Title: Are demographic correlates of White-faced Capuchin Monkeys *(Cebus capucinus)* "Gargle and Twargle" Vocalization Rates consistent with the Infanticide Risk Assessment Hypothesis?

Running title: Capuchins test bonds via vocalizations

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Graphical Abstract

The scatterplot displays average gargle (open red circles) and twargle (closed blue circles) rate data by age in months. The subplot displays average gargle and twargle rates for individuals 24 months of age and younger. Individuals gargle and twargle the most during infancy, when risk of infanticide is the highest.

Abstract:

Zahavi's "Bond Testing Hypothesis" (1977a) states that irritating stimuli are used to elicit honest information from social partners regarding their attitudes towards the relationship. Two elements of the *C. capucinus* vocal repertoire, the "gargle" and "twargle," have been hypothesized to serve such a bond-testing function (Perry & Manson, 2008). The greatest threat to *C. capucinus* infant survival, and to adult female reproductive success, is infanticide perpetrated by alpha males (Perry, 2012). Thus, we predicted that infants (<8 months), pregnant females and females with infants would gargle/twargle at higher rates than the rest of the population, directing these vocalizations primarily to the alpha male. Over 16 years, researchers collected data via focal follows in 11 habituated groups of wild capuchins in Lomas Barbudal, Costa Rica. Our hypothesis was mainly supported. Infants and females with infants (<8 months) vocalized at higher rates than the rest of the population. Pregnant females did not vocalize at high rates. Infants (age 8-23 mo.) were the only target group that vocalized more when the alpha male was not their father. Monkeys gargled and twargled most frequently towards the alpha male, who is both the perpetrator of infanticide and the most effective protector against potentially infanticidal males.

Key Words: *Cebus capucinus, Zahavian bond tests, vocal communication, infanticide*

Introduction

Much of the nonhuman primate vocalization literature focuses on how vocalizations broadcast, rather than elicit, information (Bergman, Beehner, Painter, & Gustison, 2019; Elowson, Snowdon, & Lazaro-Perea, 1998; Gros-Louis, 2002, 2006; Gros-Louis et al., 2008; Locke, 2001; Maynard Smith, 1982; Schamberg, Cheney, Clay, Hohmann, & Seyfarth, 2017; Seyfarth & Cheney, 1986). Researchers may overlook calls functioning as “Zahavian bond tests” when centering research on vocal broadcasting rather than elicitation (Zahavi 1977a). A Zahavian Bond Test is the engagement in a risky behavior, or stimulus, imposed by a “tester” to elicit an honest response regarding the sentiments of the recipient towards the tester (Zahavi, 1977b; Zahavi & Zahavi, 1977). In this paper, we examine the possibility that white-faced capuchins *(Cebus capucinus)* use two calls from their vocal repertoire, the “gargle” and “twargle,” to elicit information about a recipient’s sentiments towards the caller, especially if the caller faces infanticide risk.

Research suggests that white-faced capuchins navigate relationships by testing and reinforcing bonds via non-vocal signals (Manson, 1999; Perry, 2011; Perry et al., 2003; Perry & Manson, 2008). A bond, defined by Zahavi (1977a) as a “special relationship between two individuals,” may form between parents-offspring, sexual partners or group members and may change through time (Zahavi, 1977a). Zahavian bond tests promote honest communication within a dyad, as the tester aims to discern the attitudes of the recipient towards the tester

(Taylor, 2014; Zahavi, 1977a). A neutral or positive response from the recipient (e.g., producing an affiliative vocalization, gesturing a greeting, continuing with the same behavior, etc.) may indicate interest in relationship investment, and a negative response or premature termination of the stimuli (e.g., hitting, walking away, biting, etc.) may indicate disinterest in relationship investment (Smuts & Watanabe, 1990; Zahavi, 1977a). For example, old adult male olive baboons *(Papio anubis)*, as compared to young adult males, generally complete bond testing behaviors, indicating relationship investment. The Zahavian Bond Testing Hypothesis would predict this outcome, as old adult males are reliant on allies for coalitionary support, whereas young adult males are not (Smuts & Watanabe, 1990).

A signal is more likely to be trusted if it is costly or risky to produce, because it would be unprofitable for unmotivated individuals to produce such signals (Zahavi, 1977a; Zahavi & Zahavi, 1977). Signaling does not result in cooperation when individuals do not trust information conveyed by their partner (Silk, Kaldor, & Boyd, 2000). Some group-living primates, such as chacma baboons *(Papio ursinus)* and rhesus macaques *(Macaca mulatta)* produce honest signals and responses to coordinate coalitionary behavior (Silk et al., 2000; Silk, Seyfarth, & Cheney, 2016). Dishonest signalers potentially incur punishment from group members, resulting in negative long-term consequences for perpetrators (Cheney & Seyfarth, 2018; Poole, 1989; Silk et al., 2000, 2016).

White-faced capuchins are known to produce risky signals and perform Zahavian Bond Tests (Manson, 1999; Perry, 2011; Perry et al., 2003; Perry & Manson, 2008; Perry & Smolla, 2020). Females test bonds by holding allies' infants in risky acts of trust (Manson, 1999), and dyads of all age-sex classes engage in risky rituals. For example, individuals stick sharp and dirty objects or body parts (such as wood chips, fingers, or feet) into another individual's eye-socket, nose or mouth (Perry, 2011, 2012; Perry et al., 2003; Perry & Smolla, 2020).

We expect white-faced capuchins to test bonds with individuals with whom they have important relationships, such as parents, alloparents, allies and adult males. Relationships with alpha males are arguably some of the most critical relationships in white-faced capuchin societies, as alpha males are capable of providing great benefits (e.g., resources or coalitionary support) or imposing tremendous costs (e.g., stress or death) on individuals (Perry, 2012). Alpha males benefit from relationships with females for reproductive opportunities largely unavailable to subordinate males (Perry, 1997, 1998, 2012).

Subordinate males also, but to a lesser degree, provide invaluable resources to group members, such as coalitionary support and protection against predators and extra-group males (Perry, 1997, 2012). However, they can also pose a threat to capuchin societies by overthrowing alpha males and subsequently destabilizing social interactions, altering group behavior and committing infanticide (Jack & Fedigan, 2008; Perry, 2012; Perry et al., 2003; Perry, Godoy, & Lammers, 2012; Perry, Godoy, Lammers, & Lin, 2017). Infanticide, i.e. the killing of unweaned offspring, creates breeding opportunities for perpetrators (Hrdy, 1979; Palombit, 1999; Perry et al., 2012). Alpha males are the only known infanticide perpetrators at the Lomas Barbudal site (Perry, 2012), yet infanticide is the leading cause of infant white-faced capuchin deaths (49%-82% of deaths occurring in the wake of takeover events and 12%-18% during peaceful periods) and poses the largest threat to female reproductive success (Fedigan, 2003; Perry, 2012; Perry et al., 2012, 2017).

It is critical for individuals, especially adult females and infants, to sensibly navigate bonds with the alpha male, given the benefits and costs of these relationships. Individuals profit from accurately assessing if the alpha male is either: 1) willing to invest in the bond and provide coalitionary support, or 2) unwilling to invest in the bond and potentially threaten an infant's life. We present and test the "Infanticide Risk Assessment Hypothesis" (Perry & Manson, 2008), suggesting that individuals use Zahavian Bond Tests to assess infanticide risk. We hypothesize that white-faced capuchins use two elements of their vocal repertoire, the "gargle" and the "twargle," to assess relationship quality. We predict that individuals will gargle and twargle more frequently when the recipient of these vocalizations poses infanticide risk to the vocalizer.

Below is a list of predictions (in italics) that can be derived from the Assessment of Infanticide Risk Hypothesis, followed by clarification of the assumptions underlying each prediction. See Table 1 for each prediction's definitions, data sets and statistical approaches.

P.1. *Infants will gargle and twargle at higher rates than the rest of the population*. Unweaned infants should be highly motivated to test bonds, because they face the highest infanticide risk (Perry et al., 2012). They can more accurately navigate social situations knowing (a) if the alpha male will protect them against infanticidal males (in which case they should maintain proximity to him), (b) if the alpha male poses a threat to them (in which case they should avoid him) and (c) who may provide coalitionary support (in which case they should affiliate with those individuals). Infants will gargle and twargle at high rates until they are largely weaned, and their mothers can conceive again.

