

ANIMAL CULTURE

Cultural transmission of vocal dialect in the naked mole-rat

Alison J. Barker^{1*}, Grigorii Vevjurko^{1†}, Nigel C. Bennett², Daniel W. Hart², Lina Mograby¹, Gary R. Lewin^{1*}

Naked mole-rats (*Heterocephalus glaber*) form some of the most cooperative groups in the animal kingdom, living in multigenerational colonies under the control of a single breeding queen. Yet how they maintain this highly organized social structure is unknown. Here we show that the most common naked mole-rat vocalization, the soft chirp, is used to transmit information about group membership, creating distinctive colony dialects. Audio playback experiments demonstrate that individuals make preferential vocal responses to home colony dialects. Pups fostered in foreign colonies in early postnatal life learn the vocal dialect of their adoptive colonies, which suggests vertical transmission and flexibility of vocal signatures. Dialect integrity is partly controlled by the queen: Dialect cohesiveness decreases with queen loss and reemerges only with the ascendance of a new queen.

The naked mole-rat (*Heterocephalus glaber*) was the first eusocial mammal to be identified (1) and has received much attention for an array of extreme physiological traits (2–4). Yet often overlooked are the sounds these animals make: constant peeping, chirruping, and grunting (5, 6) (audio S1 and S2). Complex patterns of acoustic communication exist throughout the animal kingdom (7), and decades of study—notably in songbirds (8), bats (9), cetaceans (10), and primates (11)—have generated debate about the etiology of human language, with compelling evidence for anatomical (12), genetic (13), and cultural (14) drivers. The highly cooperative nature of naked mole-rat societies led us to investigate whether their vocalizations support social complexity.

The vocal repertoire of the naked mole-rat consists of at least 17 distinct vocalizations (6). The most common vocalization, the soft chirp, serves as a greeting call that has been previously shown to occur in a stereotyped call-and-response (i.e., antiphonal) manner (15).

We recorded 36,190 soft chirps from 166 animals (seven colonies), housed in Berlin, Germany, or Pretoria, South Africa, over a period of 2 years. We developed an algorithm to automatically segment, trace, and extract acoustic features of individual soft chirps (Fig. 1A). In developing our analysis pipeline, we included established parameters for vocalization analysis (16) and, whenever possible, spectrogram-extracted features, which mini-

mized variable background noise from recordings made across different locations and days. We used a type of supervised machine learning, the random forest classifier (17), to analyze eight soft-chirp features: three from the sound wave (pitch, Wiener entropy, and zero-crossings rate) and five from the soft-chirp spectrogram (asymmetry, peak frequency, height, duration, and slope) (Fig. 1A and fig. S1). By training the classifier with soft chirps from individual mole-rats, we found that it could reliably predict the identity of individuals within a colony (Fig. 1B and fig. S2).

Within naked mole-rat colonies, reproductive suppression of nearly all members is necessary to sustain the colony with limited food resources and leads to strong xenophobia (18). As such, multiple mechanisms for maintaining the social integrity of the colony and for detecting intruders might be necessary. We next tested for colony-specific signatures (15) by using soft chirps recorded from three colonies in Berlin (colonies B, M, and T) and a fourth colony, which has always been located in South Africa (colony D). Again, using a random forest classifier, we found that soft-chirp features were highly predictive of colony identity (Fig. 2, A and B, and figs. S3 to S5), with asymmetry and peak frequency found to be the best spectrogram-derived features for colony separation (Fig. 2, C and D) (15). Although soft-chirp features did not strongly predict rank, age, or sex (fig. S6), we observed a positive correlation with body size and soft-chirp pitch (supplementary text and fig. S7).

We next evaluated whether naked mole-rats recognize information communicated via soft chirps. To test this, we employed a place preference assay in which individual animals were given access to two interconnected chambers (Fig. 3A, top, and movie S1), each equipped for simultaneous audio playback and record-

ing. Animals preferred to spend most of the allotted time in the chamber with sound presentation, regardless of whether soft chirps from their home colony or a foreign colony were played (Fig. 3A). In response to the audio playback stimulus, animals frequently vocalized with their own soft chirp, consistent with the antiphonal behavior previously described (Fig. 3B) (15, 19). We observed very high response rates when animals were presented with home colony audio playbacks, much higher than and significantly different from responses to foreign colony playbacks (Fig. 3C).

