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1 **Sneeze to leave: African wild dogs (*Lycaon pictus*) use variable quorum**
2 **thresholds facilitated by sneezes in collective decisions.**

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4

5 **Abstract**

6 In despotically driven animal societies, one or a few individuals tend to have a
7 disproportionate influence on group decision-making and actions. However, global
8 communication allows each group member to assess the relative strength of preferences
9 for different options amongst their group-mates. Here, we investigate collective decisions
10 by free-ranging African wild dog packs in Botswana. African wild dogs exhibit dominant-
11 directed group living and take part in stereotyped social rallies: high energy greeting
12 ceremonies that occur before collective movements. Not all rallies result in collective
13 movements, for reasons that are not well understood. We show that the probability of
14 rally success (i.e. group departure) is predicted by a minimum number of audible rapid
15 nasal exhalations ('sneezes'), within the rally. Moreover, the number of sneezes needed
16 for the group to depart (i.e. the quorum) was reduced whenever dominant individuals
17 initiated rallies, suggesting that dominant participation increases the likelihood of a rally's
18 success, but is not a prerequisite. As such, the 'will of the group' may override dominant
19 preferences when the consensus of subordinates is sufficiently great. Our findings
20 illustrate how specific behavioural mechanisms (here, sneezing) allow for negotiation (in
21 effect, voting) that shapes decision-making in a wild, socially complex animal society.

22

23 **Key words**

24 African wild dog (*Lycaon pictus*); signal; consensus decision making;
25 social communication

26

27

28

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29 **Background**

30 Group consensus is ubiquitous in social invertebrate and vertebrate animals [1] and is
31 necessary for individuals to reap the benefits of group living—including added protection
32 from predators, greater information sharing, and better defense of resources [2]. One of
33 the most obvious instances of group coordination in social animals is the decision to
34 move off from a resting spot [3]. Signals used by individuals in the pre-departure and
35 foraging stage of group movement have been described across taxa [4] and often
36 operate in a type of quorum, where a specific signal has to reach a certain threshold
37 before the group changes activity [4, 5]. This ensures that a minimum number of
38 individuals (the actual quorum number) are ready move off [4]. Past research in
39 meerkats, *Suricata suricatta*, for example, has found that a quorum of at least two and
40 usually three meerkats emitting “moving calls” are necessary for the whole group to
41 move to a new foraging patch, and “piping signals” in honey bees, *Apis mellifera* [6], and
42 “trills” in white faced capuchin monkeys, *Cebus capucinus*, [7] are required for collective
43 departures to occur.

44 Certain individuals can also have a disproportionate influence on collective
45 behavior decisions within social systems that exhibit variation in inter-individual
46 relationships (e.g. kinship and dominance structures, see [8]) [9]. For example,
47 dominance rank and/or an individual’s social role (measured as social affiliation strength
48 to others) are often found to correlate with leadership roles, a phenomenon observed
49 pervasively in primates [10]. In social canids, research on group living has focused
50 largely on the role of dominants in directing and repressing subdominant behavior in
51 group-decision making [11].

52 Here, we investigate the collective decisions of African wild dog (*Lycaon pictus*)
53 packs in Botswana during the transition from a sedentary resting state to an active

54 moving state. African wild dogs are the “most social canid” and exhibit uniquely non-
55 aggressive, dominant directed group living, exemplified by stereotyped social rallies [12-
56 14]: high energy, socially intricate pre-departure greeting ceremonies that are
57 “conspicuous,” “highly ritualized,” and are “of high adaptive value...and serve to hold the
58 pack together” [13]. Dominant breeding pairs in an African wild dog pack affect the
59 behavior of the pack as a whole; the dominant-directed social system facilitates feeding
60 by pups at kill sites [15], suppresses sub-dominant pregnancies [16], and ensures
61 collective care for a denning female and pups [17]. However, little is known about the
62 extent to which dominants, or single individuals, drive behavior outside the reproductive
63 realm. Sueur and Petit [3], assert that African wild dogs (*Lycaon pictus*) likely use
64 “shared consensus,” in which all group members participate in the decision making
65 process, because their “open social system” is defined by pervasive cooperation.
66 However, no study has systematically investigated how these social carnivores make
67 collective decisions.

