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Call parameters and facial features in bats: a surprising failure of form following function

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We attempted to correlate echolocation call parameters to a comprehensive array of ear and nose measurements from 12 families of bats. Surprisingly, we failed to find any significant relationships. We did find consistent differences between nasal and oral emitters such as: (a) nasal emitters have higher frequencies with maximum energy for their size than oral emitters, (b) nasal emitting bats tend to have longer, narrower skulls, and (c) nasal emitters have a shorter distance from the nostril to the eye (muzzle length).

Key words: Chiroptera, call parameters, echolocation, nasal and oral sound emission, facial features, noseleaves, ears, muzzle length

INTRODUCTION

Griffin (1958) first quantified echolocation in an aerial-hawking insectivorous bat and divided the capture sequence of signals into three phases: search, approach, and feeding buzz. Identification of bats by search phase calls in the field using ultrasonic detectors is now common. The mixture of the constant frequency and frequency modulation in calls, frequency change over time, harmonic structure, duration, highest and lowest frequency, and frequency with maximum energy are standard parameters monitored for identification purposes (Fenton and Bell, 1979, 1981; Thomas *et al*., 1987; Fenton, 1994; O'Farrell *et al*., 1999). However, some species of bats cannot be differentiated by these parameters.

Across and among some families, frequencies used by bats in echolocation calls have been shown to be negatively correlated with size of bat that has been derived from a variety of indicators including skull measurements, forearm length, and body mass (Heller and Helversen, 1989; Barclay and Brigham, 1991; Vaughan *et al*., 1997; Fenton *et al*., 1998; Bogdanowicz *et al*., 1999; Jones, 1999). Average body mass for a species is not often uniformly available. Most animals produce sounds with wavelengths equal to or smaller than their body size (Jones, 1999). This relationship between size and sound production has special significance for echolocating bats because size of bat may be constrained by the frequencies needed to detect prey (Barclay and Brigham, 1991; Fenton *et al*., 1998; Jones, 1999).

Facial structures of bats are highly variable and can include noseleaves; wart-like projections; papillae and slits; differing sizes, shapes and placement of pinnae; and various pinnae accessories such as a tragus, antitragus and transverse ridges (Fig. 1). Noseleaves are found in the Rhinopomatidae, Rhinolophidae, Hipposideridae, Nycteridae, Megadermatidae, Phyllostomidae and in two genera of the Vespertilionidae. The first six families in this list are nasal emitters, while all other families of microchiropterans are oral emitters (Pedersen, 1993). Oral-emitting bats can have wrinkled, thickened lips, lips with papillae, lip pads or combinations of these and other facial foliage. The noseleaf in nasal emitting bats and the mouth and lips in oral emitting bats has been demonstrated to have different patterns of sound emission (Griffin, 1958; Simmons, 1969; Hartley and Suthers, 1987).

Freeman (1984) reported that heads of oral emitters are positively tilted relative to the basicranial axis while heads of nasal emitters are negatively tilted. This tilting is thought to cause the nasal region of nasal emitters to point directly forward during flight and affects several characters of the skull and jaws independently of the bat's size. Examining this hypothesis, Pedersen (1993, 1995, 1998) found that nasal emitters and oral emitters have distinct ontogenetic skull characteristics associated with the upward or downward movement of the hard palate to align the emission source with the direction of flight. In an effort to capture morphological diversity across most living families of bats, we investigate whether there are obvious patterns between nasal and oral emitting bats with regards to echolocation parameters, facial features, and skull morphology.

Given the wide range of echolocation strategies used in bats, we expected to find correlations with different facial features. For example, would bats that emit high frequency sounds have significantly differently shaped ears than those emitting lower frequencies. Except for the relationships between size and frequency, we had no specific a priori predictions about relationships of facial features and echolocation strategies. To this end we measured a wide array of facial features in search of possible correlations.

MATERIALS AND METHODS

Sixty-six fluid-preserved specimens of species with available echolocation data from 12 families were obtained from the American Museum of Natural History and measured (Table 1). The families represent a broad range of facial features and echolocation calls within Chiroptera. Individual specimens were in good condition, preserved in alcohol in as natural a pose as possible, with little damage to the facial features and head region, and with skull intact.

