PNAS RESEARCH ARTICLE | PSYCHOLOGICAL AND COGNITIVE SCIENCES

Puppy whines mediate maternal behavior in domestic dogs

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Edited by Raghavendra Gadagkar, Indian Institute of Science, Bangalore, India; received September 27, 2023; accepted March 27, 2024

In mammals, offspring vocalizations typically encode information about identity and body condition, allowing parents to limit alloparenting and adjust care. But how do these vocalizations mediate parental behavior in species faced with the problem of rearing not one, but multiple offspring, such as domestic dogs? Comprehensive acoustic analyses of 4,400 whines recorded from 220 Beagle puppies in 40 litters revealed litter and individual (within litter) differences in call acoustic structure. By then playing resynthesized whines to mothers, we showed that they provided more care to their litters, and were more likely to carry the emitting loudspeaker to the nest, in response to whine variants derived from their own puppies than from strangers. Importantly, care provisioning was attenuated by experimentally moving the fundamental frequency (f_o, perceived as pitch) of their own puppies' whines outside their litter-specific range. Within most litters, we found a negative relationship between puppies' whine f_o and body weight. Consistent with this, playbacks showed that maternal care was stronger in response to high-pitched whine variants simulating relatively small offspring within their own litter's range compared to lower-pitched variants simulating larger offspring. We thus show that maternal care in a litter-rearing species relies on a dual assessment of offspring identity and condition, largely based on level-specific inter- and intra-litter variation in offspring call f_o. This dual encoding system highlights how, even in a long-domesticated species, vocalizations reflect selective pressures to meet species-specific needs. Comparative work should now investigate whether similar communication systems have convergently evolved in other litter-rearing species.

domestic dog | vocal communication | individual discrimination | parental care | litter-rearing mammals

Significance

Can parents rearing multiple offspring both recognize them and assess their condition from their vocalizations? We addressed this question in domestic dogs using state-of-the-art resynthesis to create remarkably realistic synthetic puppy whines that we presented to mothers in playback experiments. Mothers provided more care in response to whines whose pitch had been resynthesized to fall within the specific range of their litter, and particularly when whines were modified to simulate one of their weaker (smaller) puppies. We thus show that vocal communication can efficiently support both kin discrimination and condition assessment in a mammal that rears multiple offspring. A better understanding of maternal behavior in this pet species is crucial for improving breeding practices by developing vocal-based welfare monitoring tools.

Misdirected, insufficient, or excessive parental care can reduce offspring survival and limit parental reproductive success (1). Selection pressures to limit alloparenting and optimize care have led to the evolution of functional signals that support the communication of offspring identity and body condition (2). For example, vocalizations mediating parent–offspring interactions have been described in a wide range of mammals rearing a single offspring (3–7), revealing how these signals fulfill specific functions within the context of a species social organization (3) or antipredatory strategies (4). Indeed, mutual mother–offspring vocal recognition has been identified in group-living or colonial species, where offspring can be relatively mobile. This includes precocial species such as reindeer (*Rangifer tarandus*) (8), sheep (*Ovis aries*) (5), goats (*Capra hircus*) (6), cows (*Bos taurus*) (7), or species in which offspring are separated from their mothers over relatively long periods such as pinnipeds (3) and bats (9). In contrast, unidirectional recognition systems where only the offspring are able to recognize their mothers' calls (4) have been identified in species that hide their vulnerable and relatively immobile offspring to protect them from predators [as observed in fallow deer (*Dama dama*) (10)].

Surprisingly, mother–offspring vocal interactions remain virtually unstudied in litter-producing species (11), despite the fact that having more than one offspring clearly increases the complexity of simultaneously performing offspring recognition and condition assessment. As such, these species offer a unique opportunity to further investigate how selection pressures linked to offspring rearing shape parent–offspring vocal communication in mammals. To our knowledge, a very small number of studies have been conducted in litter-rearing mammals (12–14). For example, sows (*Sus domesticus*) give stronger vocal responses in reaction to playbacks of their own piglets' calls (13). They also vocalize more, move more, and spend more time near the loudspeaker in response to high-pitched calls corresponding to relatively small offspring of their own litter (12). However, because the playback experiments reported in these studies used natural calls, the authors could not determine which acoustic features sows relied on to discriminate their own offspring from strangers and assess their condition.

Author contributions: M.M. and D.R. designed research; M.M., R.P., L.B.d.B., and D.R. performed research; M.M., V.A., K.R. and D.R. contributed new reagents/analytic tools; M.M., R.P., V.A., N.M., and D.R. analyzed data; K.P., V.A., and N.M. made edits on the original draft; all authors gave final approval for submission; and M.M. and D.R. wrote the paper.

The authors declare no competing interest.

This article is a PNAS Direct Submission.

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This article contains supporting information online at https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2316818121/-/DCSupplemental.

Here, we report an extensive investigation of mother–offspring vocal interactions in Beagle domestic dogs (*Canis familiaris*), combining the acoustic analyses of 4,400 whines of 220 puppies from 40 litters with playback experiments on 16 mothers. This domesticated species provides an ideal model as they rear large litters of highly vocal puppies (15, 16). Indeed, shortly after birth, puppies produce whines, a vocalization typically emitted in contexts associated with discomfort or distress, such as when puppies are hungry, cold, or separated from their mother and littermates (17–20). Crucially, whines attract the mother's attention and often elicit her care (17, 19).

First, we recorded whines during a short separation of puppies from their mothers and littermates to test whether puppies' whines contain cues to offspring identity (litter and individual identity) and offspring condition [using body weight as a proxy (21)]. We predicted that whine acoustics, particularly their fundamental frequency (hereafter f_o), would explain litter differences and within litters, individual differences. Indeed, f_o is a key contributor to individuality and/or body condition in other mammalian infant calls including fur seal pups (*Arctocephalus tropicalis*) (22), kittens (*Felis catus*) (23), goat kids (6), calves (24), piglets (25, 26), infant chimpanzees (*Pan troglodytes*) (27), and human babies (*Homo sapiens*) (28, 29). For our acoustic analyses, we extracted 10 whines from the first minute of each puppy's recording and selected five acoustic parameters, namely the mean fundamental frequency (*mean* f_o), the minor vibrato-like frequency modulations (*minor FM*), the major frequency modulations (*major FM*), the harmonicity (harmonic-to-noise ratio *HNR*), and the whine duration (*duration*) (*SI Appendix*, Table S1). These parameters characterize the pitch (perceptual correlate of f_o) and the vocal quality (perceived harmonicity) of individual whines, and are known to be perceptually salient and biologically relevant to receivers in a wide range of mammals (30, 31).

