

Individual variation in nursing vocalizations of Hawaiian monk seal pups, *Monachus schauinslandi* (Phocidae, Pinnipedia), and lack of maternal recognition

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Abstract: Vocalizations of individual Hawaiian monk seal pups, *Monachus schauinslandi*, do not have unique attributes that enable females to recognize their own offspring. Despite low aggregation density during pupping, aggressive encounters are common between females with pups. Fostering is prevalent and may reflect confusion over the identity of pups following aggressive encounters between females. All pup vocalizations were simple in structure and contained true harmonics. The coefficients of variation revealed considerable variance in vocalization structure within pups. Controlling for age, multivariate analyses of variance revealed significant differences among pups in vocalization attributes. Significant developmental changes occurred in vocalization structure for some pups but not for others. Discriminant function analysis suggested that it would be difficult for females to distinguish between the vocalizations of pups. The results of experiments conducted in the field showed that females did not discriminate between filial and alien pups by voice. In addition, females tended not to foster pups that had vocalizations similar to those of their own offspring. Thus, females seem to be unable to recognize their pups by voice. The apparent lack of vocal recognition of pups may contribute to the high frequency of fostering in this species.

Résumé : Les cris d'appels des jeunes phoques-moines *Monachus schauinslandi* ne comportent pas de caractéristiques particulières qui permettent aux mères de reconnaître leurs propres petits. Malgré la faible contagion des phoques au cours de la mise-bas, les interactions agressives entre femelles mères sont fréquentes. L'adoption est une habitude commune chez ces phoques et reflète probablement la confusion au sujet de l'identité de la progéniture après des batailles entre femelles. Tous les cris des petits sont de structure simple et comportent des harmoniques naturels. L'estimation des coefficients de variation a mis en lumière la variance considérable qui existe dans la structure des cris chez les petits. Les analyses multidimensionnelles de la variance après uniformisation de l'âge ont démontré qu'il y avait des différences significatives entre les petits quant aux caractéristiques des cris. La structure des cris subit des changements significatifs au cours du développement chez certains petits, mais pas chez d'autres. Une analyse discriminante indique qu'il est probablement très difficile pour une mère de distinguer les cris de ses petits de ceux des autres petits. Les résultats d'expériences en nature ont démontré que les femelles sont de fait incapables de distinguer les cris de leurs propres petits de ceux des autres. En outre, les femelles ont tendance à ne pas adopter de petits dont les cris ressemblent à ceux des leurs. Il semble donc que les femelles soient incapables de reconnaître leurs petits vocalement. L'absence apparente de reconnaissance vocale explique peut-être la fréquence élevée des adoptions chez cette espèce. [Traduit par la Rédaction]

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Introduction

Mechanisms for parental recognition of offspring should evolve among species in which parental investment is large, and the potential exists for parents to become confused about the identity of their offspring (Gubernick 1980; Stoddard and Beecher 1983). Vocal recognition appears to be important in gregarious vertebrates that have high colony density during parental care (Petrinovich 1974; Gelfand and McCracken 1986; Davis and McCaffrey 1989; Balcombe 1990; Balcombe and McCracken 1992; Insley 1992; Sherrer 1992). For example, Sherrer and Wilkinson (1993) showed that vocal "isola-

tion'' signatures of infant evening bats, *Nycticeius humeralis*, are sufficiently unique to enable a mother to distinguish her offspring from others in the crowded communal roost.

A similar pattern of maternal behaviour occurs in all species of fur seals and sea lions (Bonner 1984; Gentry and Kooyman 1986; Oftedal et al. 1987). Lactating females must forage at sea, but have retained the ancestral pattern of terrestrial birth and maternal care. Thus, females undertake feeding cycles, alternating between brief nursing periods on land and foraging trips at sea. When females return from foraging, they must relocate their own offspring among numerous other pups.

Many studies have reported that female otariids successfully relocate their own pups and reject the approaches of alien pups (e.g., Peterson and Bartholomew 1967; Stirling 1971; Pierson 1987; Gisiner and Schusterman 1991). In fact, foster nursing is uncommon among otariids (Stirling 1975; Bowen 1991). When non-offspring nursing occurs, it tends to be opportunistic and brief (Packer et al. 1992; but see Lunn 1992). Several studies have shown that the vocalizations of mothers and pups are distinguishable individually (Trillmich 1981; Roux and Jouventin 1987; Insley 1992). Additionally, females and pups are more responsive to recorded playbacks of vocalizations of their respective partners than to those of aliens (Trillmich 1981; Roux and Jouventin 1987; see also Schusterman et al. 1992). Hence, there appears to be a well-developed mutual recognition system underlying the successful reunion and lack of fostering in otariids.