Do naked mole-rats recognize individual voices from home colonies rather than colony dialects? We tested this by designing artificial stimuli, using two features: asymmetry and peak frequency (15). Artificial stimuli were fabricated such that our colony classifier would categorize them as belonging to “mock colony members” but they would not overlap with the vocalizations of any known individuals in the colony (fig. S8). Notably, response rates were again higher for the mock home stimulus, which suggests that naked mole-rats can distinguish colony-specific features in vocalizations (Fig. 3, D and E, and fig. S8). To test whether peak frequency or asymmetry alone were sufficient for behavioral preference, we used a pure tone of 4.5 kHz (mean colony peak frequency) and a frequency-doubled stimulus (9.0 kHz with mean colony asymmetry). We observed responses to the pure tone alone but virtually none to the frequency-doubled stimulus (Fig. 3E and fig. S8). The preferential response to home colony dialect was still found in the presence of a conflicting olfactory cue in the test chamber (Fig. 3F).

If naked mole-rats use distinct colony dialects to differentiate themselves from neighboring colonies or as a mechanism for ensuring conformity within the colony, such dialects must be maintained across generations. We cross-fostered three individuals between colonies—a nontrivial task because queens breed rarely and breeding activity cannot be synchronized across colonies. An abandoned pup (pup Mi) was cross-fostered from colony T to colony M (Fig. 4, A and D), and we simultaneously tracked two surviving foster siblings born in colony M (pups Ob and Ny; Fig. 4, B and C). In a second experiment, two orphaned pups (pups Da and Jo, colony S) were fostered into two different colonies (colony M and colony T, respectively) (Fig. 4, E to G). We observed that adult vocalizations fully develop by ~3 months of age (supplementary text and figs. S9 and S10), so we examined pup dialects at time points later than 6 months after fostering. We tested foster pup vocalizations on our colony classifier, which classified the pups as belonging to one of five

¹Department of Neuroscience, Max Delbrück Center for Molecular Medicine, Berlin, Germany. ²Mammal Research Institute, Department of Zoology and Entomology, University of Pretoria, Pretoria, Republic of South Africa.

*Corresponding author. Email: glewin@mdc-berlin.de (G.R.L.); alison.barker@mdc-berlin.de (A.J.B.) †Present address: Department of Electrical Engineering, Mathematics and Computer Science, Delft University of Technology, Delft, Netherlands.