Second, we conducted playback experiments to test whether mothers can acoustically discriminate their own offspring, and whether the f_o of puppy whines supports this ability. To do this, we used parametric acoustic resynthesis to modify f_o independently of other acoustic parameters (32–34). Unlike using natural vocal stimuli, acoustic resynthesis allowed us to experimentally test the specific communicative function of whine f_o. In the presence of their puppies, mothers were exposed to synthetic variants of their own puppies' or stranger puppies' whines, resynthesized with a f_o falling inside or outside their litter-specific range, thus mimicking litter-typical or litter-atypical calls (Fig. 1*B*, *SI Appendix*, Fig. S1, and Movie S1). We quantified the mothers' reactions to the playbacks by calculating four behavioral indices characterizing i) their provision of maternal care including grooming or feeding their puppies and carrying the speaker to the nest (15–17, 35, 36), ii) their olfactory and visual attention to puppies, iii) their olfactory and visual attention to the playback, and iv) their stress-related behaviors such as whining or moving (20) (see Table 1 for full description). These indices were quantified over the duration of the playback period and the 2 min following sound exposure. We predicted that 1) mothers would react more to synthetic variants derived from their own puppies' whines and 2) mothers would respond more to calls in which the f_o was synthesized to values falling within the range of their own litter (litter-typical).

Finally, we also conducted playback experiments to test whether mothers adapt their behavior based on their puppies' body weight. To do this, we exposed mothers to playbacks of their own puppies' or stranger puppies' whines in which the f_o was synthesized to simulate the weight-related interindividual variation in whine f_o observed between the puppies of that mother's specific litter. We quantified mothers' responses using the same behavioral indices as described above. We predicted stronger maternal behaviors in response to higher-pitched synthetic whines (simulating a

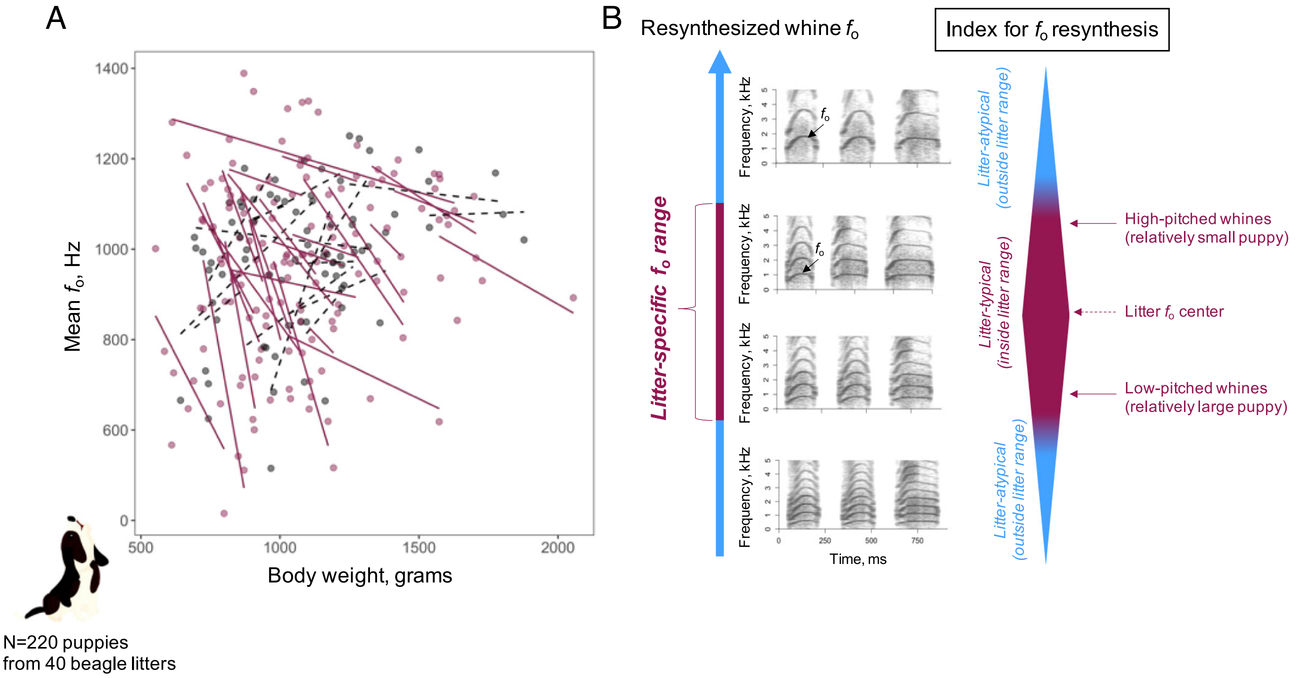

Fig. 1. Acoustic analyses and preparation of synthetic whine stimuli for playback experiments. (*A*) Litters have specific f_o ranges, and within most litters, individual puppy whine f_o is negatively correlated with body weight, as illustrated with the pink solid lines. Positive or null relationships between puppy whine f_o and body weight are indicated with dashed black lines. Each dot corresponds to a puppy, and each line represents the slope of the correlation within a litter. (*B*) To test the extent to which mothers use f_o to discriminate their own puppies from stranger puppies, we created synthetic whine variants from stranger or own-puppy natural whine exemplars with a f_o falling inside the tested mother's litter frequency range (litter-typical, central spectrograms in purple range) or with a f_o falling outside the litter range (litter-atypical, upper and lower spectrograms in blue range). To test the extent to which mothers use f_o to assess the body weight of puppies, we also created variants where the f_o was set to simulate either a relatively small puppy (relatively high f_o within litter range) or large puppy (relatively low f_o within litter range) for the given tested litter.