P.2. *Pregnant females will gargle and twargle at higher rates than the rest of the: a) adult female population and b) adult females who are not pregnant and do not have an infant <8 months old.* They benefit from knowing (a) if the alpha male will protect their expected offspring (in which case they should maintain proximity to him when the baby is born and present), (b) if the alpha male poses a threat to their expected offspring (in which case they should avoid him when the baby is born and present), and (c) who may provide coalitionary support (in which case they should affiliate with those individuals). Pregnant females will gargle and twargle throughout their pregnancy, especially as the birthing event approaches.

P.3. *Females with infants (<8 months) will gargle and twargle at higher rates than the rest of the: a) adult female population and b) adult females who are not pregnant and do not have an infant <8 months old*. They benefit from knowing (a) if the alpha male will protect their offspring (in which case they should maintain proximity to him when the baby is near), (b) if the alpha male poses a threat to their offspring (in which case they should avoid proximity to him when the baby is near), and (c) who may provide coalitionary support (in which case they should affiliate with those individuals). Females are expected to frequently test bonds with the alpha male until the end of the weaning period and especially during the three months following the birthing event when lactation has the largest impact on a female's ability to conceive again (Perry, 2012; Treves, 2000; Van Schaik & Dunbar, 1990).

P.4. *Individuals will gargle and twargle more when the current alpha male is not the offspring's father,* because individuals should be motivated to assess bonds with more group members for coalitionary support if it is uncertain that the alpha male will provide coalitionary support or pose infanticide risk (Treves, 2000).

P.5. *Individuals will gargle and twargle more to the alpha male than to any other monkey in the group*, because alpha males are the best source of coalitionary support against future potentially infanticidal alpha males (Perry, 2012). Additionally, alpha males who have recently acquired tenure (within one calendar year) (Perry, 1998) are the highest source of infant mortality and threaten female reproductive success (Perry, 1997, 2012).

Table 1. Target groups, reference groups, model/test and data for each prediction.

Prediction	Target Group	Reference Group	Model/ Statistical Test	Data Type
P.1.	Infants (<8 months)	Rest of population	NB Model	Gargle and twargle counts and hours
P.2.	Pregnant females	(2a) Non-pregnant adult females (2b) Adult females who are not pregnant and do not have an infant <8 months old	NB Model	Gargle and twargle counts and hours
P.3.	Females with young infants (<8 months)	(3a) Adult females without infants (<8 months) (3b) Adult females who are not pregnant and do not have an infant <8 months old	NB Model	Gargle and twargle counts and hours
P.4.	(4a) Infants (<24 months) whose father is not the alpha male (4b) Pregnant females whose fetus is not sired by the alpha male (4c) Females with infants (<8 months) not sired by the alpha male	(4a) Infants (<24 months) whose father is the alpha male (4b) Pregnant females whose fetus is sired by the alpha male (4c) Females with infants (<8 months) sired by the alpha male	NB Model	Gargle and twargle counts and hours
P.5.	All individuals	N/A	Binomial Test	Gargle and twargle count proportions directed towards the alpha male

Methods

(a) Ethical Note

The protocol and procedures were ethically reviewed and approved by UCLA's Animal Research Committee (ARC), which ensures compliance with the US NRC's Guide for the Care and Use of Laboratory Animals, the US PHS's policy on Humane Care and Use of Laboratory Animals, and the Guide for the Care and Use of Laboratory Animals; the ARC approved protocols relevant to this project are #1996-122, 2005-084, 2016-022 (plus various renewals of these). This work was conducted with appropriate permission from the Costa Rican authorities (SINAC, MINAET, and CONAGEBIO), which granted permits for data collection and procedures. All field work complied with Costa Rican law, the ASP's principles for ethical treatment of non-human primates, and the code of best field practices for field primatology.

(b) Study System

Data presented were collected from 2002-2018 on 11 groups of wild, well-habituated white-faced capuchin monkeys (*Cebus capucinus)* at the Lomas Barbudal Biological Reserve and surrounding forest (latitude: 10.510, longitude: -85.380). White-faced capuchins are large-brained, long-living New World monkeys (Perry, 2012). They reside in stable multi-female, multi-male, female-philopatric groups ranging in size from 7-30 individuals (Perry, 2012). Males generally disperse to neighboring groups around the time of maturity, alone or in groups of 2-8 individuals (Jack & Fedigan, 2004, 2008; Perry, 2012). White-faced capuchins have a wide range of learned and species-typical vocal and gestural behaviors (Gros-Louis et al., 2008). More information about the site, population and methods can be found in (Frankie et al., 1988; Perry et al., 2012).

(c) Description of the Behavior

The gargle vocalization is a loud, raspy, guttural, broad-band vocalization generally produced in bouts in close range (~5-10 m) of the targeted individual (Gros-Louis et al., 2008; Perry, 1998). Gargles are produced by individuals in all age-sex classes but rarely by adult males (Gros-Louis et al., 2008; Perry, 1998). Gargles are one of the first vocalizations infants produce during the first month of life (Gros-Louis et al., 2008), suggesting an urgency in an individual's ability to produce the vocalization. Individuals have been observed gargling to group members in most age-sex classes (Perry, 1998).

The twargle vocalization begins with high-pitched trill sounds and cascades into low, raspy gargle sounds (Gros-Louis et al., 2008). Trills are high-pitched vocalizations generally produced in bouts during affiliative social situations or travel (Gros-Louis, 2002; Gros-Louis et al., 2008). Individuals in most age-sex classes twargle (Gros-Louis et al., 2008; Table 2).

Gargles and twargles are primarily produced while resting, travelling or positively affiliating with the recipient (Gros-Louis et al., 2008). The recipient varies in their reaction to the vocalizer; they may leave, ignore, act affiliatively (e.g. by grooming or receiving grooming from the vocalizer) or act aggressively (e.g. by hitting or pushing the vocalizer).

We performed separate analyses on gargles and twargles, although they are often produced in conjunction. Gargles and twargles are acoustically distinct, production rates are distributed differently across age-sex classes (Gros-Louis et al., 2008), and there is no prior analysis suggesting that they fulfill the same function.

(d) Data Collection

Data were collected using a strict behavioral focal follow protocol. Focal follows were primarily 10 minutes long (86% of the time spent conducting focal follows was during 10-minute follows) conducted across demographics; however, neither individuals nor age-sex classes were evenly sampled (Table 2; Table S1). At least one research assistant in the field was required to accurately identify all individuals within a group before collecting data. Monthly coding, vocalization and data collection tests were mandated to ensure efficiency and accuracy at using the behavioral coding scheme. Data were not included in analyses unless at least one assistant in the field per day could accurately collect data. More information on the field site protocols can be found in (Perry et al., 2012).

Table 2. Column 1 refers to target populations delineated by age and developmental life history stage. “Gargle Count” and “Twargle Count” refer to the number of recorded gargles/twargles per target population. “Gargle Hours” and “Twargle Hours” refer to the amount of time, in hours, that gargle/twargle data was collected by someone trained to collect data on the respective vocalization. “Gargle Rate” and “Twargle Rate” refer to the target population’s average gargle/twargle per hour rate.

	Gargle Count	Gargle Hours	Gargle Rate	Twargle Count	Twargle Hours	Twargle Rate
Infant (<8 mo.)	7080	901.16	7.86	409	359.73	1.14
Infant (<24 mo. including <8 mo.)	11763	3163.70	3.72	863	1107.08	0.78
Juvenile (≥24 & <60 mo.)	2076	3500.30	0.59	582	1809.72	0.32
Pregnant females	451	1115.99	0.40	507	1036.24	0.49
Females with young (<8 mo.) infants	1280	1010.75	1.27	746	946.44	0.79
Non-pregnant adult females (>= 60 mo.) without young infants	867	2404.03	0.36	605	2234.96	0.27
All adult males (>= 60 mo.)	253	5621.85	0.05	57	5239.29	0.01
All adults (>= 60 mo.)	2851	10152.66	0.28	1915	9456.97	0.20
Overall population	16690	16816.65	0.99	3360	12373.78	0.27

Data were collected on 357 individuals; 221 individuals were observed producing gargles or twargles, and 136 individuals were never observed producing gargles or twargles (this does not indicate that 38% of the population does not gargle or twargle). Researchers observed 16816.65 gargle-hours, 12373.78 twargle-hours, 16,690 gargle instances, and 3,360 twargle instances

(e) Data Cleaning

Initial data cleaning and preparation were performed by querying the MySQL database housing the Lomas Barbudal Monkey Project's data. Later stages of data cleaning, exploratory data analysis and inferential statistics were conducted using Python 3.8.2 (https://www.python.org/) and R 4.0.2 (http://www.R-project.org/).