Suckling of alien offspring is more common in phocids (true seals). Often, female phocids are aware of, and accept, the suckling of alien young. Thus, the young need not sneak suckles in the opportunistic manner seen among otariid pups (Stirling 1975; Riedman and Le Boeuf 1982; Boness 1990; Riedman 1990; Bowen 1991; Boness et al. 1992). Most phocid females remain with their pups almost continuously throughout lactation. Consequently, for most phocids, the selective pressures that have promoted the highly developed recognition and reunion system of otariids are absent.

The vocal recognition abilities of phocid mothers and pups have been studied less. The ability of mother and pup to recognize one another vocally does not necessarily preclude fostering. Conversely, absence of vocal recognition does not mean that fostering invariably will occur (cf. northern elephant seals, *Mirounga angustirostris*; Petrinovich 1974; Riedman and Le Boeuf 1982; Insley 1992). However, one might expect more frequent fostering when vocal recognition is absent or limited. Hence, we investigated the possibility that maternal recognition of pups exists in Hawaiian monk seals, a species exhibiting a high frequency of fostering.

Early researchers suggested that Hawaiian monk seals recognized and suckled only their own offspring (Kenyon and Rice 1959). However, subsequent researchers reported fostering (Alcorn 1984; Johnson and Johnson 1984; Johanos and Henderson 1986). Boness (1990) noted that most females suckled alien pups at some period during lactation. Most episodes were the result of exchanges of pups between females involved in aggressive encounters. During these encounters, pups usually vocalized, and one or both females appeared confused about the identity of their pup (Boness 1990; D.A. Job, unpublished observation).

In this study, vocalizations from different monk seal pups were recorded during suckling to determine the difference

among individuals. Also, we used behavioural observations to assess whether females discriminated between the vocalizations of different pups.

Methods

Study site, age determination, and marking technique

Data were collected from May 1 to July 29, 1989, the peak of the Hawaiian monk seal pupping season. East Island (23°45'N, 166°10'W) is a small (670 m²) coral sand island located within the French Frigate Shoals Atoll in the North-western Hawaiian Islands.

