Dubreuil, 2019). Individually specific and sex dependent vocal structure suggests that receivers can likely differentiate individuals by voice and that selection may have shaped bark structure to maximize effective range and potentially exaggerate caller body size (Maynard Smith & Harper, 2003). While there is only moderate sexual dimorphism in vervet monkeys (Turner et al., 1997), previous structural analysis and the data presented in this study suggest that bark structure and usage were affected by intra-sexual selection. Future structural analysis should examine whether spectral characteristics of barks are also related to individual age and dominance rank. If so, barks may also serve as an index of male competitive ability (Benítez et al., 2016; Fischer et al., 2002, 2004; Neumann et al., 2010).

Lastly, it has recently been proposed that loud alarm calls of males might constitute costly signals that are under inter-sexual selection because females prefer to mate with males who provide anti-predation services (van Schaik et al., 2022). While it has been suggested that males tend to be more active during alarm calling events and that females recruit male calling activity (Ouattara et al., 2009b; Stephan & Zuberbühler, 2016; Wich & de Vries, 2006), it is here argued that intra-sexual selection may also account for such findings. Males may well be more vocally active than females because they are displaying their stamina to other males during a predator event and not to females. If females would prefer to mate with males who engage in frequent loud calling activity, this might also result in a potential dilemma since males might be incentivized to produce calls outside of predator events. While it may be argued that females would take context into account and only develop preferences for males who produce high loud call rates during the "correct" circumstances, it is questionable how this would be possible for females in most cases. If females could not always identify the exact context of a barking event and invariably selected for high call rates, we would expect most males to participate in the majority of barking events, which was not the case in our data. Instead, the highest-ranked males frequently barked alone, which suggests that barking activity of lower ranked males is suppressed or that they are not motivated to produce barks at high frequency. Therefore, our data provide better support for the assumption that bark production is an intra-sexually selected trait in vervet monkeys.

5.3| Outlook

In conclusion, the studies presented here suggest that call usage may vary considerably among populations and individuals in the genus *Chlorocebus*. While previous work on primate alarm calling behavior has predominantly addressed variation in call structure and call perception, future work should consider quantifying call usage in light of population specific ecological factors, group composition, seasonal variation and inter-individual social and demographic factors. Further, assessing variation in call usage during individual ontogeny is recommended. Phylogenetic comparative methods assessing variation in specific aspects of call usage rather than absence or presence of a particular call type across primate taxa may further advance insight into the selective pressure that shape vocal behavior.

To substantiate that male barks in the genus *Chlorocebus* serve a dual function of alarm call and signal of male quality, individual call rates during multi-male calling events need to be analyzed with respect to individual rank and other factors related to male competitive ability and degree of male-male competition. Future structural analyses of barks should examine whether spectral and temporal characteristics of barks are related to individual age and rank.

Population specific differences in call usage could be explored on a large scale via passive acoustic monitoring to determine whether increased barking frequencies during the mating season are a general phenomenon in the genus. Lastly, the population density of predators and their local prey preferences demand further attention to investigate whether predation pressure affects variation in call usage across populations.

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Acknowledgements

I want to thank Julia Fischer, for welcoming me into her lab as a Master student and offering me the opportunity to stay on for a PhD project. I am grateful for years of supervision, help in acquiring the funding for this project and the freedom to develop and pursue my own research questions. Julia took great part in developing my thinking and writing by always providing constructive criticism.

I wish to express my gratitude to Alexander Gail for being on my thesis advisory committee, heling to acquire the funding for the drones used in this project and taking the time to be the second reviewer for this thesis. Many thanks go to Arezoo Pooresmaeili for being on my thesis advisory committee and always providing words of encouragement after my presentations.

I am grateful to Jan Clemens, Peter Kappeler and Oliver Schülke for taking the time to be on my examination board. Special thanks go to Jan Clemens for helping me to use the DAS tool he developed and which I am eager to use in future projects.

My eternal thanks go to Roger Mundry for his invaluable efforts in teaching statistics to students from all over the world. He greatly improved my abilities to use different modeling techniques in R and I cannot emphasize enough how valuable I think his courses are for the entire research field we work in.

My sincere gratitude goes to all past and present members of the Cognitive Ethology lab, for supporting me in my work and being great companions along the way. I also want to thank Stefanie Bader, Nadja Vögtle and Durr-E-Ajam Riaz who I had the honor to supervise, for their invaluable assistance in coding all the video and audio data.

I want to thank all members of the Simenti field site, including Irene Gutiérrez Díez, Anaïs Avilés de Diego, Lisa Ohrndorf, William O´Hearn, Dominique Treschnak, Vieux Biaye, Elijah

Dansonkho, Moustapha Faye, Armel Nyafouna, Touradou Sonko, Chérif Kéba Camara, Djibril Coly and Amadou Bamba Diedhiou who helped me with my experiments and made my time in Senegal such a wonderful experience. Special thanks go to Bamba for his incredible working attitude and benevolent and calm minded approach to everything in life. He taught me how to move in the bush, what to pay attention to and how to track down monkeys who do not want to be followed. All of these abilities proved immensely useful in later years.

I thank Peter Henzi and Louise Barret for inviting me to the Samara field site and lending me Carl the Caracal for scaring monkeys. I further thank Erica van de Waal for granting me the opportunity to work at the Inkawu Vervet Project.

My thanks go to all the members of the IVP field team who helped collecting the data for this project. The IVP field site would not have survived the pandemic without the tireless efforts of each and every one of them and I look back to many joyful memories with them during this long and sometimes difficult field trip. It would not have been possible without you and I will be forever in your debt. Thanks got to: Michael Henshall, Tamsyn Henshall, Pooja Dongre, Tecla Mohr, Nokubonga Dlamini, Sashimi Wieprecht, Jose van der Geest, Camille Schroecker, Hannah Hilden-Reid, Claire Baffray, Aurelie Cortes, Charlotte Rossetti, Axelle Bouteiller, Rebekka Zing, Varun Manavazhi, Luke Quarles, Dina Mostafa, Lucas Zermatten, Alice Beaud, Asanda Ngcongo, Eliza Jones, Maarten Mommens, Damien Minchelli, Maxine Piron, Luca Hahn, Lara Zanutto, Millie German, Morgane Le Goff, Shannon Glosenger-Thrasher, Aaron Mencia, Lily Munzhedzi and Rebecca McCann. Special thanks go to iMvula, iLanga and Mr. Duke Silver for cheering me up and sharing my Biltong with me.

Finally, my warmest thanks go to my family for long years of support. None of this would have been possible without you and I cannot stress enough how grateful I am to you all.

Curriculum Vitae

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Inkawu Vervet Project, Mawana Game Reserve, KwaZulu Natal, 3115, South Africa

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External Funding

Co-Author of DFG-grant: DFG FI707/25-1 – Project Number 428036558

Co-Author of seed fund, Leibniz ScienceCampus Primate Cognition: LSC-SF2018-09

Associations

German Zoological Society

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Leibniz ScienceCampus Primate Cognition

Declaration

I hereby declare that I have written this thesis independently and with no other aids or sources than quoted.

Göttingen, November 08th 2022

Lukas Schad