Individuals born between 1994 and 2012 were genotyped using standard procedures employed by Dr. L. Vigilant's primate genetics lab at MPI-EVAN (see Godoy, Vigilant, & Perry, 2016; Muniz & Vigilant, 2008 for details). 11 individuals, in addition to those who died before fecal sample collection, have not been genotyped. Infants (<24 months) with unknown fathers produced 1,222 out of 12,626 gargle and twargle instances. We did not include these instances in analyses for P.4, as paternity is relevant.

(f) Statistical Analysis

(f.1.) Negative Binomial Models

We addressed predictions (P1 – P4) using negative binomial (NB) generalized linear mixed models (GLMM) in the glmmTMB package in the R 4.0.2 statistical environment (https://www.R-project.org/). We used the fitdistrplus and logspline packages, exploratory data analyses (Zuur, Ieno, & Elphick, 2010) and Akaike information criterion (AIC) to determine the best: a) distribution and b) models, of all considered models. NB distributions are reasonable for our data and account for gargle and twargle rate variance due to uneven focal sampling and proportionally more data collected during alpha male takeover events (Consul & Jain, 1973; Davis & Wu, 2009; Kaempf, 1995; Lindén & Mäntyniemi, 2011; Lord, Guikema, & Geedipally, 2008). We fit NB models using two NB distributions (nbinom1 and nbinom2 in the glmmTMB package) and report results from nbinom1 models, as these were better fitting models according to AIC. All models include caller identity as a random effect to account for idiosyncratic vocalization rates.

Gargle and twargle rates are dependent variables measured by vocalization count/individual/hour followed. Inconsistent follow time per monkey is accounted for by conditional probability and a log offset variable (Lindén & Mäntyniemi, 2011). Independent variables differ per prediction but always specify the target group (population subset) of interest. Reference groups are population subsets excluding target groups. Individuals are considered once or twice per prediction: a) in the target group, b) in the reference group or c) in the target group and the reference group, if data was collected on that individual during different reproductive/life history stages.

We calculated incidence rate ratios (IRR) for each model. (The estimate is the log of the IRR.) IRRs represent the ratio of event outcomes over a given time period: IRR = 1 indicates that the target and reference groups vocalize at the same rates, <1 indicates that the reference group vocalizes at a lower rate, and >1 indicates that the target group vocalizes at a higher rate. We present exponentiated confidence intervals (CI), as they relate to IRRs. If the CI includes 1, then there may not be a true difference between groups. P-values are two-tailed.

Table 1 outlines the target group and reference group for each analysis. We subcategorize infants into those aged 0-8 months and 8-23 months. Infants were defined as <8 months for all analyses except for P4a, as weaning occurs between 8-23 months of age (Carnegie, Fedigan, & Melin, 2011; Jack & Fedigan, 2008; Sargeant, Wikberg, Kawamura, & Fedigan, 2015). We used the lower-bound weaning age, because, if necessary, infants may have the ability to gain independence and avoid infanticide (Treves, 2000). Pregnant females are defined as females who will give birth in the subsequent 160 days. We define adults as individuals 60 months or older, because the youngest female to give birth in the population conceived at 60 months old (Perry, 2012).

(f.2.) Binomial tests

We use a binomial test to address this prediction, because we measure gargles and twargles as proportions, rather than rates/individual. Binomial tests compare two outcomes with the null assumption that each outcome will occur 50% of the time (Kaempf, 1995). We compare gargles and twargles directed to the alpha male, versus to all other members of the group, from infants (<8 months), pregnant females, and female with infants (<8 months). We assume that there are at least two potential gargle or twargle recipients, which is true, as the smallest group at any given time was 7 individuals. An outcome over 50% indicates that monkeys gargle and twargle more to the alpha male than to all other group members combined.

(f.3.) Data availability statement

The data supporting the findings of this study are available in the supplementary materials of this article.

Results

P.1: Infants will gargle and twargle at higher rates than the overall population.

NB models suggest that infants gargle nearly eight times as much as the overall population: ~7.86 gargle/hour compared to ~.99 gargle/hour (NB: n=411 observations, N=355 groups, Z=23.91, P<0.0001); see Table 2. Infants twargle 4.22 times as much as the overall population: ~1.14 twargle/hour compared to ~0.27 twargle/hour (NB: n=400 observations, N=347 groups, Z=5.70, P<0.0001; Figure 1; Tables 2 and 3).

Figure 1 (a plot of raw data) demonstrates the rate of change in gargle and twargle vocalizations with age. Monkeys gargle more than they twargle at almost all ages, exhibiting a general decline from four months of age onwards. The peak gargle and twargle rates occur during the 4th month of life, when infants are leaving their mothers' backs and begin exploring the world independently.

Table 3. Incident rate ratios (IRR), exponentiated confidence intervals (CI), standard errors of the estimates (SE), random intercept variance (Var) and P-values for the fixed effects for P.1: Infants will gargle and twargle at higher rates than the overall population.

	IRR	CI	SE	Var	P-value	Prediction supported?
Gargle model of infants compared to the rest of the population	10.405	8.588 – 12.608	0.098	0.724	<0.0001	yes
Twargle Model of infants compared to the rest of the population	2.902	2.012 – 4.187	0.187	1.429	<0.0001	yes

Figure 1: The raw data scatterplot displays average gargle (open red circles) and twargle (closed blue circles) rate data by age in months. The subplot displays the average gargle and twargle rates for individuals 24 months of age and younger.

P.2: Pregnant females will gargle and twargle at higher rates than the rest of the adult female population, especially adult females who are not pregnant and do not have an infant <8 months old.

Females increase gargle and twargle rates during the birthing month, as displayed by Figure 2 (a plot of raw data). Females show marked increases in gargle and twargle rates around four and five months before giving birth, respectively. We suspect the pattern is related to pregnancy recognition and hormonal changes, but we do not have data to test this theory.

Table 4. Incident rate ratios (IRR), exponentiated confidence intervals (CI), standard errors of the estimates (SE), random intercept variance (Var) and P-values for the fixed effects for P.2 models: Pregnant females will gargle and twargle at higher rates than the rest of the adult female population, especially adult females who are not pregnant and do not have an infant <8 months old.

	IRR	CI	SE	Var	P-value	Prediction supported?
Gargle model of pregnant females compared to non-pregnant adult females	0.717	0.535 – 0.961	0.150	0.312	0.026	no (wrong direction)
Twargle model of pregnant females compared to non-pregnant adult females	0.913	0.694 – 1.200	0.140	0.627	0.513	no
Gargle model of pregnant females compared to adult females who are not pregnant and do not have an infant <8 months old.	1.389	1.015 – 1.901	0.160	0.155	0.040	weak support
Twargle model of pregnant females compared to adult females who are not pregnant and do not have an infant <8 months old.	1.349	1.016 – 1.792	0.145	0.815	0.038	weak support

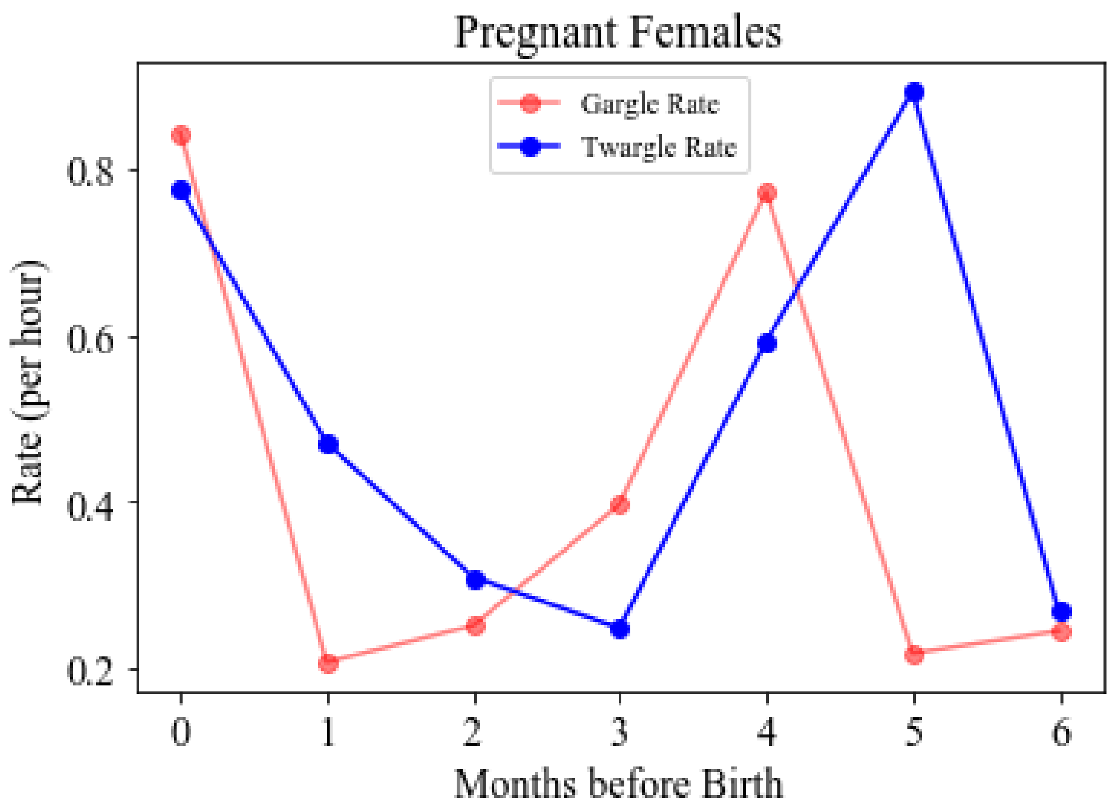

Figure 2: The raw data line graph displays the average gargle rates (red) and twargle rates (blue) of pregnant females 0-6 months before giving birth. The graph shows increases in gargle and twargle rates during the birthing month and four and five months before giving birth, respectively.