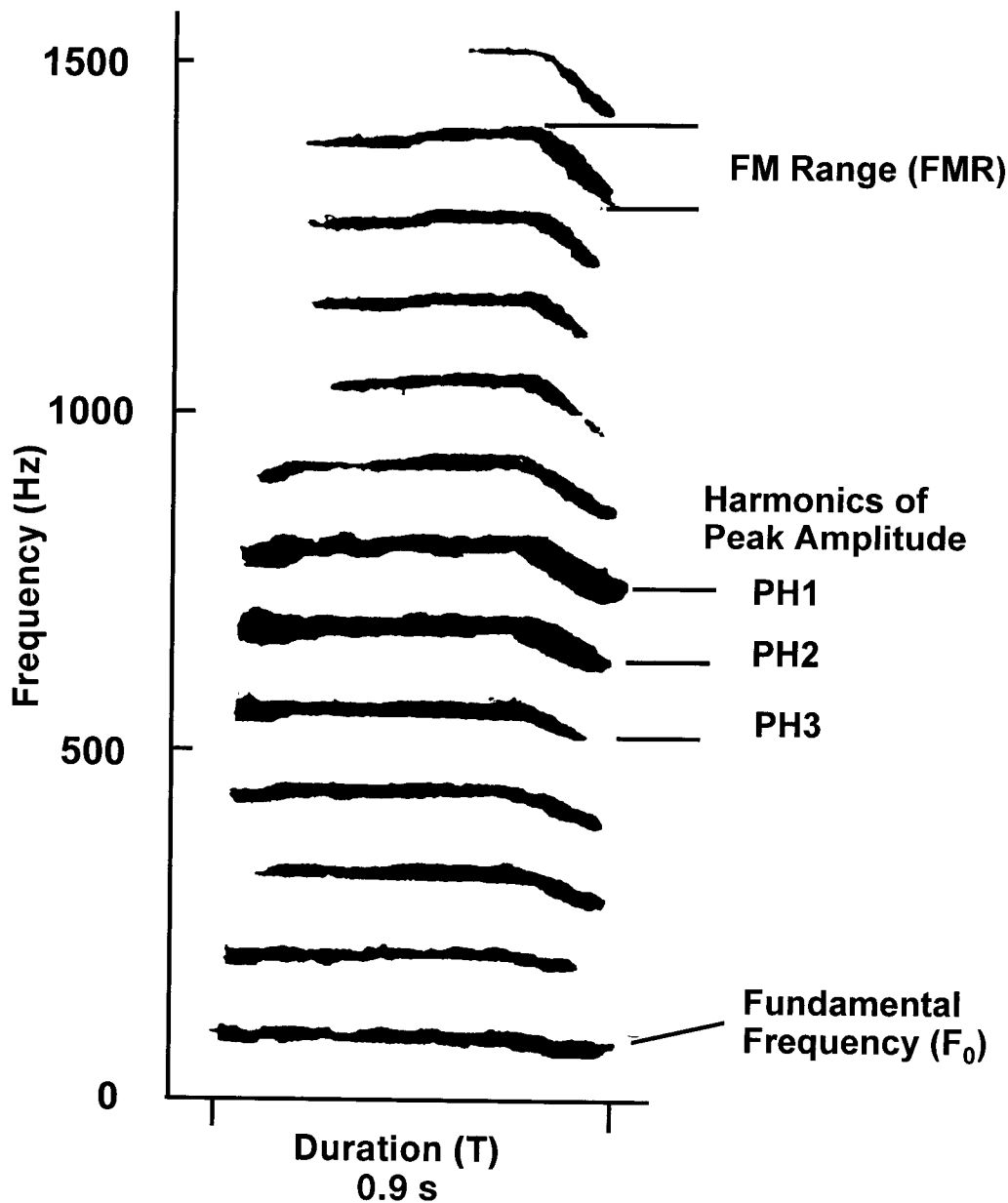
Prior to giving birth, 20 females were dye-marked remotely using a 60-cc syringe loaded with Nyanzol-D™ Dye (Belmar Products, North Andover, Massachusetts). Those females not dyed were identified from natural markings and scars. Within a few hours of birth, 34 pups were marked similarly with Lady Clairol™ bleach (Clairol Inc., New York). A few pups were not marked for 1–2 days after birth because there were no other newborn pups nearby with which to confuse them. On occasion, moulting of nearly weaned pups necessitated rebleaching. The birth dates and ages of newborn pups were estimated from observation of parturition, the presence and condition of ejected placentae, or the presence of an umbilical cord.

Recordings and sound analysis

Tape recordings of pup vocalizations were made using a Sony® Professional Walkman recorder (WM-DC6; frequency response 50 – 12 000 Hz) with a Sennheiser® directional shotgun microphone (ME-80; frequency response 40 – 15 000 Hz) shielded by a Rycote® wind sock. Recordings generally were made about 2–7 m from the pup. Where necessary, the microphone was pushed over the berm of the beach with a pole and aimed so that surf noise was minimized. Recordings were analyzed using a Kay® Elemetrics Sonograph (Model 5500; frequency response 0 – 32 000 Hz) with an analog filter having a "roll-off" frequency of 228 dB/octave. We used a Blackman window without pre-emphasis. Use of various frame sizes provided a range of precision in time and frequency domains (Miller and Job 1992). For example, a narrowband filter (15 Hz @ 2 kHz input frequency) provided optimal resolution of frequency attributes, and wideband filter settings (300 and 512 Hz @ 4 kHz input frequency) provided more precise temporal resolution. To standardize and facilitate comparison, sonograms were made as 2-s samples over 0–4 kHz, using 256 or 1024 points per frame. Description and interpretation of acoustic signals follow those of Watkins (1967), Marler (1969), and Beecher (1988).

Four hundred and twenty-eight clear recordings of nursing vocalizations were analyzed for 15 pups whose ages and mothers were known. Analysis was restricted to vocalizations emitted during nursing, and vocalizations were analyzed from different calling bouts to reduce interdependency. Six acoustic variables were measured for each vocalization, including duration (T), fundamental frequency (F_0), range of frequency modulation (FMR), and the three harmonics of greatest amplitude (PH1, PH2, PH3) (Fig. 1). F_0 was measured as the average of minimum and maximum frequencies of the first harmonic. The first harmonic above the fundamental is the second harmonic. For PH1–PH3, the harmonic number (e.g., 5 or 6) is given, not the frequency. The FMR was

Fig. 1. Sonogram illustrating parameters measured for Hawaiian monk seal pup vocalizations. Note that the FM range is not marked where it was measured; it was measured at PH1 and PH2.



determined by taking the mean value of the two harmonics having the greatest amplitude.