68 Given that African wild dog packs are characterized by pervasive cooperation
69 [12,14] and show intricate pre-departure greeting ceremonies [12-14], we expected a
70 majority or all group members to participate in group consensus about departures.
71 However, because dominant individuals are known to steer many types of group
72 activities [16-18], we expected dominants to have a disproportionate influence in this
73 process. We therefore tested the overall hypothesis that African wild dogs exhibit
74 “partially shared consensus” decisions [3, 18].

75 It is known in several other animal species that the number and identity of
76 individuals participating in the decision process can influence the outcome of collective
77 decisions, and that valuable experience may be correlated with age or dominance [9, 19,
78 20]. Moreover, specific recruitment cues or signals may help guide conspecifics [9] or

79 even be used as a type of voting mechanism [4]. Therefore, to understand the
80 mechanisms by which packs reach a consensus [15] we gathered data relating to the
81 proportion of pack engaged in social behavior, individual participation, and the role of
82 potential communication mechanisms to negotiate timing of departure. Since African wild
83 dogs display dominant-directed group living [20, 21] we examined to what extent
84 individual participation in rallies, and specifically the dominants' participation, affected
85 the likelihood of a successful group movement. Preliminary observations during rallies
86 indicated that audible, abrupt exhalations of air through the nose, 'sneezes' (*Figure 1*;
87 see supplemental video), appeared to be frequent during rallies and may serve as a pre-
88 departure cue or signal [15]. Therefore we investigated the potential for the occurrence
89 of sneezes to serve as a voting mechanism that determines on whether the pack should
90 depart [22, 4] while also considering the relative importance of other factors: the
91 dominance status of the initiator [9], the level of social participation [10], and the number
92 of other departure events that day [11].

93

94 **Methods**

95 Data were collected from five packs ($\bar{X} \pm SD$ adult group size = 8.80 ± 3.63) of African wild
96 dogs in and around the Moremi Game Reserve in the Okavango Delta from June 2014-
97 May 2015. At least one individual in each pack was fitted with a VHF radio collar (ca.
98 180 g; Sirtrack, Havelock West, New Zealand) using darting and immobilization
99 procedures described previously [23]. Collars allowed packs to be located and were
100 replaced when they failed. Some individuals remained collared following the completion
101 of this study as they formed part of a long-term study conducted by the Botswana
102 Predator Conservation Trust (BPCT) spanning the past 25 years [20]. All individuals
103 (N=49) were identified by their unique pelage patterns, and ages and life histories were

104 known for all individuals except some immigrants (N=10). We estimated the age classes
105 (adult, yearling, or pup) of these ten individuals using a combination of body size, pelage
106 development, testicular development, and tooth and ear wear. All work was conducted in
107 accordance with the guidelines for the treatment of animals in behavioural research and
108 teaching [24].

109 To explore the dynamics of collective movement decisions, packs were observed
110 from a vehicle (N=52 days; $\bar{X} \pm SE$ days/pack/month = 2.03 ± 0.50), and their behaviours
111 were recorded during rally periods via direct observation (scan and continuous sampling)
112 and video recordings (Nikon, COOLPIX S7000). Rallies were initiated when an individual
113 rose from rest in the distinctive initiation posture: head lowered, mouth open, and ears
114 folded back [13]. These initiators were identified. Not all rallies resulted in collective
115 movements, and rallies were considered to have ended when all individuals either
116 returned to rest or departed the resting site. We observed 1.92 ± 0.54 ($\bar{X} \pm SE$) rallies per
117 observation session (N = 68 rallies; $\bar{X} \pm SE$ per pack = 14.2 ± 6.75).