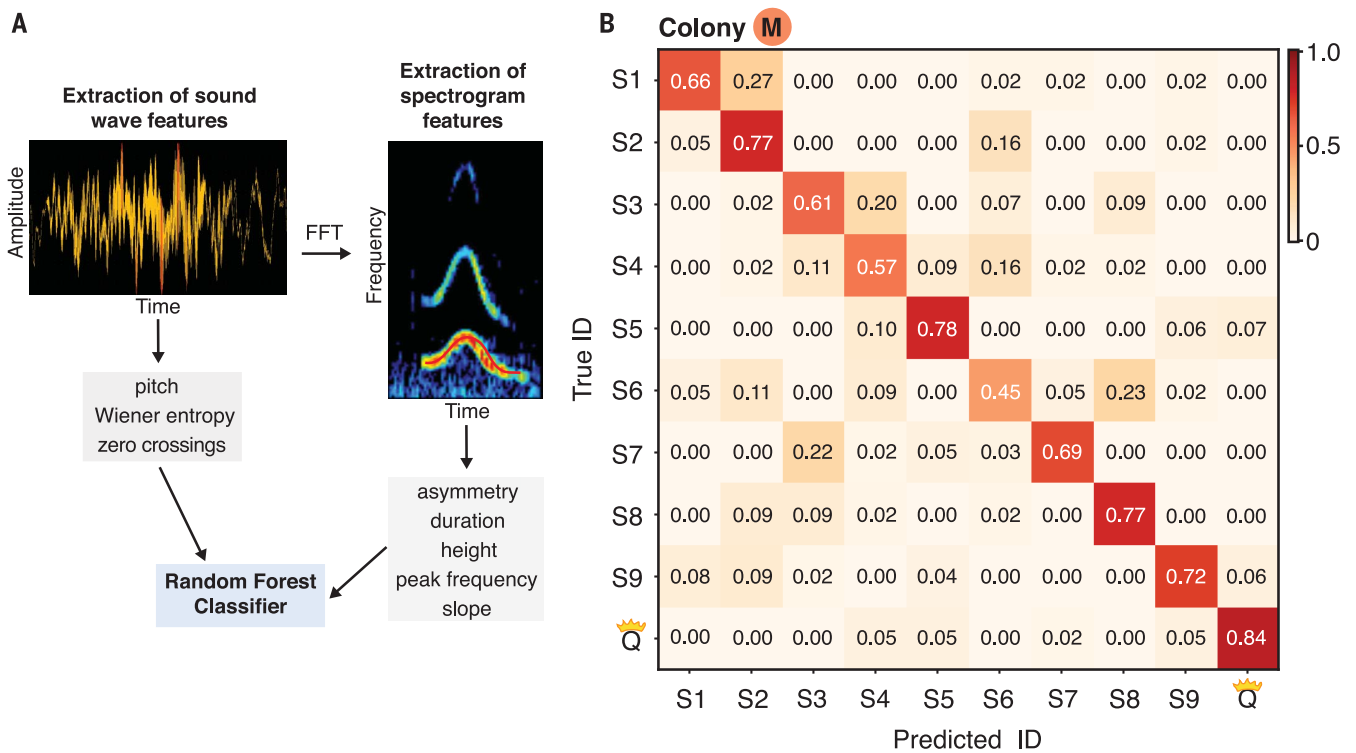


Fig. 1. Naked mole-rat soft chirps encode individual identity. (A) Soft-chirp analysis and classifier training workflow. FFT, fast Fourier transform. (B) Individuals can be identified with high accuracy using machine learning tools trained on vocal features (A). S1 to S9 represent subordinate individuals; Q represents the queen.