Responses to pup vocalizations

Vocalization playback experiments commonly have been used to assess the discrimination abilities of birds (Jones et al. 1987) and mammals (Balcombe and McCracken 1992), including pinnipeds (Petrinovich 1974; Trillmich 1981; Roux and Jouventin 1987). However, because of the endangered status of the Hawaiian monk seal, a permit allowing vocalization playback studies could not be obtained. As an alternative, naturally occurring pup vocalizations emitted during brief separations of females from pups simulated a playback situation. During ad libitum observations, when a pup vocalized, we noted whether the female responded with a vocalization or a sniff. The responses were recorded for up to four females

within five female body lengths (~10 m) of the vocalizing pup. Also recorded was the separation distance between female and pup. Thereby, we assessed whether females, at a given distance from a vocalizing pup, responded differently as a function of their "association" and "relatedness." "Association" refers to an affiliation of the pair irrespective of their immediate proximity and genetic relatedness. Thus, "associated" is used to refer to a responding female that is caring for the vocalizing pup and "not associated" to refer to the female that is not providing milk for the pup. "Relatedness" refers to the genetic status of the pair, where "filial" is used to refer to a responding female that is the mother of the vocalizing pup and "alien" to the female that is not the biological mother. Similarly, both terms are used to refer to the status of the vocalizing pup.

Twelve tests were run to determine whether a female's

Table 1. Descriptive statistics for 264 vocalizations of 12 Hawaiian monk seal pups (22 vocalizations per pup).

Variable	Grand mean \pm SD
Duration (ms)	665 \pm 59
Fundamental frequency (Hz)	99 \pm 6.2
Harmonic with peak amplitude	5 \pm 1
Harmonic with second greatest amplitude	5 \pm 1
Harmonic with third greatest amplitude	6 \pm 1
Frequency modulation range (Hz)	16 \pm 2

response to a vocalizing pup depended upon the relatedness or association status of the pair. These tests resulted from partitioning observations according to female–pup relationship (filial vs. alien and associated vs. not associated), response type (vocalizing or sniffing), and the separation distance between the pup and female (≤ 2 female body lengths vs. > 2 female body lengths).

Statistical analysis

Vocalizations

SAS[®] version 6.06 was used for all analyses (SAS Institute Inc. 1989). Data were collected across ages for individual pups, hence a repeated-measures analysis of variance would have been the most appropriate analysis to conduct. However, the need for a balanced design (Winer 1971) precluded such an analysis because of a small sample size. Thus, a separate multiple analysis of variance (MANOVA) was conducted for each of five different age groups (in 3-day intervals) to assess individual differences according to age (MANOVA, PROC, GLM). Age-related changes in vocalization attributes were assessed separately for each pup using linear regression analysis (PROC REG).

To determine the probability of correctly assigning a vocalization to a specific pup, a stepwise, cross-validated discriminant function analysis (DFA, PROC DISCRIM) was performed with all ages pooled, and with ages grouped (4–6 and 19–21 days). Variables meeting the statistic (0.15) to remain in a stepwise DFA were re-entered as data in a cross-validated DFA. The latter reduced bias in estimation of the classification error rate by removing a single pup vocalization, one variable at a time, and comparing it with the pooled vocalizations of the other pups (Wilks' test; Johnson and Wichern 1988).

Discrimination

Two additional analyses were undertaken to seek evidence of female discrimination of pup vocalizations. The naturally occurring responses of females to vocalizing pups were analyzed using the Cochran–Mantel–Haenszel test (CMH, PROC FREQ). The CMH test allows pooling into a single contingency table individuals making variable contributions. Each animal is considered to be a separate stratum in the contingency table. A CMH test was conducted only when there was homogeneity (uniformity) in females' responses to the vocalizations of pups across strata as determined by a Breslow–Day test (BD test, PROC FREQ).

The second analysis was undertaken to assess whether females were more likely to foster pups whose vocalizations were similar to those of their own pups. Information from the

DFA was used for this analysis. A particular pup vocalization may match the average call of another pup better than it matches its own. When this occurs, the DFA "assigns" the vocalization to the other pup and provides an output of the mean percentage of incorrect assignments of vocalizations. For a given female, the percentage of vocalizations assigned to pups actually fostered by the mother was compared with the percentage assigned to pups she never fostered.