Table 1. Definitions of the measured behaviors for quantifying the four types of behavioral responses in dog mothers

Behavioral response (index)	Measured behavior	Description	Variable unit	References
Maternal care	Grooming	The mother licks her puppies, mainly their anogenital parts to stimulate urination and defecation. She is in the nest or close to it	Duration	(15–17, 35, 36)
	Feeding	The mother sits or lies in the nest with at least one puppy suckling	Duration	(15–17, 35, 36)
	Feeding postures	The mother facilitates puppies' access to her nipples by sitting or lying	Count	
	Retrieval attempts	The mother carries the loudspeaker but drops it outside of the nest	Count	
	Retrieval	The mother carries the loudspeaker into the nest	Duration	(35)
Attention to puppies	Orientation toward puppies	The mother looks toward her puppies	Duration	
	Inspection of puppies	The mother inspects her puppies, sniffing or pushing them. She is inside or close to the nest	Duration	(17, 35)
Attention to the playback source	Orientation toward the loudspeaker	The mother looks toward the loudspeaker	Duration	
	Inspection of the loudspeaker	The mother inspects the loudspeaker, sniffing or pushing it	Duration	
	Headcocking	The mother titles her head, indicating relatively high attention toward the loudspeaker	Duration	(37)
Stress-related behaviors	Whining	The mother emits whines	Count	(20)
	Movement	The mother moves in her enclosure	Duration	(20)

relatively small puppy for the tested mother's litter) than to low-pitched whines (simulating a relatively large puppy).

Results

Whines Differ Acoustically among Puppies, Both between and within Litters. We performed multivariate permuted discriminant function analyses (hereafter pDFA) (38, 39) to test whether whines differed between litters and between individuals within litters.

First, we found that whines contained information about the identity of the litter. Indeed, classification models trained with the whines of three randomly selected puppies from each of 15 litters (litters selected for having six or more puppies, see *Materials and Methods*) attributed whines from the three other puppies from these litters (not included in the training set) to the correct litter in 14.2 ± 1.8% of cases against a theoretical chance level of 6.7% (1/15). This percentage of correct classification is significantly higher ($P < 0.001$) than the empirical chance level obtained on 1,000 permuted datasets (6.7 ± 0.8%, equivalent to the theoretical chance level, see *SI Appendix*, Fig. S2). The acoustic variables that most strongly contributed to interlitter differences in the acoustic structure of puppy whines were *mean* f_o and *HNR* (*SI Appendix*, Fig. S3*A*). This classification experiment demonstrates that the correct attribution of individuals to litters based on their whines relies on acoustic cues to litter identity ("litter-level signature") shared by littermates, rather than on the separate recognition of each littermate.

While this absolute classification percentage may appear relatively low, the discrimination of 15 litters corresponds to an ecologically improbable context. Indeed, a mother is much more likely to need to discriminate her puppies out of only a few litters, as reported in free-ranging dogs (15, 40, 41). When running 100 DFAs classifying the whines between only four randomly selected litters (out of 15 litters each with 6 puppies or more), 37.7 ± 7.2% of whines were attributed to the correct litter against a theoretical chance level of 1/4 (25%). This classification score was significantly higher than the empirical chance level of 25.0 ± 2.8% based on 1,000 permutations ($P < 0.001$). Our result thus confirms that whines contain a strong litter identity signal in an ecologically realistic context.

Second, we found that whines contained information about individual identity within litters. Indeed, a classification model trained with the whines (N = 10 per puppy) from the first recording session of 189 puppies nested within 35 litters, attributed the whines (N = 10 per puppy) of the second, independent recording session (not included in the training set) to the correct puppy in 3.2% of cases, against a theoretical chance level of 0.5% (1/189). This percentage of correct classification is significantly higher ($P < 0.001$) than the empirical chance level obtained on permuted datasets (1.8 ± 0.3%). The empirical chance level is higher than the theoretical chance level because in this nested design, permutations were restricted to calls within litters where calls share a litter-level signature, as demonstrated above. When lifting this restriction (allowing permutations across the full dataset), the empirical chance level obtained on 1,000 permuted datasets dropped back to 0.5 ± 0.2%, thus converging with the 0.5% theoretical chance level. The *mean* f_o and *duration* of whines were the two most strongly contributing variables to individual differences in the acoustic structure of puppy whines (*SI Appendix*, Fig. S3*B*).

Here too, when conducting these nested classification experiments in a more ecologically valid context including fewer litters (i.e., randomly selecting puppies from 4 litters corresponding to an average of 21.6 ± 2.5 puppies per experiment), classification models achieved correct attributions to individual puppies in 15.4 ± 3.5% of cases against a theoretical chance level of 4.7 ± 0.6%. This score is significantly higher than the empirical chance level of 8.0 ± 2.6% obtained when performing classification experiments on permuted datasets ($P = 0.004$). As above, when allowing permutations across litters, the empirical chance level obtained on 1,000 permuted datasets dropped to 4.7 ± 1.5%, thus converging with the theoretical chance level (4.7 ± 0.6%).

Finally, individual differences in the acoustic structure of whines were not related to puppy sex. Indeed, using the same procedure as described above, a final nested pDFA in which we permuted, within sexes, the calls of 189 individual puppies, showed that the correct classification of 3.2% obtained on the original dataset remained significantly higher than the empirical chance level of 0.5 ± 0.2% ($P < 0.001$). Furthermore, the empirical chance level was equivalent to the theoretical chance level (1/189). This indicates that puppy whines are not sexually dimorphic, as further verified with linear mixed models testing the effect of sex on each of the five acoustic variables (*SI Appendix*, Fig. S4). These results corroborate previous findings in a wide range of other offspring mammals such as calves (24), piglets (42), kittens (23), and human babies (28, 43) in which the calls of infant males and females lack sex differences.

Mothers Provide More Care in Response to Synthetic Whines from Their Own Puppies. Having shown that whines differ systematically between litters and between individuals within litters, we then investigated whether mothers modulate their maternal behavior in response to this vocal information. To do this, we performed playback experiments, exposing Beagle dog mothers (N = 16) to whines broadcasted from a speaker positioned outside of their nest during an average of 58 ± 7 s (see *Materials and Methods* and *SI Appendix*, Fig. S1 for details on the experimental setup). Mothers responded to the playback in 180 trials (out of a total of 192). Their behavioral responses included the provision of maternal care, olfactory or visual attention to their puppies, olfactory or visual attention to the playback source, and/or stress-related behaviors (see Table 1 for full details of the behavioral indices). In 16% of trials, mothers even carried the loudspeaker into the nest, indicating extremely strong maternal sensitivity to the vocalizations of offspring (Movie S1).