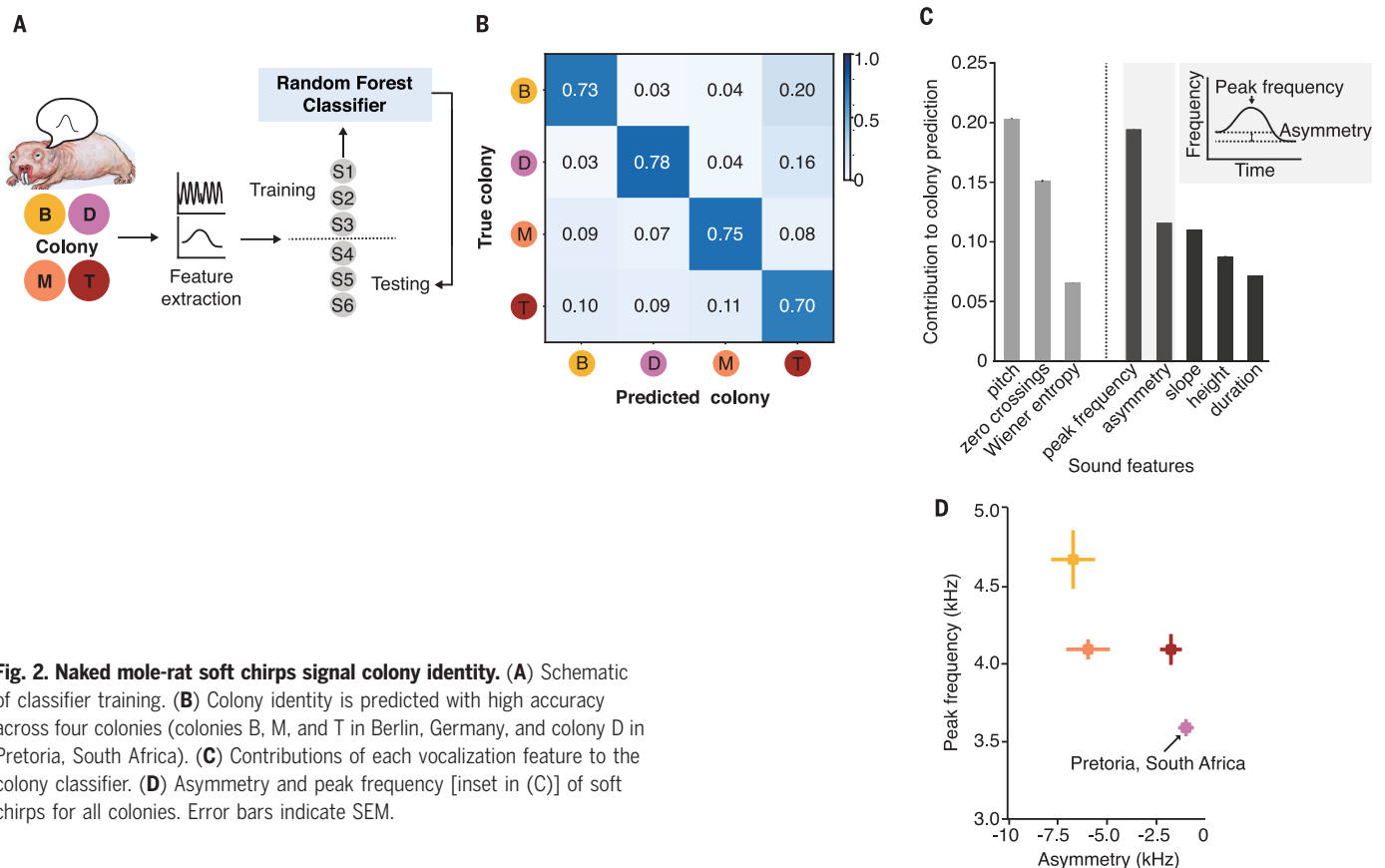


Fig. 2. Naked mole-rat soft chirps signal colony identity. (A) Schematic of classifier training. (B) Colony identity is predicted with high accuracy across four colonies (colonies B, M, and T in Berlin, Germany, and colony D in Pretoria, South Africa). (C) Contributions of each vocalization feature to the colony classifier. (D) Asymmetry and peak frequency [inset in (C)] of soft chirps for all colonies. Error bars indicate SEM.