Results

Description of acoustic structure

All pup vocalizations consist of one part and are simple in structure (see Eliason et al. 1990). They contain true harmonics with spectral energy distribution varying both within and among pups. Some vocalizations have one or more ascending, descending, or fluctuating frequency modulations (FM), while others have few or none (Fig. 2). Formants, parts of the frequency spectrum reinforced by the resonant properties of the vocal tract, also are present in the vocalizations of Hawaiian monk seals (see Miller and Job 1992). The grand mean values for frequency and temporal characteristics of the nursing vocalizations of pups are summarized in Table 1.

Variation within and among pups and changes with age

Figure 2 illustrates the variation within and among pups for nursing vocalizations. The mean and ranges of coefficients of variation (CV) show this variation in more detail (Table 2). All vocalization attributes, except the fundamental frequency, showed such variation. Controlling for age, MANOVAs revealed significant differences in vocalizations among pups for all age groups (Table 3). Fundamental frequency and, to a lesser extent, the duration and harmonic of greatest amplitude (PH1) contributed most to these differences. On average, vocalizations increased in duration and decreased in PH1 as pups grew, but these changes were not significant. Linear regression analysis showed that most vocalization attributes changed with development. However, pups showed little or no change in FM range as they grew (Table 4).

Given the variation in age-related changes in vocalizations among pups, and the fact that females are exposed concurrently to pups of various ages, we performed a DFA incorporating vocalizations at all ages. The results of this analysis, for all ages pooled, showed that individual vocalizations were assigned correctly to the pup producing the call only 14 \pm 13.4% of the time (error = 0.8609). Separation of vocalizations into age-classes did not improve these results significantly (all ages vs. 4–6 days old: $t = -0.62$, $p = 0.55$, $N = 7$; all ages vs. 19–21 days old: $t = -1.93$, $p = 0.09$, $N = 7$), although percentages increased slightly, but not significantly, among older age groups (ages 4–6 days: mean = 23 \pm 23.6% (SD); ages 19–21 days: mean = 42 \pm 30.8% (SD)). It should be noted that the average duration of lactation for females on East Island was 39.8 \pm 5.43 days.

Discrimination by females

Using vocalization playback experiments would have allowed greater control of extraneous variables than using natural observations of female responses to pup calls. Nevertheless, natural observations provided an alternative way to determine whether females discriminated between the vocalizations of

Fig. 2. Sonograms of vocalizations of two Hawaiian monk seal pups at 7 days old, illustrating variation within and among pups.