A linear mixed model with mother identity, order of presentation of the playback stimuli, and donor puppy identity (i.e., origin of the synthetic variants) as random effects revealed that the stimulus kinship (own vs. stranger puppy whines) had a significant effect on the behavioral responses of tested mothers (*SI Appendix*, Table S2). Indeed, mothers provided significantly more maternal care in response to synthetic whines from their own puppies than to those of strangers (estimate ± SE = −0.02 ± 0.01, $P = 0.02$) (*SI Appendix*, Fig. S5*B*). In particular, they were most likely to carry the loudspeaker to the nest when it broadcasted variants from their own puppies' whines (Generalized LMM, estimate ± SE = −17.1 ± 7.47, $P < 0.05$). This increase in maternal care behaviors likely led to the observed concurrent reduction of attention to the playback source itself (estimate ± SE = 0.02 ± 0.01, $P = 0.02$; *SI Appendix*, Fig. S5*A*), as well as to the lack of significant differences between conditions in other behavioral indices (namely visual and olfactory attention to puppies and stress-related behaviors, see *SI Appendix*, Table S2).

Mothers Provide Less Care in Response to Playbacks of Their Own Puppies' Whines When Their f_o Is Resynthesized to Fall Outside Their Litter-Specific Range. Having thus established that mothers can discriminate their own puppies' calls from those of strangers, our next objective was to investigate which specific acoustic features of whines are used by mothers to make this distinction. When mothers were exposed to synthetic whine variants derived from their own puppies' whines, we found that the level of maternal care elicited by the playbacks was affected by the manipulations of whine f_o (Fig. 2*A*, see *SI Appendix*, Table S3 for the detailed results of LMMs with mother identity, order of presentation of playback stimuli, and donor puppy identity as random effects). In contrast, other behavioral indices, namely the mothers' visual and olfactory attention to the loudspeaker and to their puppies, or maternal stress-related behaviors, remained unaffected (*SI Appendix*, Table S3). Thus, mothers provided less care when the f_o of the tested whine stimulus was resynthesized to be litter-atypical (LMM post hoc tests following a significant interaction between the whines' origin and f_o manipulations, estimate ± SE = −0.06 ± 0.03, $P = 0.02$). This was however not true when the synthetic whines originated from stranger puppies (post hoc tests, estimate ± SE = 0.0002 ± 0.02, $P = 0.99$). Therefore, while a litter-specific f_o (characterizing own-puppy whines) is necessary for triggering strong maternal care, the fact that merely bringing the f_o of stranger puppy whines within the tested mothers' litter-specific range does not increase care provisioning indicates that the whine f_o alone is not sufficient for mothers to identify puppies as their own.

In Most Litters, Smaller Puppies Produce Higher-Pitched Whines. Having demonstrated that litter and/or individual information encoded in the acoustic structure of puppy whines supports offspring discrimination, we then investigated whether puppies' calls also provide mothers with reliable information about their body condition. The first step to test this hypothesis was to establish how whines vary with puppy body weight within their litters.

Within the 40 recorded litters, f_o was overall significantly negatively correlated with puppy body weight (LMM with litter identity, mother identity, father identity, and puppy identity as random effects, estimate ± SE = −0.23 ± 0.1, $P = 0.01$, Fig. 1*A*). The number of litters with a significant negative relationship (N = 10) was significantly higher than the number of litters with a significant positive relationship (N = 2) (binomial test, $P < 0.001$, see *SI Appendix*, Table S5). With the exception of minor frequency modulations (*minor FM*) (LMM, estimate ± SE = −0.004 ± 0.002, $P = 0.02$), the other acoustic characteristics of whines—namely *HNR*, *major FM,* and *duration*—did not significantly vary with puppy body weight (*SI Appendix*, Table S4).

Mothers Provide More Care in Response to High-Pitched Whines Simulating Relatively Small Puppies of Their Own Litter. Having shown that, within most litters, smaller puppies produce higher-pitched (and more modulated) whines, we conducted a set of playback trials to investigate the effects of this weight-related variation in f_o on maternal behavior. A linear mixed model with mother identity, order of presentation of playback stimuli, and donor puppy identity as random effects, revealed that mothers provided significantly more maternal care in response to high-pitched variants of their own puppies' whines simulating relatively small puppies of their litter than to low-pitched variants simulating relatively large puppies (Fig. 2*B*) (LMM post hoc tests following a significant interaction between the whines' origin and f_o manipulations, estimate ± SE = 0.14 ± 0.05, $P = 0.01$). This was not observed when mothers were exposed to synthetic whines derived from whines of stranger puppies (post hoc tests: estimate ± SE = −0.05 ± 0.05, $P = 0.32$).