118 From video data, we performed behavioural scans every five seconds from
119 initiation until the end of the rally. We used critical incident sampling to record the
120 number of audible, abrupt exhalation of air through the nose, or “sneezes,” during rally
121 attempts and calculated the aggregated frequency of sneeze events per minute before
122 and after the end of rallies. “Sneezes” are atonal high-frequency bandwidth rapid
123 exhalations that are stereotyped and obvious in rallies (*Figure 1*). While it was clear from
124 video data how many sneezes occurred during a rally, the thick habitat African wild dogs
125 prefer to rest in and the unknown, if existent, cue that differentiates sneezes prevented
126 researchers from identifying which individuals sneezed. For each behavioural scan, we
127 recorded which individuals participated in one or more of three stereotypical social
128 interactions: ‘Greet,’ when individuals touched heads or approached within 1m of one

129 another; 'Parallel Run', when individuals ran flank to flank; and 'Mob,' when three or
130 more individuals gathered within 1m of one another [13,12]. The proportion of adults
131 participating in these interactions ranged from 0 (rallies in which there was no social
132 behaviour or only yearlings and pups interacted) to 1 (rallies in which all adults were
133 actively engaged at one point, though not necessarily simultaneously).

134 In a variety of animal systems, the identity, social status, or age-sex class of the
135 individual initiating a collective movement (i.e. moving away from the resting group) can
136 be critical to the likelihood of a collective departure [9, 18,19]. Because relative rank
137 beneath the dominant pair is not readily decipherable within African wild dog packs, we
138 used priority of access to carcasses (POA) as a proxy for dominance: the dominant pair
139 and their pups (<1yr) have first access to kills (POA1), followed by yearlings, (POA2),
140 and subdominant adults (> 2yr) (POA3) [20, 21].

141 We used simple bivariate tests, such as chi-square and the binomial test for
142 equality of proportions conducted in the package 'R' with significance level 0.05, to
143 initially explore relationships between rally success (departure/no departure) and
144 recorded observations of order of rally attempt, proportion of adults participating in social
145 behaviour, dominants' participation in rallies, number of sneezes, and initiator
146 demographic [25]. To further investigate the factors affecting whether a social rally
147 resulted in the pack departing (1) or not (0) from their current rest site, we ran a series of
148 binomial Generalized Linear Mixed Effects Models (GLMM's) in the package 'lme4' [26]
149 in 'R' [25]. 11/68 rallies were excluded from these specific analyses as their ultimate
150 success or failure and/or the identity of the initiator was not determined. Terms included
151 in the model set were: total number of sneezes in a rally, the initiator's priority of access
152 to kills (1, 2, 3), consecutive attempt number per observation session, and the proportion
153 of adults participating in social behaviours. Pack identity was included as a random term

154 in the models to control for repeated measures. We used Akaike's information criterion
155 to select the most plausible model from a set of credible options. All terms and their two-
156 way interactions were sequentially added to the basic model, with each retained only if it
157 reduced the AIC by 2 or more as lower AIC values correspond with better relative
158 support for each model [27]. To validate that there was no improvement to the minimal
159 model, each term was then removed sequentially from the minimal model. Terms were
160 retained only if their removal inflated AIC by more than two [28] As the Akaike weight of
161 the best model was <0.9 and several models had deviance in the AIC lower than 7 units
162 [29, 30], we conducted model averaging using the MuMIn package [31]. We selected the
163 top models whose cumulative AIC weights were >0.95 to construct model-averaged
164 estimates of the parameters [28] Model diagnostics were performed by inspection using
165 the DHARMA package, which uses a simulation-based approach to create readily
166 interpretable scaled residuals from fitted GLMMs [32]. Data from all top models included
167 in model averaging met model assumptions.

168

169 **Results and Discussion**

170 We first explored whether the likelihood of a rally resulting in the group's departure
171 increased with every failed rally. We found that first rallies rarely (26%, 9/34) ended in
172 movement away from resting spots, but the likelihood of a successful collective
173 movement increased over successive rallies (*Figure 2a*); 64% (5/8) of third rallies were
174 successful (Table 1).

175 The $\bar{X} \pm SE$ proportion of adult social participation in all recorded rallies (N=68)
176 was 0.58 ± 0.36 , but variation in proportion of adult participation was not strongly related
177 to rally success (Table 1).