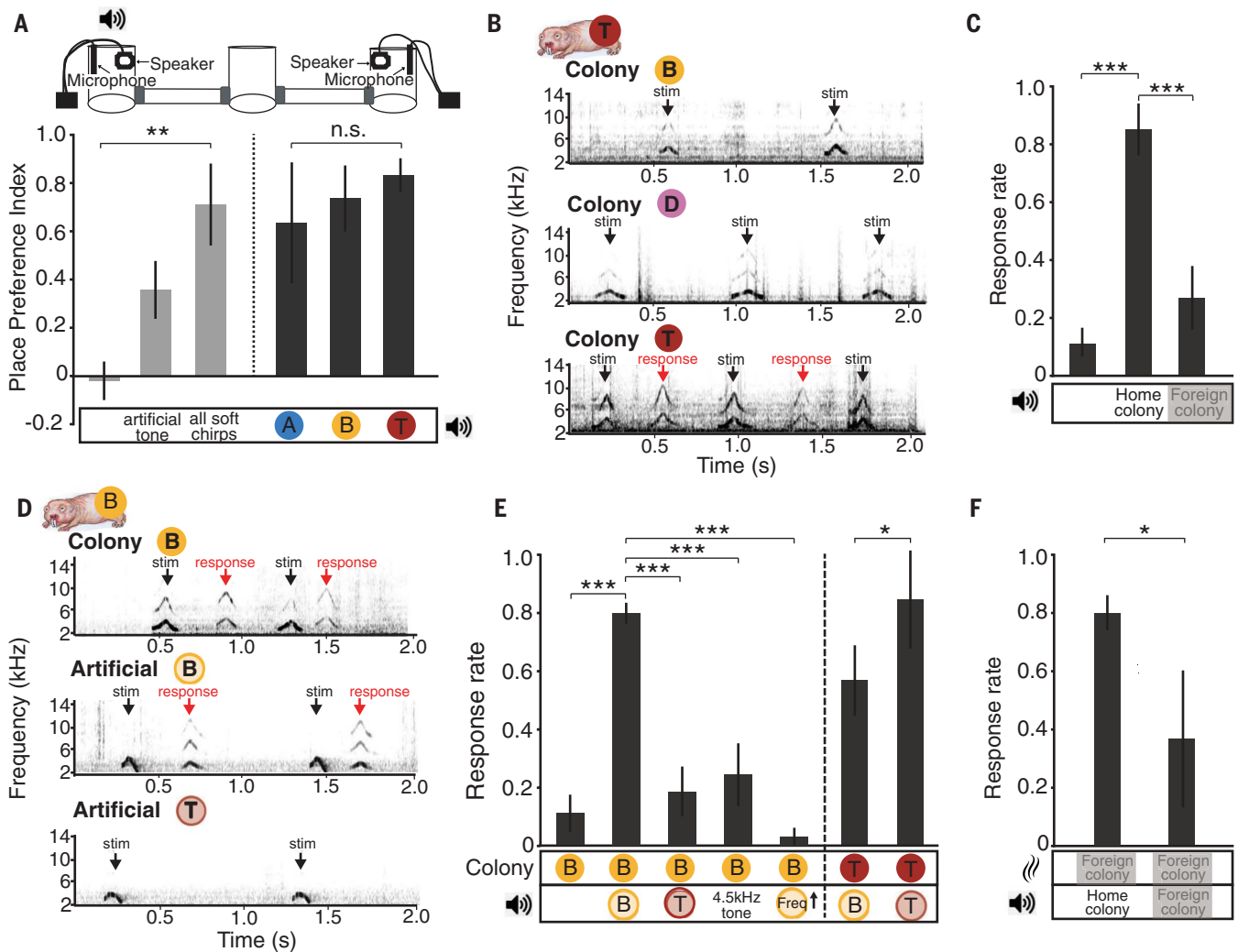


Fig. 3. Vocal response rates are modulated by colony identity. (A) (Top) Place preference assay setup. Individual animals were given access to two interconnected chambers, each equipped for simultaneous audio playback and recording. (Left) In a place preference assay, naked mole-rats spend more time in the chamber with sound presentation than in the chamber with silence [$n = 4$ animals; $N \geq 36$ trials per animal, one-way analysis of variance (ANOVA), $**P < 0.005$]. (Right) No place preference to colony-specific audio playbacks was observed. n.s., not significant. Error bars indicate SEM. (B) Soft-chirp response rates were enhanced to home colony audio playbacks. Example responses from colony T animals are indicated. stim, stimulus. (C) Response rate to home colony audio playback is greater than response rate to no playback or foreign colony playback ($n = 9$

animals; $N \geq 36$ trials, one-way ANOVA, $***P < 0.0005$). Error bars indicate SEM. (D) Example responses to home colony and artificial stimuli. The indicated responses are from colony B animals. (E) For artificially generated stimuli, soft-chirp responses to home colony-classified audio playbacks are significantly increased compared with responses to foreign colony-classified audio playbacks or when frequency and asymmetry features alone are tested ($n = 4$ animals in colony B and 5 animals in colony T, one-way ANOVA or unpaired t test, $*P < 0.05$, $***P < 0.0005$). Error bars indicate SEM. (F) Colony-specific response rates were present when conflicting olfactory cues (bedding from a foreign colony) were placed in the test chamber ($n = 6$ animals, $N \geq 36$ trials per animal, $*P < 0.05$). Error bars indicate SEM. For all experiments, a minimum of $N = 36$ behavioral trials were performed for each animal.

test colonies (including birth and foster colonies). In all three successful foster experiments, the dialect of the new colony was adopted with correct prediction rates between 59 and 95% (Fig. 4H).

Finally, we investigated whether the queen's presence might influence the vocal signature of the colony (supplementary text). During the course of this study, colony S consecutively lost two queens (Fig. 4I and fig. S11), which enabled us to record soft chirps during queen epochs and subsequent periods of anarchy. Individual variability of several features, in-

cluding peak frequency, was higher during periods of anarchy (Fig. 4J and fig. S12), and classification accuracy of the colony dialect decreased during periods of anarchy (Fig. 4K and fig. S12), which suggests that the presence of the queen enhances dialect cohesiveness.

Acoustic communication of social information has been observed in multiple mammalian species—bats (9), primates (11), cetaceans (10), pachyderms (20), and carnivores (21)—and now we expand this group to include a member of the order Rodentia. More work is needed to resolve whether naked mole-rats

are capable of true production learning, as exemplified in songbirds, or whether, like many nonhuman primates, they are exceptionally good usage learners (22). With a simple vocal greeting, humans convey individual identity (distinctive voice) and cultural identity (dialect usage); here we show that naked mole-rats also signal social membership with dialect usage. Dialect features can be transmitted across generations, a surprising feat for a rodent species, thus supporting an accumulating body of evidence that social complexity evolved concurrently with vocal complexity.