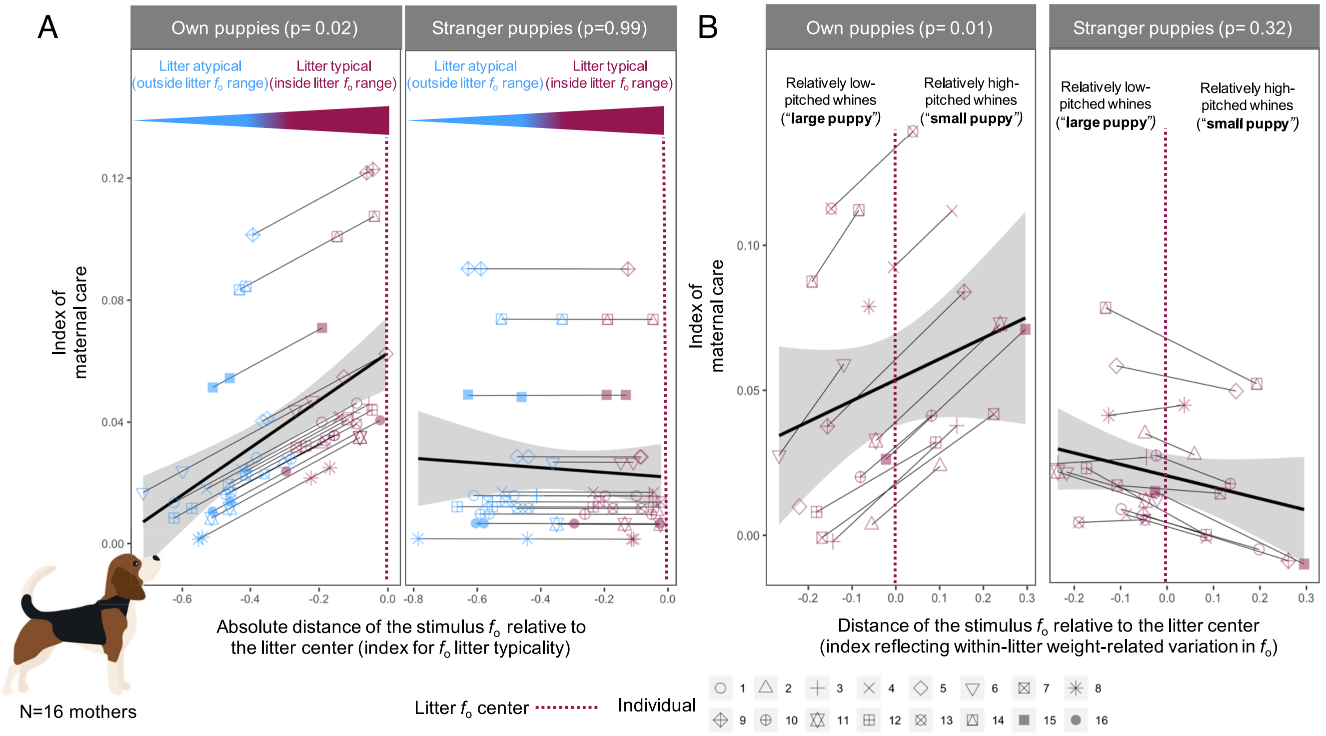

Fig. 2. The fundamental frequency f_o of puppy whines predicts maternal care responses to playbacks of her offspring. Maternal responses are quantified using a behavioral index (Table 1 and *Materials and Methods*). Each dot (fitted value) represents a single playback experiment. The dot shape indicates the mother's identity, and the dot color indicates whether the tested mother was presented with whines characterized by a f_o manipulated to fall inside (purple) or outside (blue) their litter range. The black solid lines correspond to the regression trendlines and the gray shaded areas to the 95% CIs. (*A*) Mothers provided more care in response to acoustic variants derived from their own puppies' whines where f_o was manipulated to fall inside their litter f_o range (litter-typical) than to those where f_o was manipulated to fall outside the litter f_o range (litter atypical). This response was not observed when the broadcasted whine variants were derived from the whines of stranger puppies. (*B*) Mothers provided more care in response to playbacks of their own puppies when f_o was manipulated to be relatively high (mimicking relatively small puppies for their litter) compared to those when f_o was manipulated to be relatively low (mimicking relatively large puppies for their litter). The level of maternal care was not affected by f_o manipulations in stranger puppy whines.

Thus, mothers respond to weight-related f_o variation in a way that suggests they use this information to provide more care to their own puppies only, and not to stranger puppies.

Here again, as direct maternal care behaviors such as grooming, feeding, and carrying the loudspeaker took over, the attention of mothers to the loudspeaker decreased as the f_o of their own puppies' whines increased (post hoc tests: estimate ± SE = −0.14 ± 0.06, $P = 0.02$), while other olfactory or visual attention to puppies behaviors and stress related-behaviors remained unchanged (*SI Appendix*, Table S6). In response to synthetic variants derived from the whines of stranger puppies, none of the quantified behaviors were affected by f_o manipulations (*SI Appendix*, Table S6).

Discussion

Our study aimed at unraveling the complexity of mother–offspring vocal interactions in a litter-rearing mammal, the domestic dog. We show that the structure of whines encodes litter-, individual-, and condition-related information and that mothers use this information to adjust their maternal behavior to not just one, but multiple offspring.

Specifically, we show that mothers provide significantly more maternal care in response to playbacks of synthetic variants derived from their own puppies' whines, indicating that they perceive acoustic cues to the puppy's kinship (own vs. stranger offspring). While this behavior may be adaptive in free-ranging dogs, where several females can simultaneously rear litters (15, 40, 41), it should also be taken into consideration in the context of domestic dog breeding, where human caregivers can encourage adoption by another lactating mother when the biological mother neglect or reject their own offspring (44).

Critically, whine fundamental frequency (f_o), a strong predictor of litter identity (*SI Appendix*, Fig. S3*A*), affected mothers' responses, as resynthesizing their puppies' f_o to litter atypical values outside of the litter-specific range reduced maternal responses to the same levels as for puppies from stranger litters. This result indicates that, as predicted, the f_o of whines plays a key role in offspring discrimination in domesticated dogs. However, our results also show that mothers use other acoustic cues to litter and/or individual identity because bringing the f_o of a stranger puppy's whines to litter typical values inside the litter-specific range was not sufficient to trigger a maternal response as strong as the one given in response to their own puppies' whines. We suggest that in future work, researchers investigate the extent to which mothers may use whine harmonicity or duration for offspring discrimination, two other strong vocal predictors of litter and individual identity as shown by our acoustic analyses (*SI Appendix*, Fig. S3). Our findings are also consistent with those of previous playback studies conducted on pinnipeds, where mothers rear a single offspring (3). By exposing mothers to highly controlled synthetic vocalizations derived from their own pups' calls, researchers were able to demonstrate that offspring discrimination is mediated by a combination of frequency, temporal, and/or spectral features, rather than by f_o alone. For instance, both f_o and temporality in the frequency modulations of the calls of fur seal pups enable mothers to recognize their single offspring (22).

Within most litters, we also showed that relatively small puppies produced higher-pitched whines than did their larger littermates. This result follows the well-established predictions of the principle of acoustic size allometry, whereby small puppies are expected to have shorter vocal folds that vibrate at higher rates, allowing them to produce higher-pitched whines than those of larger puppies (as reviewed in ref. 31). Crucially, in line with the negative weight-related variation in whine f_o that we observed in most litters, mothers provided more care in response to relatively high-pitched variants derived from their own puppies' whines, which simulated a relatively small puppy from their litter. This is consistent with observations that sows exhibit stronger responses to playbacks of high-pitched calls given by relatively smaller piglets (12). However, f_o manipulations did not affect maternal care when the broadcasted variants originated from stranger puppy whines, further indicating that cues to individuality other than f_o are also used as indicators of kinship.