178 We positively identified the initiator in 84% (57/68) of total observed rallies, 44%
179 (25/57) of which were successful. We found that rally success was influenced by initiator
180 demographics (Table 1; *Figure 2b*); rally attempts initiated by POA1 individuals (76.5%
181 successful, N=17) were significantly more likely to succeed than rallies initiated by POA2
182 individuals (27.3% successful, N=22) and POA3 individuals (33.3% successful, N=18)
183 individuals combined (30% successful, N=40; binomial test for equality of proportions
184 without continuity correction: $\chi^2_{(1)}=10.46$, $P<0.001$). Once packs were on the move,
185 dominants lead most pack movements (65%, N=15/23). Accounting for the relative
186 demographic proportions of the study population, these POA1 individuals were
187 significantly more likely to lead movements (n=15) than POA2 (n=1) and POA3 (n=7)
188 individuals (Chi-square test, $X_{22}=31.348$, $P<0.001$).

189 We found a statistically significant difference in the total number of sneezes in
190 successful and unsuccessful rallies (successful: $\bar{X} \pm SE$, sneeze/rally= 7.48 ± 1.49 ;
191 unsuccessful: $\bar{X} \pm SE$, sneeze/rally= 1.20 ± 0.663 ; unpaired t-test: $t=5.329$, $df=66$,
192 $p<0.0001$; *Figure 2c*) and sneezes were the most important factor predicting departures
193 in our GLMM model sets (Table 1). A sneeze has never before been documented as a
194 major communicative function of African wild dogs (see, [13]). However, it is not unique
195 in the repertoire of important signals in canids: Cohen (1976) found ubiquitous
196 “mechanical” or “unvoiced” sounds – like “panting” as a play solicitation in dogs and
197 foxes – used by all canids for short-range communication [33]. Lehner (1978) described
198 a “huff” in coyotes, as a “short range, low intensity threat that is produced by a rapid
199 expulsion of air through the mouth primarily but also the nose” [34]. He parallels the
200 behaviour to the “sneeze” documented in Golden jackals [35]. Deaux and Clark (2013)
201 describe the “snuff” of dingoes as a “broadband nasal sound produced by the expulsion
202 of air through nasal passages” that is produced in response to environmental

203 disturbance or in the context of frustration or anxiousness [36]. While we find broad
204 similarities in the description of the physical aspects of sneezes in African wild dogs and
205 the “huff,” “sneeze,” and “snuff” of other canids, the communicative function described
206 here seems to be previously undocumented in the taxa.

207 In general, noisy, abrupt vocalizations are associated with aggression or
208 frustration in the behavioural context of signal production [37]. Robbins, however,
209 documented several anomalies to general motivational-structure rules of animal
210 vocalizations in African wild dogs, which he attributed to the “muted nature of aggression
211 characteristic of African wild dog social organization” [13]. Sneezes, which seem to be
212 physically similar to signals used by other canid species as threats or alarms [33-36] are
213 produced in African wild dogs in contexts absent of anxious postures, such as pacing, or
214 threatening expressions, such as flattened ears or bared teeth. We observed sneezes
215 while individuals were walking with their heads hanging or standing with their ears alert
216 and tail relaxed (supplemental video). Other dogs did not startle in response to these
217 vocalizations, or look toward the sneezer, as might be expected if the sounds were
218 associated with a threat display or a sign of alarm. Further investigation of the
219 occurrence of sneezes suggested this signal was explicitly linked to the decision making
220 process, a correlation that future research could explore in other species exhibiting
221 similar mechanical noises.

222 We also find an interaction between total sneezes and initiator POA in rallies
223 (Table 1) indicating that the number of sneezes required to initiate a collective
224 movement differed according to the dominance of individuals involved in the rally.
225 Specifically, we found that the likelihood of rally success increases with the dominance
226 of the initiator (i.e. for lower POA categories) with lower-ranking initiators requiring more
227 sneezes in the rally for it to be successful (*Figure 2d*). In fact, our raw data and the

228 resultant model showed that rallies never failed when a dominant (POA1) individual
229 initiated and there were at least three sneezes, whereas rallies initiated by lower ranking
230 individuals required a minimum of ten sneezes to achieve the same level of success.
231 Together these data suggest that wild dogs use a specific vocalization (the sneeze)
232 along with a variable quorum response mechanism in the decision making process [19].