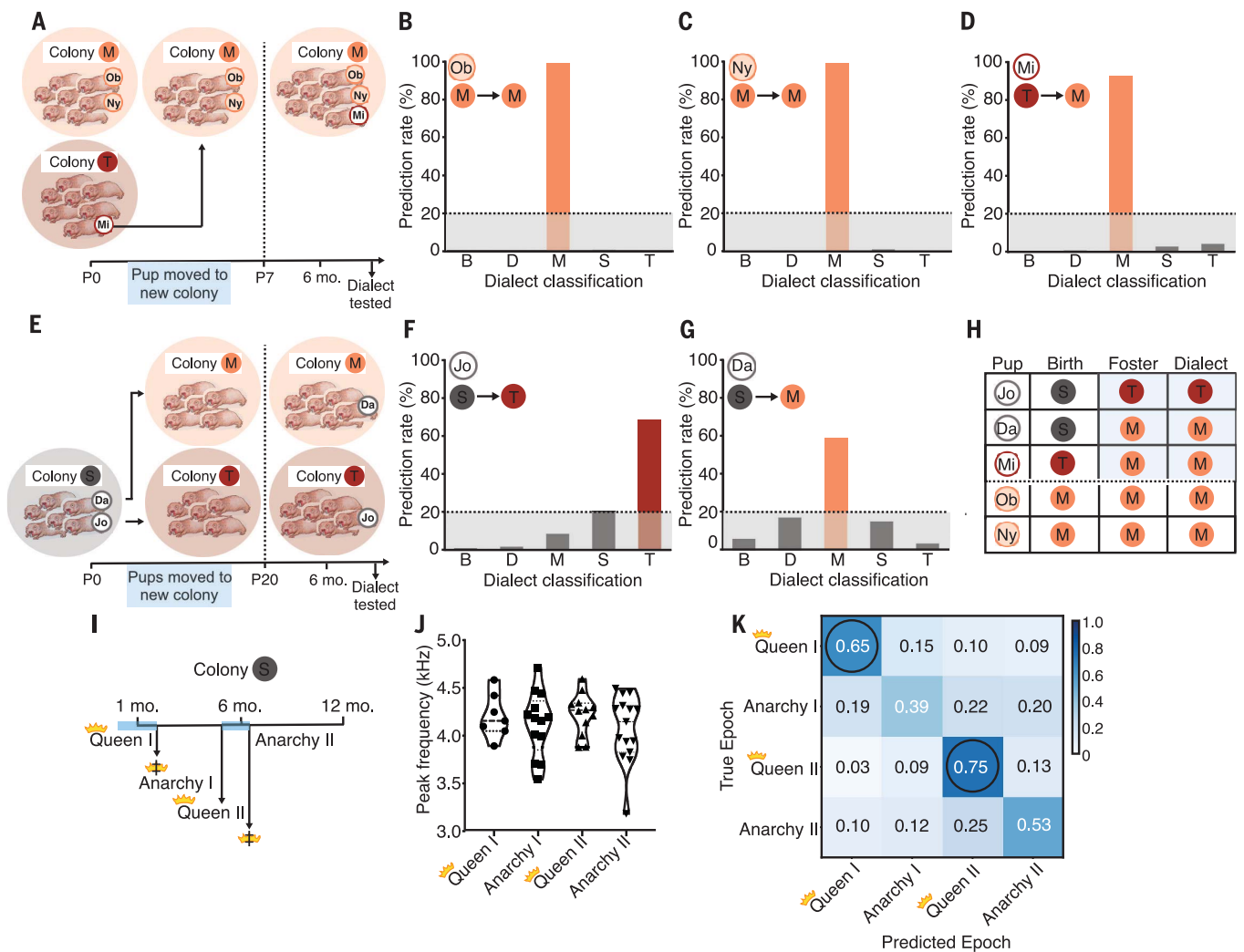


Fig. 4. Cultural transmission of colony dialects. (A) Schematic of first cross-fostering experiment. P0, postnatal day 0; P7, postnatal day 7. (B to D) Individual colony dialect predictions for each pup (Ny and Ob, nonfostered control pups; Mi, fostered pup). Prediction accuracies: pup Mi = 95.5%, pup Ob = 99.2%, pup Ny = 99.0%. (E) Schematic of second cross-fostering experiment. (F and G) Individual colony dialect predictions for

foster pups Da and Jo were 59.1% and 68.4% accurate, respectively. (H) All fostered pups adopt the dialect of their adoptive colonies. (I) Timeline of social upheaval in colony S. (J) During anarchy periods, variability in soft-chirp frequency increases. (K) Colony classification accuracy decreases during anarchy periods relative to epochs with a stable queen (black circles).

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SUPPLEMENTARY MATERIALS

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The queen's chirp rules

Naked mole-rats are known for their eusocial lifestyle, living in colonies that consist of many workers and a single breeding queen. Little is known about how individuals within these colonies navigate the many interactions that must occur in such a complex cooperative group. Barker *et al.* show that calls emitted by individuals, in particular the common "chirp" call, convey information specific to the animal's group (see the Perspective by Buffenstein). Group differences are cultural, rather than genetic, and are related to the queen: Cross-fostered pups adopt their rearing colony's dialects, and dialects change with queen replacement.

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