Our results thus suggest that litter-rearing mothers rely on group-level (litter identity) as well as individual-level (individual identity, body weight) information to adjust care provision to their large number of offspring. This is in contrast to species rearing a single offspring in which mothers discriminate between their own offspring and strangers and assess the condition of their offspring using information solely encoded at the individual level. Solving the putatively more complex task encountered by litter-rearing mothers may not have required the evolution of new abilities, but rather have relied on the extension of existing auditory and cognitive skills to larger sets of offspring. Indeed, the "multilevel" communication system identified here bears similarities to those described in species living in social groups with different matrilines, such as elephants (*Loxodonta africana*) (45) or rhesus macaques (*Macaca mulatta*) (46), where animals are able to discriminate individuals among multiple conspecifics by using both group- and individual-related information. Whether mothers actually recognize individual puppies within their litter will have to be systematically tested in future experiments using, for example, a cross-modal expectancy violation paradigm (47) that could combine auditory cues (this study) with visual and/or olfactory cues to identity (48).

Surprisingly, although large puppies produced lower-pitched whines within litters, we observed a positive relationship between whine f_o and litter weight (average body weight of littermates) across litters, where puppies from relatively heavy litters produced significantly higher-pitched whines than did puppies from lighter litters (Linear Mixed Models, estimate ± SE = 0.41 ± 0.13, $P = 0.002$). This counterintuitive correlation may arise from between-litter variation in body size linked to differences in developmental speed and associated activity levels in offspring (despite the fact that we controlled for puppy age in our experiments) superseding the within-litter, vocal fold size-related variation in f_o. Indeed, larger animals with bigger lung capacities and stronger muscles (49) may achieve higher subglottal pressures leading to the production of relatively higher f_o calls (50). These differences between litters could be inherited, as suggested by previous studies conducted on piglets (25) and goat kids (51) that have demonstrated higher levels of similarities in the acoustic structures of calls between full siblings compared to half- or nonsiblings, including in call f_o. In our study, the large between-litter variation in f_o associated with average offspring body size differences among litters could reflect the consequence of artificial selection in dog breeding leading to large size differences even within breeds (e.g., between breeders). The extent to which whine f_o is inherited, and the extent to which it is predicted by parental body weight should thus be investigated.

As human caregivers can provide care to puppies when necessary (44), thereby enhancing their chances of survival, selection pressures on dog mothers to provide optimal maternal care may have been relaxed through domestication (52). As such, one could have expected a relatively rudimentary form of mother–offspring communication in domestic dogs. Yet, we identified a multilevel system of information encoding associated with strong, functional maternal behavioral responses. In fact, we were astonished to observe that in about a fifth of playbacks (and significantly more in response to whines from their own puppies) the mothers carried the loudspeaker into the nest, as if it were their actual puppy, indicating that the whine acoustic stimulus was sufficient to trigger this key maternal behavior in the absence of specific visual or olfactory cues. We suggest that researchers could capitalize on this behavior, reminiscent of the instinctive and stereotyped egg-retrieving "fixed action patterns" described in greylag geese by Lorenz and Tinbergen in 1938 (53), to develop a paradigm aimed at testing the strength of parental behavior and the extent to which parents form unified representations of their offspring, in domestic dogs and other mammals.

Together, our observations show that offspring-mother vocal interactions in domesticated dogs involve a functional multilevel signal that simultaneously supports the assessment of litter identity, individual identity, and individual condition in multiple offspring. Our results also show that these levels of information are largely encoded in a single parameter, the f_o (responsible for perceived pitch) of a single call type, the puppy whine. Studies of domesticated litter-rearing mammals have been conducted on a limited number of species and breeds, namely the Yorkshire and Landrace breeds for domestic pigs (12, 26) and the Beagle breed for domestic dogs (this study). Future research should not only include further domesticated breeds but crucially contrast the vocal systems of these species with those of their wild relatives, such as the wild boar (*Sus scrofa*) and wolf (*Canis lupus*) to test whether these communication systems are conserved and shared across litter-rearing mammals or are just a by-product of artificial selection during domestication.

Materials and Methods

We collected data at four dog breeding facilities in France (Ecole Vétérinaire Maison-Alfort, Elevage des Pins de Meluzzine, Elevage le Clos du Bonheur, and Elevage d'Aurphie) as follows: i) collecting distress whines in 3-wk-old Beagle puppies recorded over a total of 440 sessions (N = 220 puppies from 40 litters); ii) measuring body weight [proxy for condition (21)]; and iii) conducting nearly 200 playback trials on Beagle mothers (N = 16 mothers).

Whine Analysis.

Acoustic recordings. We recorded puppies' whines with a Sennheiser MKH70 directional microphone connected to an audio recorder Zoom H4n (44.1 kHz, 24 bit), positioned at approximately 30 cm from the animal's mouth. To limit pseudoreplication, the whines of each individual were recorded during two sessions separated by a minimum of 4 h. Puppies were recorded in a context of separation from their mother and littermates. They were carried to a separate room and placed alone in a pen (roughly 100 × 50 cm) without any visual and vocal contact with their mother and littermates. The recordings lasted for a maximum of 5 min once the puppy had emitted a first whine.

At the end of each recording session, puppies were immediately reunited with their mother and siblings. All puppies displayed normal behaviors, including suckling or interacting with their mother and littermates, indicating that any stress experienced during the recording had been low and temporary. None of the recorded puppies showed signs of distress such as excessive panting, yawning or lip licking (20, 54), which otherwise would have led to the immediate interruption of the experiment. Mothers, which were habituated to being temporarily separated from their litter (e.g., during daily walks) and accustomed to breeders handling puppies during daily care (e.g., weight measurements evaluating physical condition of puppies), showed no signs of stress during separations from their puppies.

Acoustic analyses. For each 5 min recording, we selected 10 whines produced during the first minute of separation to ensure a balanced dataset of calls emitted at relatively low arousal levels. More specifically, given that puppies typically produce long sequences of repeated whines, we extracted one whine for every three consecutive whines. Such selection limited homogeneity in the acoustic structure of the selected whines associated with the production of consecutive calls.

We used a custom script in Praat (55) to measure acoustic parameters related to the sound source (i.e., vocal fold vibrations), but not to the filter (i.e., resonances of the supralaryngeal vocal tract) (30). Indeed, like the infant distress calls of many other mammals, puppy whines are high-pitched with widely spaced harmonics and a low spectral density (Fig. 1*B*). As such, filter-related parameters corresponding to formant frequencies (or vocal tract resonances) are not clearly emphasized (56) and thus not expected to play a crucial role in mother–offspring vocal interactions. In contrast, source-related parameters of offspring calls, and particularly their highly salient f_o, have been demonstrated to encode cues to identity and/or condition in a wide range of infant mammals (3, 12, 13, 24–29). We thus decided to measure a total of five independent source-related parameters consisting of the *mean* f_o of whines, their harmonicity (harmonic-to-noise ratio *HNR*), their minor vibrato-like frequency modulations (*minor FM*), their major frequency modulations (*major FM*), and their *duration* (*SI Appendix* for details on the acoustic measurements and *SI Appendix*, Table S1 for definitions of each acoustic parameter).

