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

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

1. Background

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

Certain individuals can also have a disproportionate influence on collective behaviour decisions within social systems that exhibit variation in

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inter-individual relationships (e.g. kinship and dominance structures, see [8,9]). For example, dominance rank and/or an individual's social role (measured as social affiliation strength to others) are often found to correlate with leadership roles, a phenomenon observed pervasively in primates [10]. In social canids, research on group living has focused largely on the role of dominants in directing and repressing subdominant behaviour in group decision-making [11].

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

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

It is known in several other animal species that the number and identity of individuals participating in the decision process can influence the outcome of collective decisions, and that valuable experience may be correlated with age or dominance [9,19,20]. Moreover, specific recruitment cues or signals may help guide conspecifics [9] or even be used as a type of voting mechanism [4]. Therefore, to understand the mechanisms by which packs reach a consensus [15] we gathered data relating to the proportion of the pack engaged in social behaviour, individual participation, and the role of potential communication mechanisms to negotiate timing of departure. Since African wild dogs display dominant-directed group living [20,21] we examined to what extent individual participation in rallies, and specifically the dominants' participation, affected the likelihood of a successful group movement. Preliminary observations during rallies indicated that audible, abrupt exhalations of air through the nose, 'sneezes' (figure 1; see electronic supplementary material video), appeared to be frequent during rallies and may serve as a pre-departure cue or signal [15]. Therefore we investigated the potential for the occurrence of sneezes to serve as a voting mechanism that determines whether the pack should depart [4,22] while also considering the relative importance of other factors: the dominance status of the initiator [9], the level of social participation [10], and the number of other departure events that day [11].

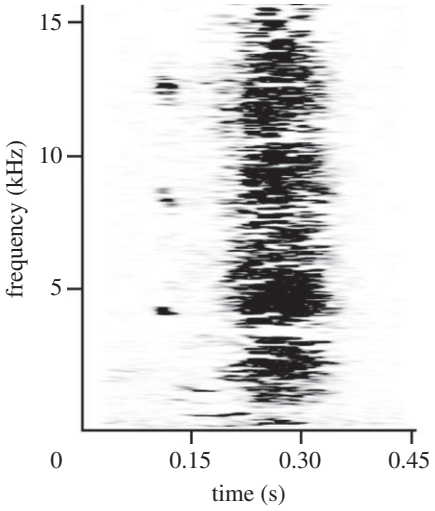


Figure 1. Spectrogram of dominant male African wild dog 'sneeze' recorded prior to a group departure event. This example spectrogram was prepared in CoolEdit Pro 2002 (v. 2.0, Syntrillium Software Corporation, Phoenix, AZ), with 44 100 sampling rate visualized in Hamming window, resolution 1024 bands, and linear energy plot at 20% scaling. The spectrogram shows linear bars (likely an intake of breath), followed by atonal high-frequency bandwidth rapid exhalation, or 'sneeze'. Energy is shown from light (low) to dark (high).

2. Methods

Data were collected from five packs ($\bar{X} \pm$ s.d. adult group size = 8.80 ± 3.63) of African wild dogs in and around the Moremi Game Reserve in the Okavango Delta from June 2014 to May 2015. At least one individual in each pack was fitted with a VHF radio collar (ca. 180 g; Sirtrack, Havelock West, New Zealand) using darting and immobilization procedures described previously [23]. Collars allowed packs to be located and were replaced when they failed. Some individuals remained collared following the completion of this study as they formed part of a long-term study conducted by the Botswana Predator Conservation Trust (BPCT) spanning the past 25 years [20]. All individuals ($N = 49$) were identified by their unique pelage patterns, and ages and life histories were known for all individuals except some immigrants ($N = 10$). We estimated the age classes (adult, yearling, or pup) of these 10 individuals using a combination of body size, pelage development, testicular development, and tooth and ear wear. All work was conducted in accordance with the guidelines for the treatment of animals in behavioural research and teaching [24].

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

From video data, we performed behavioural scans every 5 s from initiation until the end of the rally. We used critical incident sampling to record the number of audible, abrupt exhalation of air through the nose, or 'sneezes', during rally attempts and calculated the aggregated frequency of sneeze events per minute before and after the end of rallies. 'Sneezes' are atonal high-frequency bandwidth rapid exhalations that are stereotyped

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and obvious in rallies (figure 1). We observed sneezes while individuals were walking with their heads hanging or standing with their ears alert and tail relaxed (electronic supplementary material video). Other dogs did not startle in response to these vocalizations, or look toward the sneezer, as might be expected if the sounds were associated with a threat display or a sign of alarm. While it was clear from video data how many sneezes occurred during a rally, the thick habitat prevented us from being able to routinely identify which individuals sneezed, and so we only measure frequency, and not identity, of sneezers. For each behavioural scan, we recorded which individuals participated in one or more of three stereotypical social interactions: 'Greet', when individuals touched heads or approached within 1 m of one another; 'Parallel Run', when individuals ran flank to flank; and 'Mob', when three or more individuals gathered within 1 m of one another [12,13]. The proportion of adults participating in these interactions ranged from 0 (rallies in which there was no social behaviour or only yearlings and pups interacted) to 1 (rallies in which all adults were actively engaged at one point, though not necessarily simultaneously).