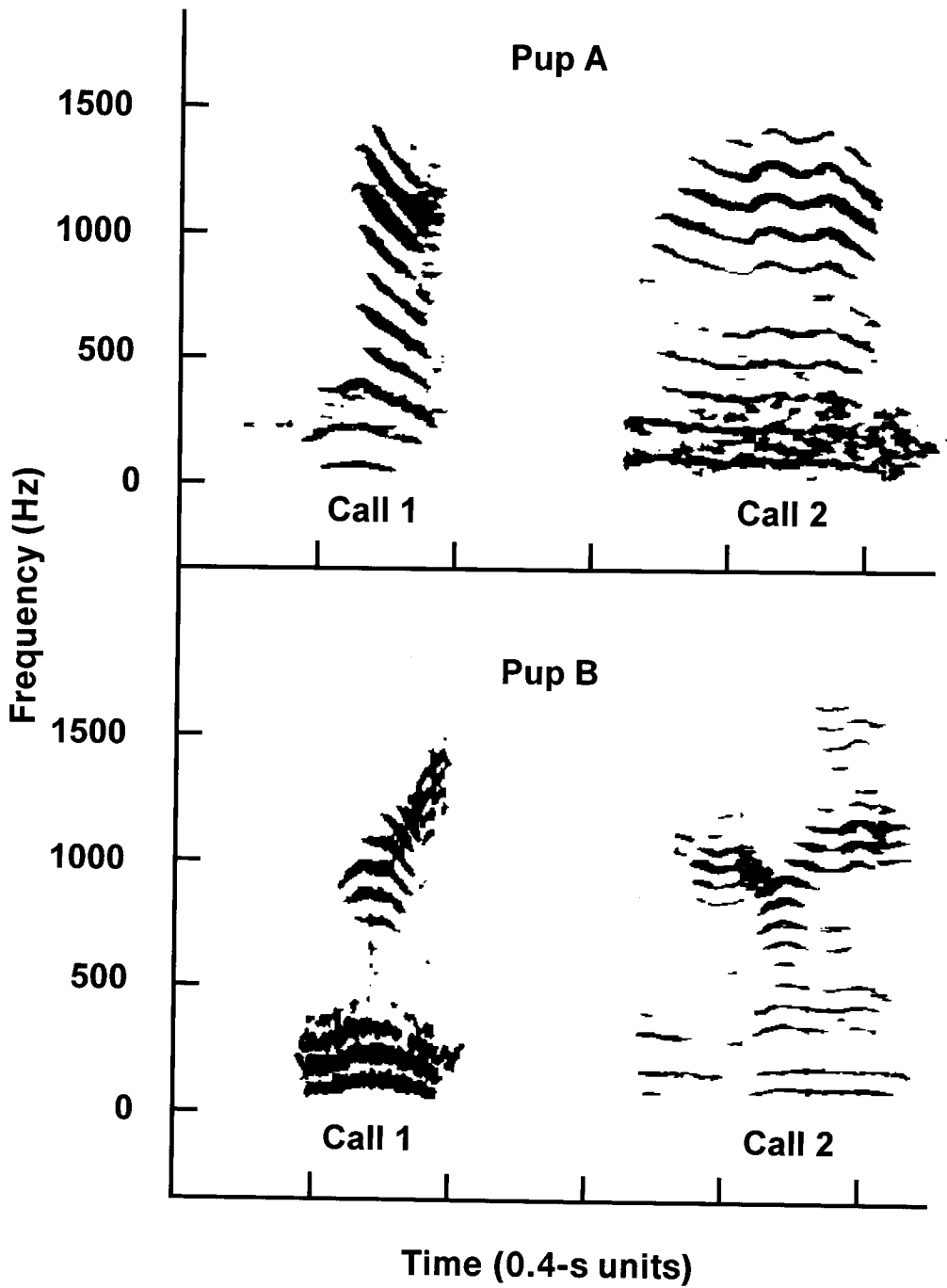


Table 2. Means and ranges of the coefficients of variation (CV) for parameters of vocalizations of 12 Hawaiian monk seal pups (22 vocalizations per pup).

Variable	Mean CV \pm SD	Range of CVs
Duration (ms)	41.3 \pm 7.09	24.1–53.3
Fundamental frequency (Hz)	10.2 \pm 2.82	5.9–15.0
Harmonic with peak amplitude	63.3 \pm 12.36	46.3–87.4
Harmonic with second greatest amplitude	61.9 \pm 10.79	44.3–80.9
Harmonic with third greatest amplitude	56.0 \pm 6.51	49.5–70.6
Frequency modulation range (Hz)	45.2 \pm 9.06	29.3–61.7

Table 3. Multivariate analyses of variance of Hawaiian monk seal pup vocalizations according to age group (Wilks' lambda F ; $n = 9$ pups).

Age group (days)	F	df
0-3	2.46***	48
4-6	1.80***	60
7-9	2.26***	48
10-12	2.23***	42
19-21	3.24***	48
All ages	3.70**	24

** $p = 0.001$.
*** $p = 0.0001$.

Table 4. Regression analysis of 12 Hawaiian monk seal pup vocalization attributes with age, showing the number of pups with a significant positive slope ($\beta+$), no change in slope (β_0), or a negative slope ($\beta-$).

Attribute	$\beta+$	β_0	$\beta-$
Duration	7	5	0
Fundamental frequency	0	7	5
Harmonic with peak amplitude	8	4	0
Harmonic with second greatest amplitude	7	5	0
Harmonic with third greatest amplitude	5	7	0
Frequency modulation range	0	11	1

filial and alien pups or between pups with which they were or were not associated.

Results of 12 tests of differential female response to vocalizations from pups of different relatedness and association status are shown in Table 5. Generally, these results indicated that females did not respond significantly more often to the vocalizations of their own pups than to those of alien pups. Nor do the results show that females responded significantly more often to the vocalizations of pups with which they were associated than to those with which they were not associated.