Statistical analyses of acoustic data. First, to investigate whether whines differed among litters, we performed multivariate permuted discriminant function analyses [pDFA fitted with the MASS R package (57)]. This procedure allows for classification experiments when data are hierarchically structured, for instance when grouping variables (e.g., individuals) are grouped into higher-level classes (e.g., sex, social groups, etc.). As argued by Mundry and Sommer (38), the potential nonindependence arising from these higher-level groupings can affect the empirical correct classification chance level because attributions can be driven by variation at these levels (e.g., if there are sex or social group differences). Permuted DFAs were conducted on a sample of 35/40 litters (corresponding to 189 puppies) that did not share the same mother.

Discriminant models included litter membership as a grouping variable, and the five acoustic parameters measured from whines (*mean* f_o, *HNR*, *minor FM*, *major FM*, and *duration*) as predictors. The whines of three randomly selected puppies from each of 15 litters (selected from our sample of 35 litters for having six or more puppies) were used to train the model to attribute calls to the correct litter, and the whines of three other puppies from the same litters were used as independent testing datasets to examine the accuracy of the model to classify whines among litters. We used a two-step procedure, in which we performed 100 traditional DFAs on our original dataset and then 1,000 DFAs on new, permuted datasets (i.e., data associated with each individual call were randomized across litters). Because in most cases a mother would only need to discriminate the whines of her own puppies from those of a small number of litters (15, 40, 41), we performed an additional 100 pDFAs, each on four randomly selected litters (out of the 15 included in the first analysis), to replicate our above analysis in a more ecologically valid context.

Second, we conducted a nested pDFA to examine whether whines were different among puppies within litters. We trained classification models with the whines of 189 puppies (corresponding to 35 litters) recorded in a first recording session and tested the models' predictions with independent data corresponding to the whines of the same individuals recorded in a second session. As above, we performed a traditional DFA on our original dataset and then 1,000 DFAs on permuted datasets, in which the data associated with each individual call were randomized within each of the 35 litters. Here too, we replicated our analysis in a more ecologically valid context, performing 100 nested pDFAs on 4 randomly selected litters (corresponding to 21 ± 0.5 puppies). We performed a final nested pDFA classifying whines between 189 individual puppies in which we permutated data within sexes to ensure that individual differences were not partly due to potential sex differences in the acoustic structure of whines.

For all pDFAs, we compared whether the percentage of correct classifications obtained with our original nonpermuted dataset was significantly different from the rate of correct classifications obtained with our permuted dataset (empirical chance level). A P-value ≤ 0.05 indicates that the correct attribution percentage is significantly higher than the empirical chance level, thus confirming the presence of grouping-level (litter or puppy) information in whine acoustics.

Finally, to test whether within litters, interindividual variation in puppy body weight predicted interindividual puppy whine acoustics, we performed linear mixed models [fitted with lme4 R package (58)] for each of our five selected acoustic variables. Models included puppy body weight (nested within litters) as a main fixed effect, and litter identity, mother identity, father identity and puppy identity as random effects. We used a likelihood ratio test to evaluate the significance of each predictor (59). All model residuals were normally and homogeneously distributed, except for the model fitted with the whine duration that was subsequently log-transformed. P-values ≤ 0.05 were considered statistically significant. Datasets and R codes for performing statistical analyses can be downloaded at https://osf.io/ws5am/.

Playback Experiments. To investigate whether mothers can acoustically discriminate their own puppies and assess their condition, we performed playback experiments on 16 Beagle mothers. Because, as predicted, the results of acoustic analyses revealed whine f_o as a key feature for conveying cues to offspring identity (at both litter and individual levels) and condition (Fig. 1*A*), we manipulated whine f_o using methods of parametric sound resynthesis (see below). Specifically, we resynthesized f_o to be litter typical vs. atypical, and also to mimic whines produced by a relatively small vs. large puppy (Fig. 1*B*). Playback experiments were conducted over 2 d at 22 ± 1 d postpartum. During this period mothers provide relatively strong maternal care (feeding, grooming, warmth, and protection) (15–17, 35, 36) to compensate for their puppies' limited hearing, vision, thermoregulation, and locomotion abilities (20, 60).

Whine stimuli. First, we prepared 1-min audio stimuli (60 ± 1 s) that only consisted of whine sequences (either produced by the puppies of the tested mother or by stranger puppies). We removed a small number of whines that overlapped with covocalizing dogs (in the rare instances where other dogs were present in surrounding rooms and vocalized), while preserving the temporal calling dynamic. We also filtered or attenuated any background noise.

Second, we prepared four synthetic variants derived from the natural exemplar using the TD-PSOLA algorithm (61) in Praat. Indeed, playback designs using synthetic sounds allow to experimentally test the communicative function of specific acoustic features whereas designs using natural sounds cannot disentangle the effects of features that may covary. We thus used parametric sound resynthesis to perform independent manipulations of the whine f_o, while leaving all other acoustic features intact (32–34).

More specifically, we resynthesized whine f_o to be litter typical by manipulating f_o to fall inside the litter f_o range of the tested mother and to be litter atypical by manipulating f_o to fall outside their range (Fig. 1*B*). Whine f_o was also modified to characterize the weight-related variation typical for the litter of the tested mother (Fig. 1*A*). Low and high f_o variants were created to simulate whines produced by respectively relatively large or small puppies within the litter-typical f_o range (Fig. 1*B*). In order to determine the f_o range of each litter, we analyzed f_o variation in two 1-min whining sequences (recorded on different sessions, see "*Acoustic recordings*") for each puppy using the Voice Report function in Praat. The detection range was manually adjusted after visual inspection of the spectrograms corresponding to each sequence. Examples of stimuli can be downloaded at https://osf.io/ws5am/.

On both days of experimentation, mothers were exposed to four synthetic stimuli, which were either derived from the whines of their own puppies or from those of strangers. Mothers were also presented with two natural stimulus sequences (from own puppies and strangers) which served as control trials to verify that females' responses were not qualitatively altered by the resynthesis (*SI Appendix*, Table S7). This resulted in the presentation of two sets each comprising six stimuli. In total, 192 playback trials were conducted across the 16 mothers.