233 This quorum response mechanism observed is similar to the type of vocal
234 coordination observed in foraging meerkats [4], and appears to be similar to the
235 increased rate of “grunts” that occur before Mountain gorillas (*G. g. beringei*) groups
236 moved off from their resting sites [38]. In African wild dogs, individuals occasionally
237 sneezed while lying down during resting periods (pers. obs), the significant increase in
238 frequency during rallies, especially in successful rallies, suggests this sound carries
239 contextual meaning (*Figure 2d*). Both sneezes in African wild dogs and grunts in gorillas
240 occur in multiple behavioural contexts, but their rates are significantly positively
241 correlated with departure events [38]. Note, however, that our analyses fail to
242 differentiate between whether sneezes act as a true voting mechanism or reflect a purely
243 physiological response to a consensus already achieved through other signals that we
244 did not observe [39, 40]. Physiologically, the rapid exhalation may function to prepare
245 the pack to hunt by clearing the nasal cavity to make scenting and running easier, but
246 this does not preclude that sneezing may also be a true voting mechanism. Further
247 research is required to confirm causality.

248 Perhaps most interestingly, our data further suggest that the quorum number
249 (indicated by the number of sneezes) is variable and not wholly dependent on the
250 involvement of dominant individuals during rallies. These data are also consistent with
251 evidence of quorum thresholds shifting with context, described in ants (*Temnothorax*
252 *albipennis*) [41]. In dominant-initiated rallies, a threshold of only three sneezes was

253 required, a result consistent with a commonly observed quorum threshold of two to three
254 individuals “acting as signalers” in groups “ranging from six to 22 individuals” found
255 across taxa [4]. Because the number of adults involved in greeting, parallel running, or
256 mobbing did not affect rally success, mutual appeasement seems not to be a crucial
257 motivating factor for departure even though those behaviours are typical of rally displays
258 [12, 14, 15]. We observe that appeasement signals, generally considered to enforce
259 group cohesion, and signals intended to motivate the group to move, are separate
260 features of African wild dog rally behaviour.

261

262 **Conclusion**

263 Our study is the first to quantitatively assess behaviour and decision-making processes
264 in African wild dog pre-departure rallies. We found that sneezes, a previously
265 undocumented unvoiced sound in the species, are positively correlated with the
266 likelihood of rally success preceding group movements and may function as a voting
267 mechanism to establish group consensus in an otherwise despotically driven social
268 system. While our research focused on the decision-making aspect and movement
269 consequences of social rallies, further work might include a quantitative study of mutual
270 appeasements and social bonding characteristics of rallies. Our results contribute to a
271 growing trend in the literature that finds voting mechanisms and quorum thresholds
272 utilized in decision-making processes across taxa. Further research identifying specific
273 signals utilized to establish group consensus will help us to better understand the
274 evolution of social behaviour in carnivores and other social mammals.

275

276 **Author Contributions**

277 R.H.W. designed the methods, conducted the fieldwork and data collection, and wrote
278 the paper with input from all authors. N.R.J. conceived the study, helped design the
279 methods, hypotheses, and conducted the GLMM analysis. A.J.K. contributed to
280 methodology, analyses and interpretation of the data. J.W.M. established and directs the
281 research site and funded the study.

282

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293

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400 10.1098/rstb.2008.0224.

401 Table 1. Model averaged Generalized Linear Mixed Effects Model (GLMM) outputs from all models whose c
 402 were >0.95 showing: a) Effect sizes, relative importance of terms and confidence intervals and b) AICc model
 403 in the model set . Terms included in the model set were: total number of sneezes in a rally (“TotSneeze”),
 404 access to kills (“InitPOA”), the interaction between sneeze frequency and initiator POA (“InitPOA:TotSneeze”),
 405 number per observation session (“Attempt”), and the proportion of adults participating in social behaviours (“AdSoc”)

406 (a)