P.2.a. Results suggest that pregnant females do not gargle and twargle more than adult females who are not pregnant. (Gargle NB: n=208 observations, N=112 groups, Z=-2.23, P=0.026; Twargle NB: n=202 observations, N=111 groups, Z=-0.65, P=0.513).

P.2.b. Results suggest that pregnant females do not gargle and twargle more than adult females who are not pregnant and do not have an infant <8 months old (Gargle NB: n=206 observations, N=110 groups, Z=2.05, P=0.040; Twargle NB: n=201 observations, N=110 groups, Z=2.073, P=0.038; Table 4; Figure S1 – Figure S2).

P.3: Females with infants (<8 months) will gargle and twargle at higher rates than the rest of the adult female population, especially adult females who are not pregnant and do not have an infant <8 months old.

P.3.a. Results suggest that females with infants (<8 months) gargle and twargle more than the rest of the adult female population (Gargle NB: n=210 observations, N=112 groups, Z=9.09, P<0.0001; Twargle NB: n=206 observations, N=111 groups, Z=5.62, P<0.0001).

P.3.b. Results suggest that females with infants (<8 months) gargle and twargle more than adult females who are not pregnant and do not have an infant <8 months old (Gargle NB: n =210 observations, N=112 groups, Z=8.46, P<0.0001; Twargle NB: n=205 observations, N=110 groups, Z=6.21, P<0.0001; Table 5; Figures S3 – Figure S4).

Table 5. Incident rate ratios (IRR), exponentiated confidence intervals (CI), standard errors of the estimates (SE), random intercept variance (Var) and P-values for the fixed effects for P.3 models: Females with infants (<8 months) will gargle and twargle at higher rates than the rest of the adult female population, especially adult females who are not pregnant and do not have an infant <8 months old.

	IRR	CI	SE	Var	P-value	Prediction supported?
Gargle model of females with infants (<8 months) compared to the rest of adult females	3.086	2.421 – 3.935	0.124	0.237	<0.0001	yes
Twargle model of females with infants (<8 months) compared to adult females who are not pregnant and do not have an infant <8 months old.	2.087	1.615 – 2.698	0.131	0.582	<0.0001	yes
Gargle model of females with infants (<8 months) compared to adult females who are not pregnant and do not have an infant <8 months old.	3.416	2.570 – 4.541	0.145	0.201	<0.0001	yes
Twargle model of females with infants (<8 months) compared to adult females who are not pregnant and do not have an infant <8 months old.	2.341	1.790 – 3.061	0.137	0.645	<0.0001	yes

Females with infants (<8 months) gargle the most 1-2 months after giving birth and twargle the most 4 months after giving birth (Figure 3). They gargle more than they twargle during the first 3 months post-partum.

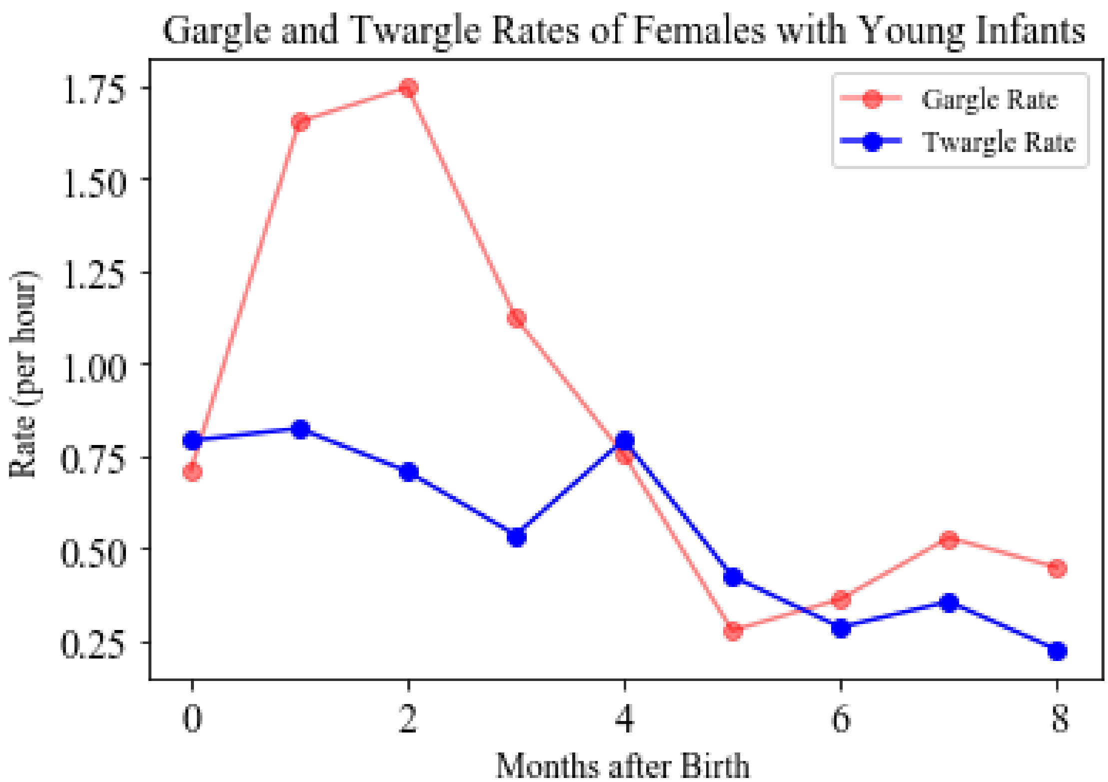

Figure 3: The raw data line graph displays the average gargle rates (red) and twargle rates (blue) of females with young infants (<8 months). The graph suggests that females with infants (<8 months) gargle at high rates 1-2 months after giving birth and at slightly higher rates 7-8 months after giving birth. Females twargle at high rates 1-4 months after giving birth.

An alternative modeling approach to answering P2 and P3 is presented in the SI (Table S5).

P.4: Individuals will gargle and twargle more when the alpha male is not the offspring's (or fetus') father.

P.4.a. Our results suggest that infants (<8 months) do not gargle or twargle more when the alpha male is not their father (Gargle NB: n=42 observations, N=40 groups, Z=0.173, P=0.863; Twargle NB: n=36 observations, N=33 groups, Z=0.334, P=0.738). However, infants (8-23 months) gargle, but may not twargle, more when the alpha male is not their father (Gargle NB: n=63 observations, N=48 groups, Z=3.436, P<0.001; Twargle NB: n=49 observations, N=45 groups, Z=1.880, P=0.060).

P.4.b. Our results suggest that pregnant females do not gargle or twargle more when the alpha male is not their father (Gargle NB: n=61 observations, N=51 groups, Z=0.223, P=0.824; Twargle NB: n=55 observations, N=46 groups, Z=-3.24, P=0.001).

P.4.c. Our results suggest that females with infants (<8 months) do not gargle or twargle more when the alpha male is not their father (Gargle NB: n=73 observations, N=58 groups, Z=0.433, P=0.665; Twargle NB: n=67 observations, N=53 groups, Z=-1.80, P=0.072; Table 6).

Table 6. Incident rate ratios (IRR), exponentiated confidence intervals (CI), standard errors of the estimates (SE), random intercept variance (Var) and P-values for the fixed effects for P.4 models: Individuals will gargle and twargle more when the alpha male is not the offspring's (or fetus') father.