Whine stimuli were broadcast in a random order by a Sound Bose Mini Link II (±3 dB in 0.2 to 20 kHz frequency range) at an average sound pressure level SPL of 67dB (at 1 m from the sound source as determined by measuring SPL in 3-wk-old puppies of this study) to mimic natural whine loudness of 3-wk-old puppies. The loudspeaker was positioned outside of the nest and hidden behind a wooden screen approximately 1.5 m away from the nest (*SI Appendix*, Fig. S1).

Playback procedure. Mothers were presented with whine stimuli in their home enclosure, with their puppies resting inside the nest (*SI Appendix*, Fig. S1).

Maternal behaviors were observed, and simultaneously recorded, using a GoPro Camera (see Movie S1 for an example of maternal response). Both the loudspeaker and camera were connected to a computer via a Bluetooth connection. This enabled us to broadcast stimuli and perform observations from a separate room, away from the tested mother's enclosure and thus avoiding any bias potentially associated with the presence of the experimenters. With this experimental setup, we were also able to stop the playback if the mother carried the loudspeaker to the nest before the end of the sound exposure, increasing the ecological validity of the experiment, as puppies typically relax and stop whining when they receive care (17, 19). As such, the average duration of a sound exposure was 58 ± 7 s.

Between two successive experiments, we included a recovery period during which mothers returned to baseline and calm behaviors such as resting. This period lasted between 20 min and 4 h (58 ± 41 min). We delayed the next playback experiment by at least 25 min if we observed the tested mother providing care during the recovery period because the timing of nursing sessions has been demonstrated to affect responses to offspring calls (62).

Behavioral analyses of mothers' responses to whines. To quantify mothers' behavioral responses to playbacks, we measured 12 behaviors (Table 1) over the duration of the playback trial which comprised the playback duration and the 2 min following the sound exposure. We used Boris open-source software for behavioral coding (63).

These behaviors were grouped into four reaction indices characterizing i) the females' provision of maternal care, ii) their olfactory and visual attention to puppies, iii) their olfactory and visual attention to the playback source, and iv) their stress-related behaviors (Table 1). More specifically, the four indices were calculated dividing each playback trial period into 1,000 bins and encoding the occurrence of each of the 12 behaviors with a 0-1 variable. Then, for each bin, we associated a score corresponding to the sum of behaviors simultaneously displayed. For instance, a score of 1 indicated that the tested mother displayed a single type of behavior, whereas a score of 2 indicated that she displayed two simultaneous behaviors such as grooming and feeding the puppies. In addition, we multiplied each score per bin by a latency weight (i.e., 1-1/number of bins) to adjust the relative weights of behaviors according to their latency (with behaviors that occurred sooner after stimulus presentation having heavier weights). Finally, to compute four indices of behavioral reactions (attention to the playback source, attention to puppies, maternal care, and stress-related behaviors), the scores were summed over the total number of bins (i.e., entire duration of the playback trial).

Statistical analyses of behavioral data. Data from playback experiments were analyzed using linear mixed models fitted with lme4 R package (58). The response variables of models corresponded to the four indices of reaction characterizing maternal responses and were modeled with a Gaussian distribution. Normality and homogeneity of the models' residuals were verified. All models included the mother's identity, the order of presentation of playback stimuli, and the puppy's identity from which we derived the synthetic variants (puppy donor identity) as random effects.

First, we conducted linear mixed models with the whine origin as a main fixed effect to investigate whether mothers can acoustically discriminate between the whines of their own puppies vs. those of strangers. Then, we tested whether mothers used whine f_0 to make this distinction. To do this, we ran models assessing the fixed effect of a two-way interaction between the whine origin and f_0 manipulations (modeled as the frequency distance derived from the litter f_0 center). Finally, we examined whether whine f_0 provided mothers with information on puppies' body condition by running similar models with an interaction between the whine origin and f_0 manipulations that remained within the litter-specific f_0 range of the tested mother. When the effect of an interaction was statistically significant, we conducted post hoc tests to assess the relationship between f_0 manipulations and behavioral responses when variants were derived from own and stranger puppies [emtrends( ) function from emmeans R package (64)].

All statistical analyses were conducted on our sample of maternal responses to synthetic whines. Prior analyses indeed revealed that the behavioral responses of mothers were not impacted by the synthetic component of our synthetic stimuli (*SI Appendix*, Table S7). This "control" ensured that the nature of the responses to synthetic whines was ecologically realistic and allowed for systematically testing the effects of f_0 manipulations on maternal behaviors. In addition, we assessed possible outliers that could influence the models' predictions by calculating Cook's distances (65). Because all analyses performed with and without outliers led to similar conclusions, in the manuscript we present the results obtained from analyses excluding identified outliers. P-values ≤ 0.05 were considered statistically significant. Datasets and R codes for performing statistical analyses can be downloaded at https://osf.io/ws5am/.

Ethics Statement. All experiments, including recordings of puppy whines and playback experiments on Beagle mothers, were performed under ethical approval no. E-42-218-0901 (ENES Bioacoustics Research Lab agreement, Direction Départementale de la Protection des Populations, Préfecture du Rhône).

Data, Materials, and Software Availability. Audio stimuli examples, a video example of maternal responses to playbacks, datasets, and R codes for analyzing data can be downloaded at https://osf.io/ws5am/ (66). All other data are included in the manuscript and/or supporting information.

ACKNOWLEDGMENTS. We thank the dog breeders, including Sandra Thoumire, Marina Bardet, Catherine Gigot, and Sophie Garel, who allowed us to record puppies at their facilities. We also thank Aurélie Pradeau and Elisabeth Reby for making the fleece covers for the loudspeaker. M.M., R.P., K.P., L.B.d.B., and D.R. were supported by the IDEXLYON project as part of the "Programme Investissements d'Avenir" (ANR-16-IDEX-0005) to D.R. M.M., K.P., and D.R. were supported by a French National Research Agency grant ("SCREAM" ANR-21-CE28000701). N.M. and D.R. were funded by the Institut universitaire de France. Funding was also provided by LabEx CeLyA, CNRS, Inserm, and the University of Saint-Etienne. This publication was completed while N.M. was Visiting Miller Professor at the University of California, Berkeley (Miller Institute for Basic Research in Science). The article processing charges were covered by the University of Quebec in Chicoutimi and the University of Saint-Etienne.

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