When the pup was associated with the female, irrespective of the separation distance between them, she did not call consistently more often in response to vocalizations of her own pup than to those of aliens (Table 5). Similarly, when either her own or an alien pup vocalized, a female did not sniff consistently in response. This heterogeneity of response (i.e., not significant according to the BD test) precluded using the CMH test to determine a relationship between a female's response and the relatedness of the pair. In a comparison of filial and alien pups, where female and pup were not associated, there was significant homogeneity in the relationship between the female's response and pup relatedness: females responded by calling more often in response to the vocalizations of alien pups (Table 5). However, the relationship between the female's vocal response and relatedness to the pup was not significant. Females also responded by sniffing alien pups more often than filial pups that vocalized, but this was not significant.

While controlling for relatedness, in tests comparing the

Table 5. Summary of the Breslow-Day (BD) test for consistency of female response to pup vocalizations and of the Cochran-Mantel-Haenszel (CMH) test for a relationship between the female's response (vocalization or sniffing) and relatedness or association of the pair.

Female's response	Separation distance ^a (m)		BD test (χ^2)	N_v	N_p	CMH test (χ^2)
	≤ 2	> 2				
Relatedness when the pup is associated						
Vocalization	≤ 2		118.85	11 132	22/15	—
Vocalization	> 2		52.02	764	18/10	—
Sniffing	1		57.85	4 759	23/15	—
Relatedness when the pup is not associated						
Vocalization	≤ 2		16.65	3 376	21/8	—
Vocalization	> 2		0.04 ^b	8 068	23/2	0.35
Sniffing	1		11.03 ^b	848	17/6	0.00
Association when the pup is alien						
Vocalization	≤ 2		54.95	7 346	21/15	—
Vocalization	> 2		26.72	7 608	23/10	—
Sniffing	1		32.61	2 600	18/12	—
Association when the pup is filial						
Vocalization	≤ 2		16.37	7 162	23/9	—
Vocalization	> 2		5.77 ^b	1 224	17/4	38.09*
Sniffing	1		7.80 ^b	3 007	23/9	0.02

Note: N_v , number of vocalizations; N_p , number of pups entered into CMH / number used in calculating χ^2 value. *, $p \leq 0.05$.

^aDistance separating vocalizing pup and responding female.

^bBD test in which $p > 0.05$ indicates homogeneity of females' responses, permitting a valid CMH test to be conducted.

association status of the vocalizing pup and the responding female, females did not respond consistently, either vocally or by sniffing, when the vocalizing pup was not their own (Table 5). However, females responded consistently by sniffing their own offspring more when it was associated with her than when it was alone or nearby with a foster mother (i.e., not associated) (Table 5). Similarly, females consistently vocalized in response to their own pups more often when they were associated with them and 2 m or more from their side than when they were with a foster mother. The latter, however, was the only situation in which there was a significant relationship between a female's response and pup status.

Using the assignment of pup vocalizations to incorrect pups in the discriminant function analysis described above, we sought further evidence of vocal discrimination of pups by females. If females were able to discriminate among pups, one would expect them to foster pups whose calls were more similar to those of their own pups. Hence, for each pup we compared the percentage of vocalizations assigned to pups which were fostered by the mothers of the calling pup with that assigned to pups which were not fostered by her. There was no significant difference in the percentage of incorrect assignments of vocalizations to these two groups of pups (paired t test; mean difference = -0.3750 , $t = -0.3019$, $p = 0.7715$, $N = 8$). Hence, females selectively did not foster pups that had vocalizations similar to those of their own offspring.

Discussion

Our objective was to determine whether variation in vocal structure of Hawaiian monk seal pups was adequate for females to recognize individuals by call and to assess whether females showed evidence of discriminating between their own and alien pups. Based on the nursing vocalizations of pups, our results suggest that the vocalizations of different pups are not distinguishable by females. Similarly, the behaviour of females suggests that they do not respond preferentially to vocalizations of pups on the basis of their relatedness or association. Thus, females are unlikely to use pup vocalizations to discriminate between pups or to recognize their own pup.

Variation in vocalizations within and among pups

A prerequisite for individual vocal recognition is stereotypy in vocalizations within individuals and variability among them (Falls 1982; Chapman and Weary 1990). We found considerable variability in the nursing calls of individual pups (Table 2). There was sufficient similarity among vocalizations of different pups to distinguish individuals only when age was controlled statistically (Table 3). When age was not controlled, there was poor predictability in assigning vocalizations to the correct pup. The reason may be that ontogenetic changes were not consistent among individuals. For a given vocalization attribute, some pups showed changes with age while others did not, or such changes were in the opposite direction (Table 4). The pupping season is prolonged for the Hawaiian monk seal (see Boness 1990) and females may be exposed simultaneously to pups ranging in age from newborns to weanlings (more than 40 days old). Therefore, the vocalizations of individual pups are variable and the differences among pups are small in comparison with the differences within pups. This probably makes it more difficult for females to discriminate between the calls of their own pups and others.