	IRR	CI	SE	Var	P-value	Prediction Supported?
Gargle model of infants (<8 months) whose father is not the alpha male compared to infants (<8 months) whose father is the alpha male	1.043	0.644 – 1.690	0.246	0.101	0.863	no
Twargle model of infants (<8 months) whose father is not the alpha male compared to infants	1.211	0.394 – 3.723	0.573	0.339	0.738	no

(<8 months) whose father is the alpha male						
Gargle model of infants (8 – 23 months) whose father is not the alpha male compared to infants (8 – 23 months) whose father is the alpha male	2.235	1.413 – 3.536	0.234	0.470	<0.001	yes
Twargle model of infants (8 – 23 months) whose father is not the alpha male compared to infants (8 – 23 months) whose father is the alpha male	1.914	0.973 – 3.766	0.345	0.598	0.060	no
Gargle model of pregnant females whose fetus' father is not the alpha male compared to pregnant females whose expected offspring's father is the alpha male	1.092	0.503 – 2.373	0.396	0.283	0.824	no
Twargle model of pregnant females whose fetus' father is not the alpha male compared to pregnant females whose expected offspring's father is the alpha male	0.350	0.185 – 0.660	0.324	1.486	0.001	no (wrong direction)
Gargle model of females with infants (<8 months) whose offspring's father is not the alpha male compared to females with infants (<8 months) whose offspring's father is the alpha male	1.158	0.597 – 2.244	0.338	0.374	0.665	no
Twargle model of females with infants (<8 months) whose offspring's father is not the alpha male compared to females with infants (<8 months) whose offspring's father is the alpha male	0.646	0.402 – 1.040	0.243	1.548	0.072	no

P.5: Individuals will gargle and twargle more to the alpha male than to any other monkey in the group.

Individuals gargled and twargled more to the alpha male than to all other individuals combined (binomial tests: both P<0.0001; see tables Table S2, S3 and S4 for further details) despite multiple subordinate males and only one alpha male occupying a group at any point in time. Throughout the entire study population, alpha males received 7628 (57.9%) of the 13185 gargles produced, and 2243 (82.2%) of the 2729 twargles produced. Infants (<8 months) twargled more to the alpha male, but they did not gargle more to the alpha male; 46% of gargles were directed at the alpha male (see SI Tables 2-4 for further information).

Discussion

Our research explores our proposed, “Assessment of Infanticide Risk Hypothesis,” suggesting that white-faced capuchins use two elements of their vocal repertoire, the gargle and the twargle, to perform Zahavian bond tests. We predicted that individuals will gargle and twargle more frequently when facing infanticide risk, and we predicted that individuals will gargle and twargle more frequently to individuals posing infanticide risk, namely the alpha male. Our results provide some support for our hypothesis, but a few questions remain unclear. Individuals facing infanticide risk (to themselves or their offspring) gargled and twargled at the highest rates out of all target groups in the study. However, pregnant females, whose fetuses were at risk for future infanticide, did not gargle and twargle at high rates. Furthermore, infants (8-23 months) were the only demographic group included in the study that gargled more to the alpha male when he was not their father. Infants (<8 months) were also the only demographic group included in the study that did not gargle more to the alpha male than to any other group member.

Infants (<8 months) gargle and twargle more than any other demographic group included in our study (Figure 1, Table 2). However, infants do not gargle or twargle more to the alpha male when he is not their father, and they do not gargle more to the alpha male than to any other group member. Our results suggest that assessing infanticide risk is not the sole motivation for infant gargling and twargling. One potential explanation is that infants may be strongly motivated to test bonds with multiple group members, because they may not have prior knowledge regarding allies and enemies. Infants (8-23 months) gargle more when the alpha male is not their father, and this could potentially represent the age at which individuals begin developing a sense of the social hierarchy. Also, this is the age in which infants begin spending less time around their mothers (Perry et al., 2012), and they may recognize the necessity of testing bonds with the alpha male when they receive less protection from their mothers. They could also be motivated to test bonds to: 1) assess coalitionary support or 2) assess access to valuable resources.

Our study does not provide support for our prediction that pregnant females gargle and twargle at especially high rates (Table 4). We suspect that pregnant females, as compared to females with infants (<8 months), experience less selective pressure to test bonds, as their threat of infanticide is not so imminent as that of females with infants.

Adult females with infants (<8 months) gargle and twargle at high rates, especially when infants are young (<3 months old) (Figure 3). Mothers may vocalize at high rates during this time to convey gargle and twargle function and context to offspring, as researchers have found that mothers across many non-human primate species convey vocal context and function (Bergman et al., 2019; Elowson et al., 1998; Seyfarth & Cheney, 1986). Future analyses should investigate gargles and twargles in the context of mother-offspring dyads to address this possibility and the relationship between weaning and gargles and twargles.

Our results suggest that, with the exception of infants (8-23) months, individuals do not gargle nor twargle more when the alpha male is not their father (Table 6). We expected increased bond testing when the alpha male did not sire the offspring, as these are expected to be times when individuals are particularly at risk of infanticide and/or in need of coalitionary support and resources (Perry, 2012). However, most of our studied demographic groups test bonds regardless of who holds the current alpha male position. We suggest several potential explanations: a) Individuals are motivated to test bonds, because they need coalitionary support and access to resources in many situations (e.g. during fights or inter-group encounters), b) Bond testing indicates long-term sentiments of a relationship that are likely to carry forward well into the future (Zahavi, 1977b;

Zahavi & Zahavi, 1977), so individuals may preemptively test bonds in preparation of a risky situation, or c) Individuals may not recognize their father or trust that their father recognizes them as kin. However, according to the logic of (b), we would expect pregnant females to gargle and twargle at high rates if individuals preemptively test bonds, which we did not find, so explanation (b) seems unlikely.

The majority of gargles and the overwhelming majority of twargles were directed to the alpha male, across almost all demographic groups. This finding supports our hypothesis that individuals use gargles and twargles to test important bonds. The difference in gargle and twargle rates throughout the study seems to indicate that gargles and twargles are at least sometimes used for distinct purposes. Elements of the benign trill vocalization are incorporated into the twargle (Gros-Louis, 2002; Gros-Louis et al., 2008), so it is possible that twargles are produced with more benign intent than gargles. This may explain the difference in gargle and twargle rates of females with infants (<8 months). Females gargle, rather than twargle, at high rates 0-3 months post-partum (Figure 3). Perhaps this is an especially crucial time for females to bond test (Perry et al., 2012), because infants are nutritionally dependent and at highest risk for infanticide, which may influence vocalization selection.

Alternative hypotheses could explain gargle and twargle functions. We considered alternative hypotheses previously (Perry 1998; Perry & Manson, 2008) and they were not supported because of the context in which gargles and twargles are produced. If gargles were used to formally acknowledge another's superior rank, we would expect them to be frequent and unidirectional in most dyads of disparate rank and least frequent in adjacently ranked individuals during times when relative rank was being disputed. If the gargles were used to test bonds with adjacently ranked individuals, they should be more frequently exchanged (in both directions) within these dyads (Preuschoft, 1999; Smith et al., 2011). Neither of these situations is true, as gargles are primarily used by infants and their mothers towards adult (and primarily alpha) males. If individuals use (gargle) vocalizations as appeasement, to mitigate conflict and tension, they would be expected to occur before, during or shortly after conflicts if (Dias, Luna, & Espinosa, 2008; Hohmann & Fruth, 2000; Smith et al., 2011); however, gargles and twargles are produced primarily during peaceful interactions. If gargles/twargles are indicative of respect by the vocalizer towards the recipient, we would expect the recipient to respond neutrally or affiliatively; however, a negative response is often produced (Gros-Louis et al., 2008; Perry & Manson, 2008). And if gargles and twargles are a sign of allegiance, then alpha males should be concerned when they hear gargles being directed towards other group members, yet they pay no attention when these situations arise (Perry & Manson, 2008).

Therefore, "The Assessment of Infanticide Risk" remains our leading hypothesis explaining gargles and twargles.

(a) Limitations

Although this study produces results consistent with the Assessment of Infanticide Risk hypothesis by comparing gargle and twargle rates across demographic categories, it would be desirable to also conduct a fine-grained temporal analysis of how relationships change within each dyad, looking at the causes and consequences of producing gargles and twargles. Are these vocalizations produced when the relationship is under particular strain? Is the vocalizer's subsequent behavior contingent on the affective responses of the recipient to the gargle or twargle? The current data set is not well suited to this goal, because of the sampling density within each dyad. However, these would be exciting analyses to conduct with a more limited sample of individuals that have dense focal sampling within time periods characterized by changes in relationship quality.