407	Term name	Term code	Importance	N containing models	Estimate	SE	z	CI (95%)
408	Intercept			4	-1.69	2.10	0.79	-6.14
	TotSneeze	1	1	4	2.03	1.66	1.20	-1.14
409	InitPOA	2	0.93	3				
	InitPOA1				0.00	0.00	0.00	0.00
410	InitPOA2				-1.29	2.04	0.62	-5.51
	InitPOA3				-2.62	2.17	1.18	-7.01
411	InitaPOA:TotSneeze	3	0.93	3				
	InitPOA1:TotSneeze				0.00	0.00	0.00	0.00
412	InitPOA2:TotSneeze				-1.66	1.65	0.98	-5.11
	InitPOA3:TotSneeze				-1.18	1.63	0.70	-4.61
413	Attempt	4	0.58	2	0.75	0.90	0.83	-0.31
	AdSoc	5	0.12	1	-0.08	0.65	0.12	-4.21

414

415 (b)

Model (incl. term codes)	df	logLik	AICc	delta	weight
1234	8	-17.32	53.63	0	0.46
123	7	-18.94	54.16	0.53	0.35
12345	9	-17.25	56.32	2.69	0.12
1	3	-25.43	57.32	3.69	0.07

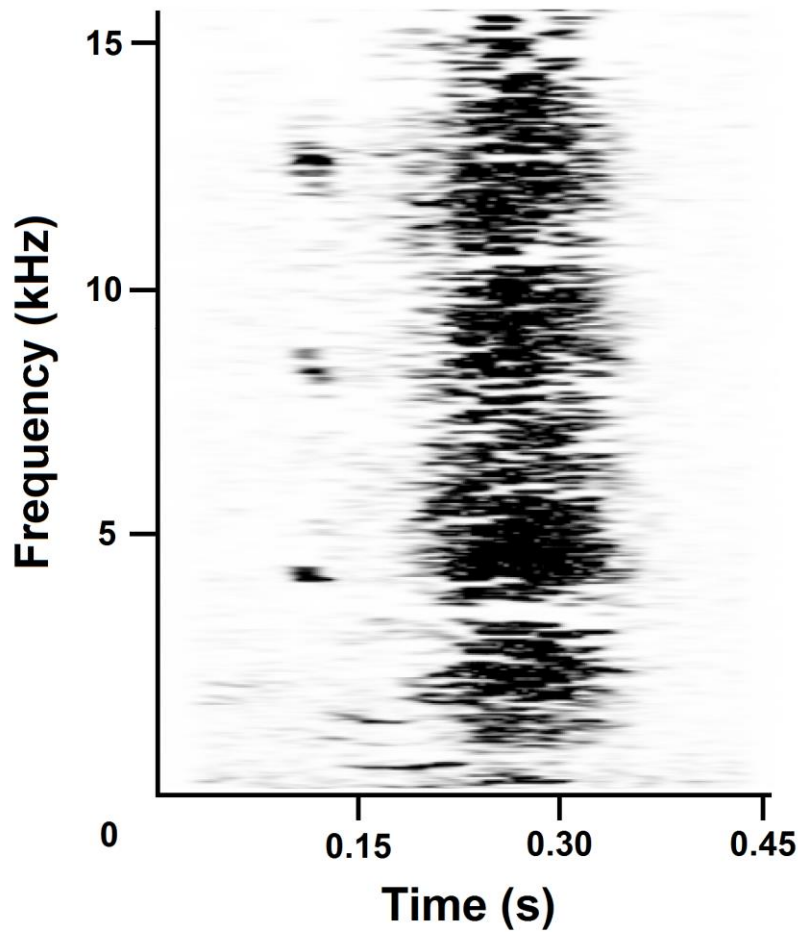
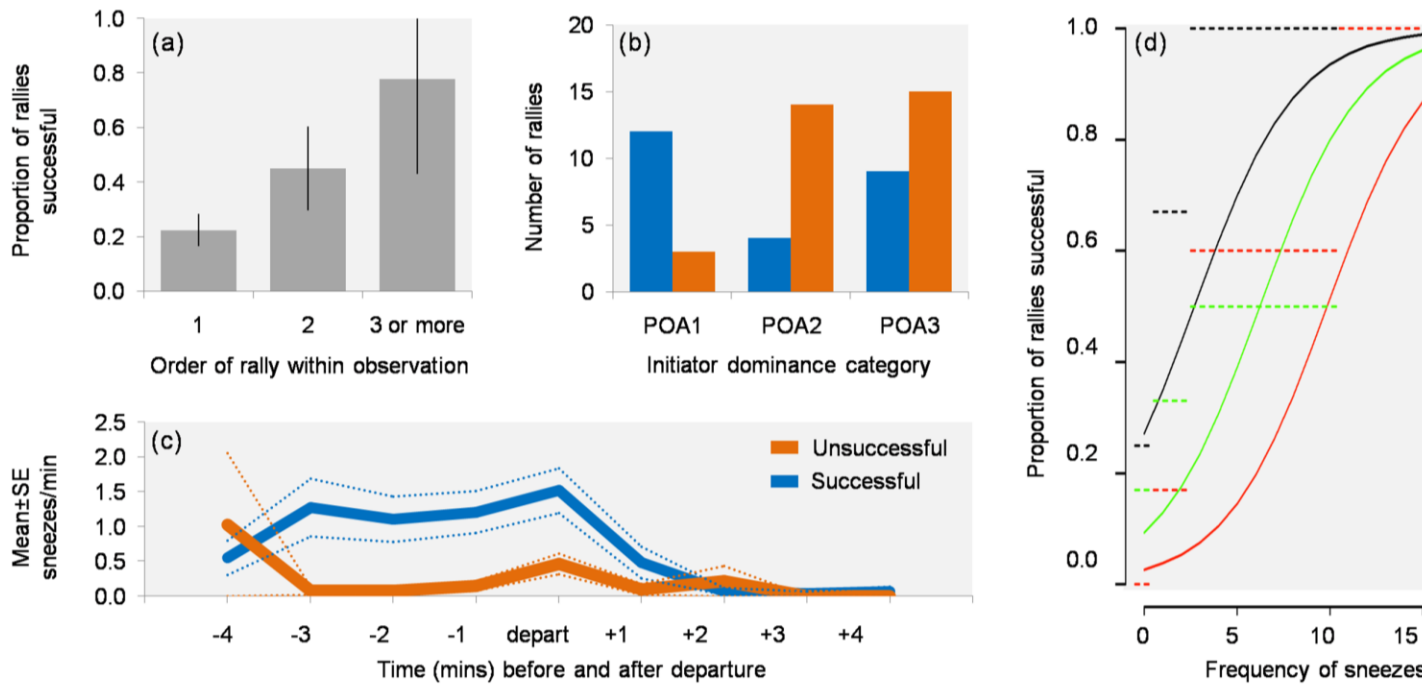