Only a few studies of parental recognition and discrimination of young by call have addressed the role of vocal ontogeny (Beecher et al. 1981; Jones et al. 1987; Sherrer 1992). Most studies of vocal recognition of young in pinnipeds do not take into consideration changes with age (Trillmich 1981; Thomas et al. 1983; Perry 1986; Roux and Jouventin 1987; Gisiner and Schusterman 1991; Insley 1992). Where age-related changes are consistent among individuals, females may have evolved the ability to detect changes with age and to discriminate between the vocalizations of her own and alien offspring, despite being faced with vocalizations from pups of widely differing ages.

Discriminatory ability of females

Overall, analyses suggested that females do not discriminate acoustically between filial and alien pups nor between pups with which they are and are not associated. In our analysis of the effects of association and relatedness upon female discriminatory behaviour, in only 1 of 12 tests was there any suggestion that females may be discriminating by voice (Table 5). In this test, when a female's own pup vocalized more than 2 m away, females were more likely to respond vocally when they were caring for the pup than when the pup was alone or in foster care. Although a differential response might imply recognition, such an interpretation should be made with caution. Eleven other tests do not support this

conclusion. Furthermore, there are ambiguities inherent in using naturally occurring responses to pup vocalizations because of an inability to control specific conditions in the field. For example, the frequency of response by females may have been low because females already had a foster pup by their side. A female's potential response, or lack of response, to her own pup that was not associated with her may have been influenced by the location and behaviour of the pup she was fostering, thereby producing spurious results.

It has been reported that vocalizations are important in maintaining proximity of female–pup pairs in phocids (Perry and Renouf 1988). It is possible that the greater vocal response of females to their own pups, when the pups were associated with them, merely reflects the use of vocalizations for maintaining proximity rather than providing evidence of vocal recognition. Among 12 tests of differential response of females, one positive result is likely to occur by chance alone. Furthermore, results of the DFA showed a lack of similarity between the vocalizations of pups fostered by a particular female and those not fostered by her. Absence of differential female responses may mean either that females are incapable of discriminating between filial and alien pups or that conditions were not appropriate to reveal vocal discrimination (cf. Holmes 1990). Insley (1992) concluded that vocal recognition was unlikely in the northern elephant seal. He found 64% of calls assigned correctly to pups in a DFA, a score considerably higher than we obtained for Hawaiian monk seals (14%).

It was not possible to control for the use of other senses in discrimination by females. Olfaction probably plays some role in female–pup recognition among Hawaiian monk seals, as it appears to do in other species (Insley 1992). However, anecdotal observations suggesting that females are confused about the identity of pups imply that olfaction either is not very important or is not very well developed. Furthermore, females readily foster older and larger aliens, suggesting that visual cues may not be very important either (Boness 1990).

Lack of vocal recognition may contribute to fostering

Casual observations showing that female Hawaiian monk seals were confused about the identity of pups following bouts of interfemale aggression support the suggestion by Boness (1990) that individual recognition between female and pup may be absent, poorly developed, or poorly used. Fostering behaviour often follows incidents of female aggression. In 1987, 73% ($N = 32$) of observed fostering episodes involved female–female aggression (Boness 1990). A similar percentage (75%, $N = 18$) of fostering episodes involved such aggression in this study (Job 1992). Poorly developed or deficient female recognition ability may be a proximate factor leading to such frequent fostering.

During lactation, female Hawaiian monk seals typically are well dispersed from other female–pup pairs compared with other phocids (Boness 1990). Furthermore, fostering behaviour is frequent among female Hawaiian monk seals. Boness (1990) reported that 87% of 30 females fostered at least one pup during lactation in 1987. A similarly high proportion of females (9 of 10) did so in 1989 (Job 1992). Boness (1990) followed pups to 1 year of age and found no difference in survival of fostered pups, suggesting that there is little or no immediate cost to fostering. The dispersed

spacing pattern of Hawaiian monk seals during lactation and the low reproductive cost of fostering may contribute to the lack of recognition by voice in this species.

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