(b) Conclusion

Our results largely support the Assessment of Infanticide Risk Hypothesis. Infants and females with infants (<8 months), i.e. individuals/their offspring at greatest infanticide risk, gargle and twargle at higher rates than the overall population and population subsets. Pregnant females did not gargle and twargle at exceptionally high rates, perhaps because their potential infanticide risk was too far in their future. Most demographic groups gargle and twargle more to the alpha male than to any other and all other individuals in the group. However, with the exception of infants 8-23 months of age, individuals do not gargle or twargle more when the alpha male is not their father. Overall, we found that individuals are motivated to test bonds during infanticidal risk periods, but our results suggest that that individuals may be motivated to test bonds for alternative reasons as well.

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Data set:

Access to the data set and code can be found here: https://osf.io/59gmw/

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Title: Are Demographic Correlates of White-faced Capuchin Monkeys *(Cebus capucinus)* "Gargle and Twargle" Vocalization Rates Consistent with the Infanticide Risk Assessment Hypothesis?

Supporting Information

Characteristics of the Data Set

Table S1 Distribution of behavioral sampling effort across demographic categories

Target Population	Estimated Percentage of Total Population	Percentage of Gargle Hours	Percentage of Twargle Hours
Infants (< 24 months)	21%	19%	9%
Juveniles (24 – 59 months)	21%	21%	15%
Adult Males (>= 60 months)	26%	33%	42%
Adult Females (>= 60 months)	32%	27%	34%

To estimate % of total population we do the following: Each monkey that has been identified has been assigned an estimated birth date, which is used to compute its (estimated) age on every date when it is seen. We count a monkey as having been seen during a month of its life (e.g. at the age of 21 months) if that was its estimated age (discarding fractional months) any of the times it was seen. The fraction of monkeys estimated to be some age (in months) is the number of monkeys seen at that age divided by the sum of the numbers seen for all ages. Clearly a monkey who was seen at age 9 months and then again at 11 months was alive at 10 months, but is not counted. The latter two columns are computed on the basis of the time spent collecting focal follows of monkeys observed by researchers who could reliably identify the specified vocalization.

Additional Results

Distribution of gargles and twargles across age-sex categories for vocalizers and targets of vocalizations:

Tables S2 and S3 show the distribution of the sample according to the age-sex class of vocalizers and their recipients. Note that these are raw frequencies, not rates of behavior, i.e. the amount of focal follow time is not included here, so the percentages in columns 2-5 are for the entire pooled sample, not for the percentage directed specifically by that age-sex class to another age-sex. Focal animals are always the vocalizers in our analyses. Therefore, in the final column, we present the percentage of all vocalizations for this age-sex class that are directed towards adult males, defined as being >5 years of age. We also define adult females as those being >5 years of age. Except for adult males, all other age-sex classes direct their gargles and twargles overwhelmingly towards adult males.

Table S2: Number of gargles in the sample, according to age-sex class of vocalizer and age-sex class of recipient, for all cases in which age-sex classes of both are known, followed by the corresponding % of all vocalizations in the entire sample in parentheses. The final column is the % of vocalizations by that particular age-sex class that are directed towards adult males.

Age-sex class of vocalizer	Age-sex class of recipient				% of gargles directed towards males (>5 years of age) for the specified age-sex class of vocalizer
	Females (<5 years of age)	Females (>5 years of age)	Males (< 5 years of age)	Males (>5 years of age)	
Females (≤5 years of age)	35 (0.24%)	50 (0.34%)	16 (0.11%)	6636 (45.73%)	98.50%
Females (>5 years of age)	7 (0.05%)	2 (0.01%)	5 (0.03%)	2297 (15.83%)	99.39%
Males (≤5 years of age)	19 (0.13%)	334 (2.30%)	55 (0.38%)	4966 (34.22%)	92.41%
Males (>5 years of age)	23 (0.16%)	23 (0.16%)	33 (0.23%)	33 (0.23%)	29.46%
Total	84 (0.58%)	409 (2.82%)	109 (0.75%)	13932 (96.00%)	

Table S3: Number of twargles in the sample, according to age-sex class of vocalizer and age-sex class of recipient, for all cases in which age-sex classes of both are known, followed by the corresponding % of all vocalizations in the entire sample in parentheses. The final column is the % of vocalizations by that particular age-sex class that are directed towards adult males.

Age-sex class of vocalizer	Age-sex class of recipient				% of twargles directed towards males (>5 years of age) for the specified age-sex class of vocalizer
	Females (< 5 years of age)	Females (>5 years of age)	Males (< 5 years of age)	Males (>5 years of age)	
Females (< 5 years of age)	17 (0.61%)	10 (0.36%)	5 (0.18%)	1003 (36.20%)	96.91%
Females (>5 years of age)	17 (0.61%)	10 (0.36%)	34 (1.23%)	1375 (49.62%)	95.75%
Males (<5 years of age)	0 (0.00%)	5 (0.18%)	7 (0.25%)	245 (8.84%)	95.33%
Males (>5 years of age)	7 (0.25%)	9 (0.32%)	12 (0.43%)	15 (0.54%)	34.88%
Total	41 (1.48%)	34 (1.23%)	58 (2.09%)	2638 (95.20%)	

P.1: Infants will gargle and twargle at higher rates than the overall population.

Fifty-six monkeys were observed both as infants and non-infants, permitting a more longitudinal approach than was used in the main text. These 56 individuals gargled at 8.23/hour when <8 months old and 0.96/hour when >8 months old. Forty-five gargled at higher rates during infancy as compared to adulthood. The 11 exceptions are mostly accounted for by small observation times as infants. One individual was observed for 9, one for 4.5 hrs, one for 2.2 hrs and the rest for < 2 hours. Only 2 of these 11 exceptions were observed gargling as infants. Twenty-seven monkeys were observed for > 10 hours as infants (and also for > 10 hours as non-infants), and all of these individuals gargled at higher average rates as infants than as non-infants.

Twargles are less commonly observed than gargles, so more observation time is required to obtain a similar sample size to the gargle data. Fifty-three individuals were observed (by observers competent to identify twargles) both as infants and non-infants, and only 8 were observed for at least ten hours as infants (and >100 hours as non-infants.) One individual twargled at a higher average rate as a non-infant than as an infant, and the other 7 displayed higher rates as infants. In total, only 20 of the 53 displayed higher average twargle rates as infants, but none of the others (N=33) were observed twargling as infants (i.e. an average rate of zero). Twelve individuals also displayed zero rates as non-infants. Eleven individuals were observed for over 100 hours as non-infants, all of whom were observed twargling at least once.

P.5: Individuals will gargle and twargle more to the alpha male than to any other monkey in the group.

Table S4: Percentage of vocalizations directed towards alpha males as opposed to all other group members combined.

Vocalization type	Percentage of Vocalizations directed to alpha male	Number of vocalizations directed to the alpha male	Number of vocalizations directed to all other individuals	P-value
Gargles	57.9%	7628	5557	<0.0001
Twargles	82.2%	2243	486	<0.0001

Table S5: Counts and percentages of gargles and twargles directed by infants to (a) the alpha male, or (b) all other individuals in the group.

Behavior	To Alpha	Not to Alpha	Percentage to Alpha
Infant (<8 months) gargles	2611	3061	46%
Infant (<8 months) twargles	259	105	71%
Infant (8-23 months) gargles	1611	1697	49%
Infant (8-23 months) twargles	275	116	70%

Table S6: Counts and percentages of gargles and twargles directed by adults (>60 months old) to (a) the alpha male, or (b) all other individuals in the group.

Behavior	To Alpha	Not to Alpha	Percentage to Alpha
Adult (>60 months) gargles	2006	348	85%
Adult (>60 months) twargles	1283	192	87%

Interactions between Group Size and Gargle and Twargle Rates

In response to a request from reviewers, we explore how group size and age of vocalizer might affect the proportion of gargles and twargles directed towards the alpha male, using Generalized Linear Mixed Model, using the glmmTMB function in R (http://www.R-project.org/) (results below in S7). Age and group size are fixed effects, and monkey id is a random effect:

alpha ~ age5 + size + offset(log(total)) + (1 | id)

"Alpha" is the fraction of gargles or twargles directed towards the alpha male, "age5" is the age category (as described below), "size" is the group size, "total" is the number of gargles or twargles produced, and "id" is the identity of an individual monkey. In the model, individuals are grouped into 6 age categories: each of the first 5 years of life is treated as a separate category (age 0 to 4) and the 6th category lumps all individuals age 5 years or more (i.e. adults). Group size ranges from 5 to 41 individuals. We ran models using the nbinom1 and nbinom2 distributions, but we only report the nbinom2 results, as models using this distribution performed better according to AIC (Table S7). See the code and output file for further details.