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

We used simple bivariate tests, such as chi-square and the binomial test for equality of proportions conducted in the package R with significance level 0.05, to initially explore relationships between rally success (departure/no departure) and recorded observations of order of rally attempt, proportion of adults participating in social behaviour, dominants' participation in rallies, number of sneezes, and initiator demographic [25]. To further investigate the factors affecting whether a social rally resulted in the pack departing (1) or not (0) from their current rest site, we ran a series of binomial generalized linear mixed effects models (GLMMs) in the package 'lme4' [26] in R [25]. Eleven out of 68 rallies were excluded from these specific analyses as their ultimate success or failure and/or the identity of the initiator was not determined. Terms included in the model set were: total number of sneezes in a rally, the initiator's priority of access to kills (1, 2, 3), consecutive attempt number per observation session, and the proportion of adults participating in social behaviours. Pack identity was included as a random term in the models to control for repeated measures. We used Akaike's information criterion to select the most plausible model from a set of credible options. All terms and their two-way interactions were sequentially added to the basic model, with each retained only if it reduced the AIC by two or more as lower AIC values correspond to better relative support for each model [27]. To validate that there was no improvement to the minimal model, each term was then removed sequentially from the minimal model. Terms were retained only if their removal inflated AIC by more than two [28] As the Akaike weight of the best model was less than 0.9 and several models had deviance in the AIC lower than seven units [29,30], we conducted model averaging using the MuMIn package [31]. We selected the top models whose cumulative AIC weights were more than 0.95 to construct model-averaged estimates of the parameters [28] Model diagnostics were performed by inspection using the DHARMa package, which uses a simulation-based approach to create readily interpretable scaled residuals from fitted GLMMs [32] Data from all top models included in model averaging met model assumptions.

3. Results and discussion

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

The $\bar{X} \pm$ s.e. proportion of adult social participation in all recorded rallies ($N = 68$) was 0.58 ± 0.36, but variation in proportion of adult participation was not strongly related to rally success (table 1; supplemental social participation results).

We positively identified the initiator in 84% (57/68) of total observed rallies, 44% (25/57) of which were successful. We found that rally success was influenced by initiator demographics (table 1; figure 2*b*); rally attempts initiated by POA1 individuals (76.5% successful, $N = 17$) were significantly more likely to succeed than rallies initiated by POA2 individuals (27.3% successful, $N = 22$) and POA3 individuals (33.3% successful, $N = 18$) individuals combined (30% successful, $N = 40$; binomial test for equality of proportions without continuity correction: $\chi^2_1 = 10.46$, $p < 0.001$). Once packs were on the move, dominants lead most pack movements (65%, $N = 15/23$). Accounting for the relative demographic proportions of the study population, these POA1 individuals were significantly more likely to lead movements ($n = 15$) than POA2 ($n = 1$) and POA3 ($n = 7$) individuals (chi-square test, $X_{22} = 31.348$, $p < 0.001$).

We found a statistically significant difference in the total number of sneezes in successful and unsuccessful rallies (successful: $\bar{X} \pm$ s.e., sneeze/rally$= 7.48 \pm 1.49$; unsuccessful: $\bar{X} \pm$ s.e., sneeze/rally$= 1.20 \pm 0.663$; unpaired *t*-test: $t = 5.329$, d.f. $= 66$, $p < 0.0001$; figure 2*c*) and sneezes were the most important factor predicting departures in our GLMM model sets (table 1). A sneeze has never before been documented as a major communicative function of African wild dogs (see, [13]). However, it is not unique in the repertoire of important signals in canids: Cohen [33] found ubiquitous 'mechanical' or 'unvoiced' sounds—like 'panting' as a play solicitation in dogs and foxes—used by all canids for short-range communication [33]. Lehner [34] described a 'huff' in coyotes, as a 'short range, low intensity threat that is produced by a rapid expulsion of air through the mouth primarily but also the nose' [34]. He parallels the behaviour to the 'sneeze' documented in golden jackals [35]. Deaux & Clark [36] describe the 'snuff' of dingoes as a 'broadband nasal sound produced by the expulsion of air through nasal passages' that is produced in response to environmental disturbance or in the context of frustration or anxiousness [36]. While we find broad similarities in the description of the physical aspects of sneezes in African wild dogs and the 'huff', 'sneeze', and 'snuff' of other canids, the communicative function described here seems to be previously undocumented in the taxon.