Figure 1. Spectrogram of dominant male African... recorded prior to a group departure event. The spectrogram was prepared in CoolEdit Pro 2... Syntrillium Software Corporation, Pheonix, A... sampling rate visualized in Hamming window... bands, and linear energy plot at 20% scaling... shows linear bars (likely an intake of breath),... high-frequency bandwidth rapid exhalation, c... shown from light (low) to dark (high).



429

430

431 *Figure 2. Effects of attempt number, initiator demographic, and sneeze frequency on rally success. Panel A shows*
 432 *of successful rallies (those which resulted in collective movements) increased with every failed rally in an ob*
 433 *indicate the standard error of the mean. Panel B shows the frequency of successful (n=28) and unsuccessful*
 434 *by individuals from each demographic category of priority of access to carcasses (POA): POA1, dominants and*

435 yearlings (1-2yo); and POA3, subdominant adults (>2yo) with bars indicating standard error. Panel C shows t
436 sneezes per minute before and after the end of successful and unsuccessful rallies. Hatched lines represent
437 were gathered by critical incident sampling of sneezes from all packs' (N=5) successful (n=28) and unsuccessful
438 presented data are limited to the sneezes four minutes before the end of the rally and four minutes after the fi
439 or individuals returned to rest, which includes 80% (209/260) of total observed sneezes in rallies. Panel D co
440 interaction total number of sneezes in a rally and initiator POA effect on rally success. Solid lines show the estim
441 GLMM model (Table 1) across a range of sneeze counts (increasing along the x-axis and scaled to the range
442 25). These lines are color-coded to initiator POA. Raw data are represented by the dashed lines, the lengths
443 four bins into which raw data were directed on the basis of frequency of sneezes observed in the rally (0, 1-2, 2