The models show how age and group size are related to the fraction of gargles and twargles directed towards the alpha male. For every year of age, up to age 5, there is an increase by a factor of 1.094 in the fraction of gargles, and an increase by a factor of 1.032 in the fraction of twargles, directed to the alpha male. Also, for each individual added to the group, the fraction of gargles directed to the alpha male changes by a factor of 0.985 (i.e. decreases), and the fraction of twargles directed to the alpha male changes by a factor of 0.994 (also decreasing).

Summaries of the raw data showing how the proportion of gargles directed to the alpha male vary according to age and group size are presented after the model results, in Tables S8 & S9.

Table S7: Results from the GLMMs predicting the impact of (a) age of vocalizer and (b) group size on the proportion of gargles and twargles directed towards the alpha male. Monkey ID is a random effect.

	Age exp(est)*	CI Age	SE Age	P-value	Group Size exp(est)*	CI Group Size	SE Group Size	P-value
Gargle Model	1.094	1.067 – 1.212	0.013	<0.001	0.985	0.979 – 0.991	0.003	<0.001
Twargle Model	1.032	1.006 – 1.059	0.013	0.015	0.994	0.987 – 1.000	0.003	0.055

*exp(est) is the exponential of the estimate reported by R's summary of the glmmTMB function. In other contexts when only two groups are being compared we refer to it as IRR. In this more general case, it is the ratio between the estimate of the probability of the gargle being directed towards the alpha of n+1-year-olds vs. n-yr-olds, or, in the case of group size, it is the ratio between the estimate of the probability of the gargle being directed towards the alpha in group size n+1 vs. size n. The confidence intervals refer to these quantities, i.e., 1.067 - 1.212 is the confidence interval around 1.094.

For the gargle model, there are 1040 observations, 193 groups, and the variance in the random effects intercept is 0.074. For the twargle model, there are 477 observations, 135 groups, and the random effects intercept variance is 0.010.

The raw data (Tables S8-9, below) show that for most ages and group sizes, individuals gargle and twargle most frequently to the alpha male. Note that for age 5+, the proportion of gargles/twargles directed to the alpha male is well over 0.50 for all group sizes with a reasonable sample size. Data are scant for group sizes below 10 and above 39.

Table S8: Proportions of gargles directed to the alpha male for different age groups and group sizes (raw data). NA values indicate a complete absence of data for that category. * indicates a sample size of <10 gargles in that category, and † indicates a sample of ≥100 gargles in that category. Age 0-1 indicates the first year of life.

Proportion of Gargles directed to the Alpha Male by Group Size and Age

Group Size

Age	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44
0-1	0.0*	0.69†	0.54†	0.63†	0.52†	0.47†	0.34†	NA
1-2	1.0*	0.40	0.82†	0.55†	0.39	0.51†	0.48†	0.36
2-3	1.0	0.74†	0.85†	0.91†	0.70	0.61†	0.59†	0.13*
3-4	NA	0.93	0.89†	0.83†	0.83	0.73	0.49†	NA
4-5	1.0*	1.0	0.92	0.97	0.77	0.11*	0.75	NA
5+	0.95	0.96†	0.88†	0.82†	0.85†	0.80†	0.81†	NA

Table S9: Proportions of twargles directed to the alpha male for different age groups and group sizes (raw data). NA values indicate a complete absence of data for that category. * indicates a sample size of <10 twargles in that category, and † indicates a sample of ≥100 twargles in that category. Age 0-1 indicates the first year of life.

Proportion of Twargles Directed to the Alpha Male by Group Size and Age

Group Size

Age	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44
0-1	0.50*	0.75	0.66†	0.77†	0.66†	0.75	0.44	NA
1-2	NA	0.0*	0.71*	0.50	0.0*	0.73	0.92†	0.17*
2-3	1.0*	1.0	1.0*	0.89	0.67*	0.69	0.83	0.43*
3-4	NA	0.0*	0.78	0.82	0.98	0.83*	0.36	NA
4-5	NA	0.43*	0.93	0.93	0.92	0.0*	1.0*	NA
5+	0.92†	0.89	0.89†	0.87†	0.88†	0.82†	0.33*	NA

As group size increases to 30+ members, individuals gargle relatively less to the alpha male, especially when young (Table S8). We suspect this to be related to the threshold at which groups are prone to fission. In large groups, monkey "cliques" form, which may eventually separate into independent groups should a fission event occur. In the event of a fission, the current alpha male may no longer be a primary provider of valuable resources and protection, thus this vocalization dynamic may display bet-hedging behavior. However, the same trend is not true for twargles (Table S9). This suggests that gargles and twargles may serve distinct functions, although it is unclear what these distinctions are.

Multiple Linear Regression Models with Pregnant Females and Females with Infants (<8 months) (Relevant to P2 and P3): Pregnant females (P2) and females with infants (<8 months) (P3) were predicted to gargle and twargle at higher rates than the rest of the adult female population (>60 months and neither pregnant nor having an infant <8 months old).**)**
We ran multiple linear regression models with glmmTMB in R (http://www.R-project.org/). This approach differs from the modeling approach in the main text in that it includes the two reproductive states of interest – pregnancy and early lactation (i.e. having an infant <8 mo old) as fixed effects in the same model, rather than creating multiple separate models, each containing a single fixed effect. As in the other models, we include individual monkey ID as a random effect and include observation time as a log offset variable.

We predicted that pregnant females and adult females with infants (<8 months) gargle and twargle more than all other adult (> 60 months) females. Our results show that pregnant females display slightly higher gargle rates, and females with infants (<8 months) display much higher gargle rates. (Gargle GLMM: n=306 observations, N=112 groups, random intercept variance=0.206; Twargle GLMM: n=297 observations, N=111 groups, random intercept variance =0.611) (Table S10).

Table S10: Results of multiple linear regression models in which (a) pregnancy and (b) having an infant <8 months old are fixed effects in the same model predicting gargle and twargle rates, in separate models. Incident rate ratios (IRR), exponentiated confidence intervals (CI), standard errors of the estimates (SE), P-values and Z-scores are presented for the fixed effects for GLMMs for Predictions 2 & 3.