In general, noisy, abrupt vocalizations are associated with aggression or frustration in the behavioural context of signal production [37]. Robbins, however, documented several anomalies to general motivational-structure rules of animal vocalizations in African wild dogs, which he attributed to the 'muted nature of aggression characteristic of African wild dog social organization' [13]. Sneezes, which seem to be physically similar to signals used by other canid species as threats or alarms [33–36], are produced in African wild dogs in contexts absent of anxious postures, such as pacing, or threatening

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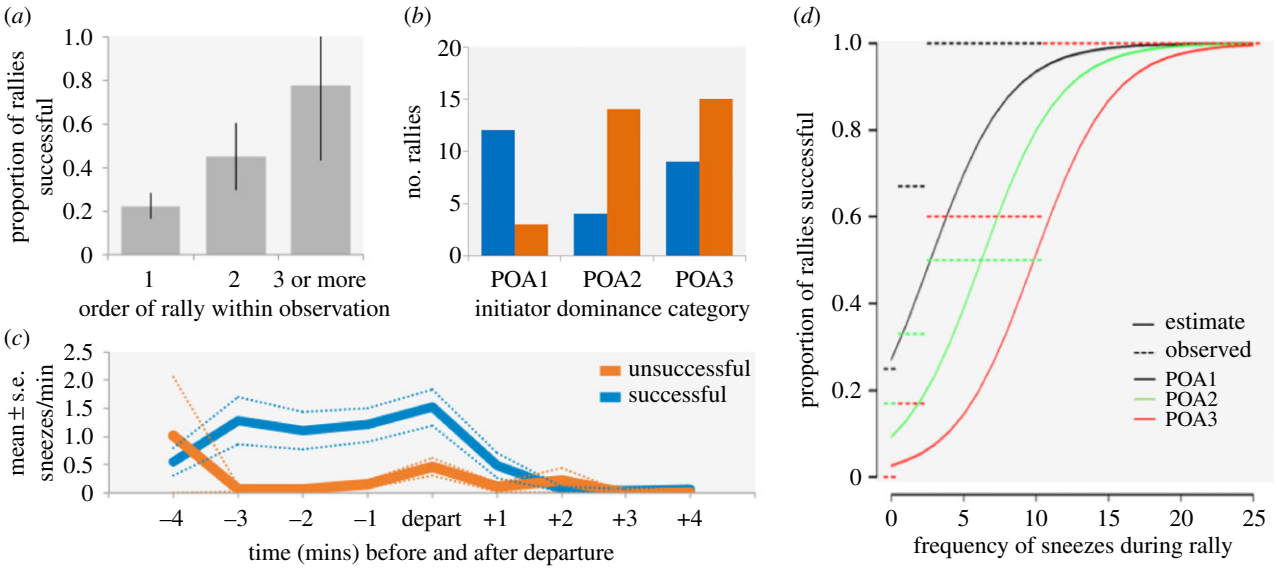


Figure 2. Effects of attempt number, initiator demographic, and sneeze frequency on rally success. Panel (*a*) shows that the proportion of successful rallies (those that resulted in collective movements) increased with every failed rally in an observation period. Bars indicate the standard error of the mean. Panel (*b*) shows the frequency of successful ($n = 28$) and unsuccessful ($n = 40$) rallies initiated by individuals from each demographic category of priority of access to carcasses (POA): POA1, dominants and pups (less than 1 year old); POA2 yearlings (1–2 years old); and POA3, subdominant adults (more than 2 years old) with bars indicating standard error. Panel (*c*) shows the mean frequency of sneezes per minute before and after the end of successful and unsuccessful rallies. Hatched lines represent standard error. Data were gathered by critical incident sampling of sneezes from all packs' ($N = 5$) successful ($n = 28$) and unsuccessful ($n = 40$) rallies. The presented data are limited to the sneezes 4 min before the end of the rally and 4 min after the first individual departed or individuals returned to rest, which includes 80% (209/260) of total observed sneezes in rallies. Panel (*d*) contains the plot of the interaction total number of sneezes in a rally and initiator POA effect on rally success. Solid lines show the estimated effects from the GLMM model (table 1) across a range of sneeze counts (increasing along the *x*-axis and scaled to the range of the actual data 0–25). These lines are colour-coded to initiator POA. Raw data are represented by the dashed lines, the lengths of which indicate the four bins into which raw data were directed on the basis of frequency of sneezes observed in the rally (0, 1–2, 2–9, more than 10).