We used 27 measurements to quantify facial features or size of bat (Fig. 1). Because of difficulty in measuring soft tissues of alcoholic specimens and the breadth of this analysis, we measured to nearest millimeter using dial calipers or a millimeter scale. We quantified pinna length, greatest pinna width, total pinnae breadth, distance between pinnae, length of noseleaf, horseshoe length, and spear length with a millimeter ruler and took all other distance measurements with calipers. We used a protractor to measure the angle of the free standing pinna to the lower jaw, and recorded the body mass of each blotted specimen. Our measurements came from the left side of a wet specimen where possible and are illustrated in Fig. 1. Measurements taken include: forearm length through the skin from the olecranon process to the shallow notch proximal to the thumb (includes carpals; not shown); (a) greatest length of head through the skin from occiput of a bent over head to anteriormost gum line at incisors or premaxilla; (b) greatest width of head through the skin across the braincase at the mastoid region, which includes muscle and ears; (c) greatest height of head from the braincase on either side of the sagittal crest at the region of the parietal bone to the region of the basioccipital bone; (d) width of eye across eyeball within the eyelid; (e) distance between eyes between the medial corners of the eyes; (f) distance between nostril and eye from lateral edge of nostril to medial corner of the eye on the same side, which we designate here as muzzle length; (g) distance between pinna and eye from notch of pinna to lateral corner of the eye; (h) distance between