	IRR	CI	SE	P-value	Z-score	Prediction supported?
Gargle pregnancy variable in GLMM	1.486	1.087 – 2.032	0.160	0.013	2.484	weak
Gargle female with infant (<8 months) variable in GLMM	3.570	2.707 – 4.710	0.141	<0.0001	9.005	yes
Twargle pregnancy variable in GLMM	1.332	0.983 – 1.805	0.155	0.064	1.851	no
Twargle female with infant (<8 months) variable in GLMM	2.281	1.732 – 3.005	0.141	<0.0001	5.865	yes

```
#This file contains the code used to run  analyses in R,  prepared with assistance from D. Cohen.
#We explain  the code, using the model presented in Table 3 as an annotated example for
#interpreting the output.

$ R
# ... omit output showing version, copyright, platform ...

> library(glmmTMB)
# we use glmmTMB package

# Change the working directory, which must be set to where you (the user)  saved the data files.
> datadir=""

# Create the function to compute IRR and its confidence interval, which only  needs to be
defined once.

> expci <- function(coef, se){c(exp(coef),se*exp(coef),exp(coef + se*qnorm(.025)),exp(coef -
se*qnorm(.025)))}
# See description below of IRR computation.

# function (constructed after our data analysis) to show results of
# R models constructed from imported data (again, only  needs to be defined once)
# More explanation appears after the first example.

> showresult <- function(model,datafile){
  data <- read.csv(paste(datadir,datafile,sep=""),na.strings="!@#$%");
  m <-summary(glmmTMB(model, data=data,family=nbinom1));
  print(m);
  irr=expci(m$coefficients$cond[2,1],m$coefficients$cond[2,2])
  cat("IRR = ",irr[1]," CI: ",irr[3]," - ",irr[4],"\n")}


# Now an annotated first example:

> showresult(nvn~infant+offset(log(vnhr))+(1|focal),"P1_gargle.csv")
 Family: nbinom1  ( log )
Formula:         nvn ~ infant + offset(log(vnhr)) + (1 | focal)
Data: data

     AIC      BIC   logLik deviance df.resid
```

```
  2621.0   2637.0  -1306.5   2613.0     407

Random effects:

Conditional model:
 Groups Name        Variance Std.Dev.
 focal  (Intercept) 0.7244   0.8511
Number of obs: 411, groups:  focal, 355

Overdispersion parameter for nbinom1 family (): 27.9

Conditional model:
            Estimate Std. Error z value Pr(>|z|)
(Intercept) -0.89425    0.10291   -8.69   <2e-16 ***
infant       2.34232    0.09795   23.91   <2e-16 ***
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
IRR =  10.40539  CI:  8.587776  -  12.6077

# The text below explains how the output in the example above relates to  the
# results presented in the manuscript.
#   showresult(nvn~infant+offset(log(vnhr))+(1|focal),"P1_gargle.csv")
# the first argument, nvn~infant+offset(log(vnhr))+(1|focal)
# is the model
# each data row contains:
#  nvn - the number of gargles [would say nve for twargles]
#  infant - 1 if the row refers to an infant, and otherwise 0 [other models have
# different fixed effects, but the same regime follows,
# i.e. a 1 if the group  fulfills the criterion and a 0 if the group does not]
#  vnhrs - number of hours in which gargles could be observed by a trained
#   research assistant in the field [would say vehrs for twargle hours]
#  focal - id of monkey
#
# the second argument to showresult is the name of the data file
#
# In read.csv the na.strings argument is required in order to read
# the monkey id NA as a regular ID rather than a missing id
#
# the function showresult
#  reads the data file
#  constructs the model (actually the summary of the model)
```

```
#  prints the summary
#  and finally computes the IRR and confidence interval with the
#   function expci.
# The arguments of this function are the estimate and std.error
# of the fixed effect, which are extracted from the summary.
# (only the first fixed effect is shown - two of the models
# below have two fixed effects, so require additional code.
# Both models appear in the SI, not in the main text.)


# We are mainly interested in the output line near the bottom:
#   infant      2.34232    0.09795   23.91   <2e-16 ***
# showing the fixed effect of being an infant
# (Other models have different fixed effects.)
#
# The paper shows the following results:
# #observations and #groups are shown in the output above:
#   Number of obs: 411, groups:  focal, 355
# Z value is 23.91, in the z value column of the infant line
# P value is shown as <2e-16, in the Pr(>|z|) column of the infant line
#  (the paper describes this as <.0001)
#
# In table 3 we also see:
# SE, .098, corresponding to the Std. Error column of the infant line
#  (which says .09795, rounded to .098 in the table)
# Var, .724 is shown in the Variance column of the line
#   focal  (Intercept) 0.7244   0.8511
#  (again the value .7244 is rounded in the table to .724)
# The other entries in table 3, IRR and CI, are computed by the
# function expci with two arguments, the estimate and std. error of
# the infant line.
# IRR is exp (exponential function) of the estimate: e^(2.34232)=10.405.
# CI is the last two values in the output of expci, showing the exponential
# of the 95% confidence interval around the estimate, i.e., 95% confidence
# interval of IRR.

# Below is the code for the remaining models, which should produce all of
# the statistical results including IRR and CI

#P1 twargle
> showresult(nve~infant+offset(log(vehr))+(1|focal),"P1_twargle.csv")
```

```
# Pregnant females will gargle and twargle at higher rates than the rest of
# the adult female population, especially adult females who are not pregnant
# and do not have an #infant <8 months old.
#P2a gargle
> showresult(nvn~pregnant+offset(log(vnhr))+(1|focal),"P2a_gargle.csv")

#P2a twargle
> showresult(nve~pregnant+offset(log(vehr))+(1|focal),"P2a_twargle.csv")

#P2b gargle
> showresult(nvn~pregnant+offset(log(vnhr))+(1|focal),"P2b_gargle.csv")

#P2b twargle
> showresult(nve~pregnant+offset(log(vehr))+(1|focal),"P2b_twargle.csv")

#P3a gargle
> showresult(nvn~nursing+offset(log(vnhr))+(1|focal),"P3a_gargle.csv")

#P3a twargle
> showresult(nve~nursing+offset(log(vehr))+(1|focal),"P3a_twargle.csv")

#P3b gargle
> showresult(nvn~nursing+offset(log(vnhr))+(1|focal),"P3b_gargle.csv")

#P3b twargle
> showresult(nve~nursing+offset(log(vehr))+(1|focal),"P3b_twargle.csv")

# now we will use a different function for P4
> showresult2 <- function(model,datafile,subset){
  data <- read.csv(paste(datadir,datafile,sep=""),na.strings="!@#$%");
  m <-summary(glmmTMB(model,
data=eval(parse(text=paste("data[data$",subset,",]",sep=""))),family=nbinom1));
  print(m);
  irr=expci(m$coefficients$cond[2,1],m$coefficients$cond[2,2])
  cat("IRR = ",irr[1]," CI: ",irr[3]," - ",irr[4],"\n")}

#the difference between showresult2 and showresult is that there is an additional subset
argument
# which describes which subset of the data to use.
```

```
#P4 gargle
> showresult2(nvn~fatherNOTalpha+offset(log(vnhr))+(1|focal),"P4_gargle.csv","X8mo==1")

# While the lines above, e.g., for P.1, compute a summary of a model like this:
# > summary(glmmTMB(nvn~infant+offset(log(vnhr))+(1|focal), data=data,family=nbinom1))
# showresult2 uses only a subset of the data,  like this:
# > summary(glmmTMB(nvn~fatherNOTalpha+offset(log(vnhr))+(1|focal),
data=data[data$X8mo==1,],family=nbinom1))
# In this case it is using only the data rows with column X8mo equal to  1
# (in other words the data for monkeys less than 8 months old)

> showresult2(nvn~fatherNOTalpha+offset(log(vnhr))+(1|focal),"P4_gargle.csv","X24mo==1")

> showresult2(nvn~fatherNOTalpha+offset(log(vnhr))+(1|focal),"P4_gargle.csv","nursing==1")

> showresult2(nvn~fatherNOTalpha+offset(log(vnhr))+(1|focal),"P4_gargle.csv","pregnant==1")


#P4 twargles
> showresult2(nve~fatherNOTalpha+offset(log(vehr))+(1|focal),"P4_twargle.csv","X8mo==1")

> showresult2(nve~fatherNOTalpha+offset(log(vehr))+(1|focal),"P4_twargle.csv","X24mo==1")

> showresult2(nve~fatherNOTalpha+offset(log(vehr))+(1|focal),"P4_twargle.csv","nursing==1")

>
showresult2(nve~fatherNOTalpha+offset(log(vehr))+(1|focal),"P4_twargle.csv","pregnant==1")


#We needed a different function to look at the results for TableS10,
# because we included more than one fixed effect.
#This is almost the same as showresult except that it shows the IRR and CIs for
# 2 separate fixed effects.
# This model is relevant to both Predictions 2 & 3.

> showresult3 <- function(model,datafile){
  data <- read.csv(paste(datadir,datafile,sep=""),na.strings="!@#$%");
  m <-summary(glmmTMB(model, data=data,family=nbinom1));
  print(m);
  irr=expci(m$coefficients$cond[2,1],m$coefficients$cond[2,2])
  cat(attributes(m$coefficients$cond)$dimnames[[1]][[2]],": IRR = ",irr[1]," CI: ",irr[3]," -
```

```
",irr[4],"\n")
  irr=expci(m$coefficients$cond[3,1],m$coefficients$cond[3,2])
  cat(attributes(m$coefficients$cond)$dimnames[[1]][[3]],": IRR = ",irr[1]," CI: ",irr[3]," -
",irr[4],"\n")}

> showresult3(nvn~pregnant+nursing+offset(log(vnhr))+(1|focal),"Table_S10_gargles.csv")

> showresult3(nve~pregnant+nursing+offset(log(vehr))+(1|focal),"Table_S10_twargles.csv")

### The groupsize model [Table S7] needs a slightly different function since it uses nbinom2
> showresult4 <- function(model,datafile){
  data <- read.csv(paste(datadir,datafile,sep=""),na.strings="!@#$%");
  m <-summary(glmmTMB(model, data=data,family=nbinom2));
  print(m);
  irr=expci(m$coefficients$cond[2,1],m$coefficients$cond[2,2])
  cat(attributes(m$coefficients$cond)$dimnames[[1]][[2]],": IRR = ",irr[1]," CI: ",irr[3]," -
",irr[4],"\n")
  irr=expci(m$coefficients$cond[3,1],m$coefficients$cond[3,2])
  cat(attributes(m$coefficients$cond)$dimnames[[1]][[3]],": IRR = ",irr[1]," CI: ",irr[3]," -
",irr[4],"\n")}

> showresult4(alpha ~ age5 + size + offset(log(total)) + (1 | id),"Table_S7_gargles.csv")

> showresult4(alpha ~ age5 + size + offset(log(total)) + (1 | id),"Table_S7_twargles.csv")
```