Table 1. Model averaged generalized linear mixed effects model (GLMM) outputs from all models whose cumulative AIC weights were more than 0.95 showing: (*a*) effect sizes, relative importance of terms and confidence intervals and (*b*) AICc model weights for all models in the model set. Terms included in the model set were: total number of sneezes in a rally ('TotSneeze'), the initiator priority of access to kills ('InitPOA'), the interaction between sneeze frequency and initiator POA ('InitPOA:TotSneeze'), consecutive attempt number per observation session ('Attempt'), and the proportion of adults participating in social behaviours ('AdSoc').

(*a*)							
term name	term code	importance	*N* containing models	estimate	s.e.	*z*	CI (2.5–97.5%)
Intercept			4	21.69	2.1	0.79	−6.04 to 2.64
TotSneeze	1	1	4	2.03	1.66	1.2	−1.18 to 5.49
InitPOA	2	0.93	3				
InitPOA1				0	0	0	0
InitPOA2				−1.29	2.04	0.62	−5.59 to 2.8
InitPOA3				−2.62	2.17	1.18	−7.08 to 1.43
InitPOA:TotSneeze	3	0.93	3				
InitPOA1:TotSneeze				0	0	0	0
InitPOA2:TotSneeze				−1.66	1.65	0.98	−5.1 to 1.52
InitPOA3:TotSneeze				−1.18	1.63	0.7	−4.61 to 2.07
Attempt	4	0.58	2	0.75	0.9	0.83	−0.33 to 2.95
AdSoc	5	0.12	1	−0.08	0.65	0.12	−4.23 to 2.92

(*b*)					
model (incl. term codes)	d.f.	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

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expressions, such as flattened ears or bared teeth. Further investigation of the occurrence of sneezes suggested this signal was explicitly linked to the decision-making process, a correlation that future research could explore in other species exhibiting similar mechanical noises.

We also find an interaction between total sneezes and initiator POA in rallies (table 1) indicating that the number of sneezes required to initiate a collective movement differed according to the dominance of individuals involved in the rally. Specifically, we found that the likelihood of rally success increases with the dominance of the initiator (i.e. for lower POA categories) with lower-ranking initiators requiring more sneezes in the rally for it to be successful (figure 2*d*). In fact, our raw data and the resultant model showed that rallies never failed when a dominant (POA1) individual initiated and there were at least three sneezes, whereas rallies initiated by lower ranking individuals required a minimum of 10 sneezes to achieve the same level of success. Together these data suggest that wild dogs use a specific vocalization (the sneeze) along with a variable quorum response mechanism in the decision-making process [19].

This quorum response mechanism observed is similar to the type of vocal coordination observed in foraging meerkats [4], and appears to be similar to the increased rate of 'grunts' that occur before Mountain gorilla (*G. g. beringei)* groups moved off from their resting sites [38]. In African wild dogs, individuals occasionally sneezed while lying down during resting periods (NR Jordan, RH Walker, JW McNutt 2014, personal observation), the significant increase in frequency during rallies, especially in successful rallies, suggests this sound carries contextual meaning (figure 2*d*). Both sneezes in African wild dogs and grunts in gorillas occur in multiple behavioural contexts, but their rates are significantly positively correlated with departure events [38]. Note, however, that our analyses fail to differentiate between whether sneezes act as a true voting mechanism or reflect a purely physiological response to a consensus already achieved through other signals that we did not observe [39,40]. Physiologically, the rapid exhalation may function to prepare the pack to hunt by clearing the nasal cavity to make scenting and running easier, but this does not preclude that sneezing may also be a true voting mechanism. Further research is required to confirm causality.

Perhaps most interestingly, our data further suggest that the quorum number (indicated by the number of sneezes) is variable and not wholly dependent on the involvement of dominant individuals during rallies. These data are also consistent with evidence of quorum thresholds shifting with context, described in ants (*Temnothorax albipennis*) [41]. In dominant-initiated rallies, a threshold of only three sneezes was required, a result consistent with a commonly observed quorum threshold of two to three individuals 'acting as signallers' in groups 'ranging from six to 22 individuals' found across taxa [4]. Because the number of adults involved in greeting, parallel running, or mobbing did not affect rally success, mutual appeasement seems not to be a crucial motivating factor for departure even though those behaviours are typical of rally displays [12,14,15]. We observe that appeasement signals, generally considered to enforce group cohesion, and signals intended to motivate the group to move, are separate features of African wild dog rally behaviour.

4. Conclusion

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

Ethics. The authors confirm that we have read and abided by the Royal Society publishing ethics policy and that all work was conducted in accordance with the guidelines for the treatment of animals in behavioural research and teaching [24].

Data accessibility. Our data are made publically available via Dryad at: http://dx.doi.org/10.5061/dryad.d6q6b [42].

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

Competing interests. We have no competing interests to report that may influence the objective presentation of our manuscript.

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