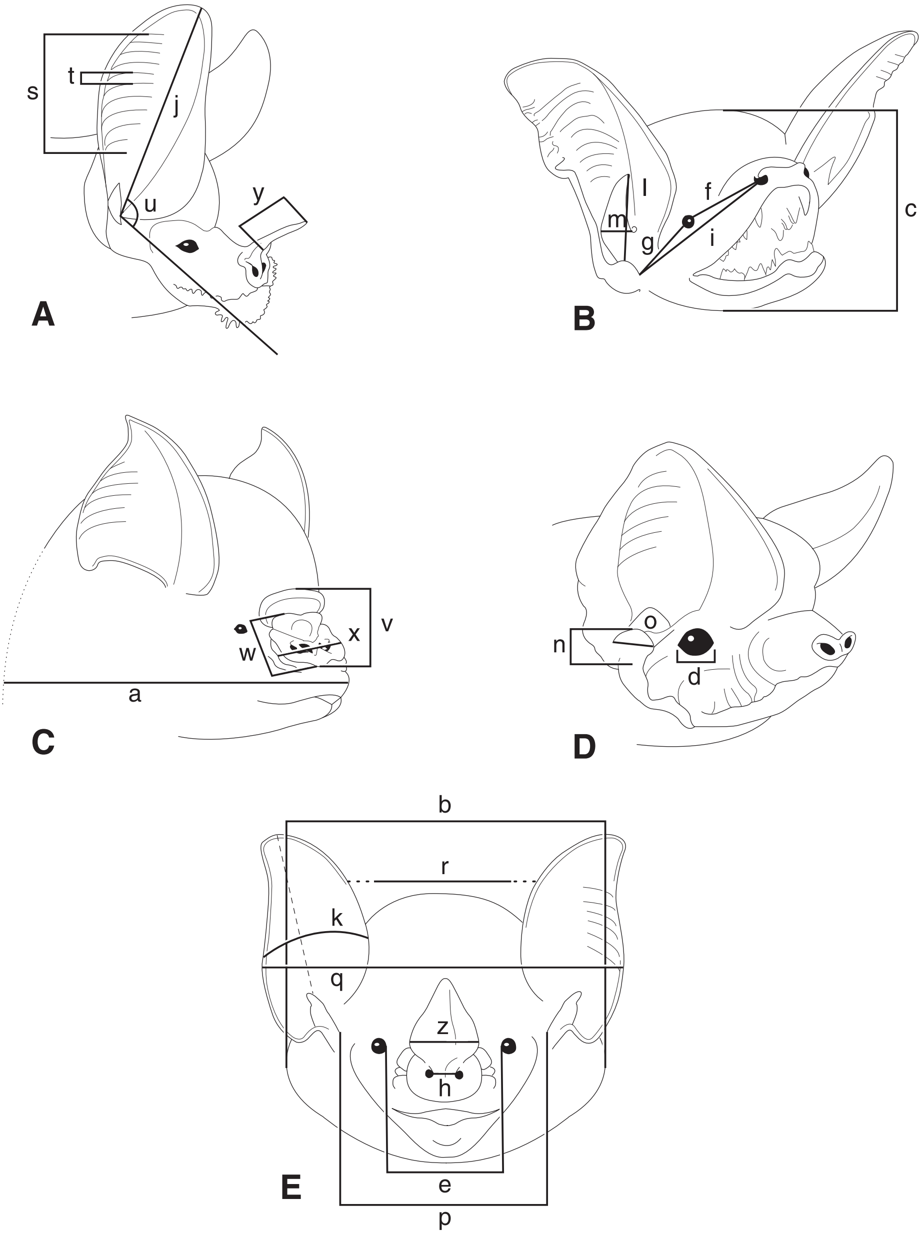

FIG. 1. Facial features of nasal and oral emitting microchiropterans. (A) *Trachops cirrhosus*, (C) *Hipposideros caffer*, and (E) *Carollia perspicillata* are nasal emitting bats, and (B) *Myotis myotis* and (D) *Tadarida aegyptiaca* are oral emitting bats. Drawings in A–D are adapted from Altringham (1996), E — from Husson (1962), and names of structures from Hill and Smith (1984). Measurements illustrated here and detailed in Materials and Methods are: (a) length of head; (b) width of head; (c) greatest height of head; (d) width of eye; (e) distance between eyes; (f) distance from nostril to eye; (g) distance from ear to eye; (h) least distance between nostrils; (i) distance from nostril to ear; (j) pinna length; (k) pinna width; (l) length of tragus; (m) width of tragus; (n) length of anti-tragus; (o) width of anti-tragus; (p) distance between meatuses; (q) breadth across pinnae; (r) distance between pinnae; (s) number of ridges on pinna; (t) spacing of ridges; (u) angle of pinna to head; (v) total length of nose leaf; (w) horseshoe length; (x) width of horseshoe; (y) spear or lancet length; (z) spear or lancet width

Table 1. Species, characteristics of echolocation calls and their sources, and emission types of bats in this study

Genus/Species	Duration (ms)	Highest Frequency (kHz)	Lowest Frequency (kHz)	Frequency with Max. Energy (kHz)	Reference	Emission Source
			Rhinopomatidae			
Rhinopoma hardwickei	48	32–33			Habersetzer, 1981	Nasal
	6–10	40	36	40–36	Simmons *et al.*, 1984	
			Emballonuridae			
Mosia nigrescens	1.1	61	37		Grinnell and Hagiwara, 1972	Oral
Saccopteryx bilineata	3.5–15	22–32			Griffin and Novick, 1955	Oral
	5.9	45.5	42.1		Barclay, 1983	
	5.4–9.4	48.7	44.5		O'Farrell and Miller, 1997	
	8	37–40	37		Pye, 1966b	
	9.0–9.4			45.1–47.1	Kalko, 1995	
Taphozous mauritianus	16	25–28		25–28	Fenton *et al.*, 1980	Oral
	20	59	15		Aldridge and Rautenbach, 1987	
	2.4–18	15.6–59	9.9–23.2	12.8–25	Taylor, 1999	
			Nycteridae			
Nycteris macrotis	0.6	116.2	57.3	84.0	Fenton and Fullard, 1979	Nasal
N. thebaica		97	61		Fenton, 1985	Nasal
	2.0	97	61	94	Fenton and Bell, 1981	
	2	97	61		Aldridge and Rautenbach, 1987	
	1.5–2	26.8–97	20.4–61	21.8–94	Taylor, 1999	
			Megadermatidae			
Megaderma lyra	<1.0	55	40		Leippert, 1994	Nasal
	0.4–1.2	22			Fiedler, 1979	
	1.0	43.6			Marimuthu *et al.*, 1995	
	1.1	17			Novick, 1958	
				48	Schmidt *et al.*, 2000	
M. spasma	1.0	22–17			Novick, 1958	Nasal
			Rhinolophidae			
Rhinolophus ferrumequinum	52–53	83	64	83	Jones and Rayner, 1989	Nasal
	49.9		69.3	82.3	Vaughan *et al.*, 1997	
		83	67–63		Trappe and Schnitzler, 1982	
	7.8–60	83	70–75.2		Vogler and Neuweiler, 1983	
	40	80–85	60–65		Pye, 1966*a*	
		85–86	66–71		Roberts, 1972	
R. hildebrandtii	40	48	42–47		Suthers *et al.*, 1988	Nasal
		46	29		Fenton 1985	
	15	46	29	46	Fenton and Bell, 1981	
	15	40	24		Aldridge and Rautenbach, 1987	
	15	37–46	24–29	37–46	Taylor, 1999	
R. rouxii	40–50	76	56–58		Schnitzler *et al.*, 1985	Nasal
	52	75–78	65		Neuweiler *et al.*, 1987	
	30–38	66–68	57–60		Novick 1958	
R. simulator		78	64		Fenton, 1985	Nasal
	20	78	64	78	Taylor, 1999	
	20	78	64	78	Fenton and Bell, 1981	
			Hipposideridae			
Hipposideros bicolor		157			Jones *et al.*, 1994	Nasal
	5–7				Novick, 1958	
				131, 142	Lara *et al.*, 2001	
H. caffer		150			Pye, 1972	Nasal

TABLE 1. Continued

Genus/Species	Duration (ms)	Highest Frequency (kHz)	Lowest Frequency (kHz)	Frequency with Max. Energy (kHz)	Reference	Emission Source
	8.0	140	119.3		Fenton, 1986	
		128–153			Jones *et al*., 1993	
	10.0	140			Fenton and Thomas, 1980	
		137	99–117		Roberts, 1972	
	7	138	105		Aldridge and Rautenbach, 1987	
	6.2–8	138–145.4	105–131	138–143.5	Taylor, 1999	
H. commersoni		55–56			Pye, 1972	Nasal
		62	51		Fenton, 1985	
	12	62	55	61	Fenton and Bell, 1981	
		65–69	50–58		Roberts, 1972	
	12	62	55		Aldridge and Rautenbach, 1987	
	12	62	55	61	Taylor, 1999	
H. diadema	11–12	54.9	50.9	54.9	Fenton, 1982	Nasal
		62	48–54		Roberts, 1972	
	9	58	47		Grinnell and Hagiwara, 1972	
H. lankadiva	8–14	74	69		Novick, 1958	Nasal
H. speoris		136–139			Jones *et al*., 1994	Nasal
	6–10	120	110		Novick, 1958	
	5.1–8.7			125.7–134	Pavey *et al*., 2001	
Noctilionidae						
Noctillo labialis	10	70	40		Suthers and Fattu, 1973	Oral
N. leporinus	14.3	58–61	30–36		Suthers, 1965	Oral
	13.3–17	52–60	27–34		Schnitzler *et al*., 1994	
	5.2	34–44	23–31		Griffin and Novick, 1955	
	10	60			Pye, 1966*a*	
	9	60	30		Suthers, 1967	
Mormoopidae						
Pteronotus davyi	5.5	68.1	58		O'Farrell and Miller, 1997	Oral
	3.1	78	63		Novick, 1963	
	6.6			68	Ibáñez *et al*., 1999	
P. parnellii	16–30	64	56		Novick, 1963	Oral
	10–30				Griffin and Novick, 1955	
	11–20	50	38		Pye, 1967	
	9–31	60	45	60–45	Pollak and Henson, 1973	
	30.4	63.5	54.5		O'Farrell and Miller, 1997	
		60.5–61.5	45–48		Roberts, 1972	
P. personatus	4.0	63	59		Novick, 1965	Oral
	2.4	33			Griffin and Novick, 1955	
Phyllostomidae						
Carollia perspicillata	0.9–2.3	76–92	70		Griffin and Novick, 1955	Nasal
	0.5–1.0	80	55		Pye, 1967	
Centurio senex	2.0	115	70		Pye, 1967	Nasal
Desmodus rotundus	1.2–1.8				Novick, 1963	Nasal
		75–60			Griffin and Novick, 1955	
	0.8–1.6	75	48		Pye, 1967	
Macrotus waterhousii	2.5–3.4	78	54		Novick, 1963	Nasal
Phyllostomus hastatus	1.6	42–55			Griffin and Novick, 1955	Nasal
	0.5–4.0	42–50	25–30		Pye, 1967	
Trachops cirrhosus	0.58	79	53		Barclay *et al*., 1981	Nasal
Vampyrum spectrum	0.3–1.8	95–100	65		Bradbury, 1992	Nasal

TABLE 1. Continued

Genus/Species	Duration (ms)	Highest Frequency (kHz)	Lowest Frequency (kHz)	Frequency with Max. Energy (kHz)	Reference	Emission Source
			Vespertilionidae			
Antrozous pallidus	5	49	26	30	Fenton and Bell, 1981	Oral
	3–6	55	30	40–45	Fuzessery *et al*., 1993	
	3.2	60	34		Griffin, 1958	
Corynorhinus townsendii	6–7	40	28		Thomas *et al*., 1987	Oral
Eptesicus capensis	2–10	80	40		Fenton and Thomas, 1980	Oral
	5	65	35	40	Fenton and Bell, 1981	
	5	65	35		Aldridge and Rautenbach, 1987	
	3.3–6.3	65–74.8	35–36.7	38.4–40	Taylor, 1999	
E. serotinus	3–6	60	25		Miller and Degn, 1981	Oral
	3.2				Troest and Mohl, 1986	
	5.22	57.4	27.7	32.3	Vaughan *et al*., 1997	
Lasionycteris noctivagans	9.4	46	25	28.2	Barclay, 1986	Oral
	10–15	30	28		Thomas *et al*., 1987	
	6	41	27		Fenton *et al*., 1983	
	10	65	30		Barclay, 1984	
Lasiurus cinereus	8	37	25	28	Belwood and Fullard, 1984	Oral
	10	20	17		Barclay, 1986	
	9	30	20		Fenton *et al*., 1983	
	15	39	26	28	Fenton and Bell, 1981	
	13	32	20		Barclay, 1984	
Myotis adversus	5.14	80	31	47	Jones and Rayner, 1991	Oral
	4–5	60	40		Thompson and Fenton, 1982	
M. californicus	2		40		Thomas *et al*., 1987	Oral
	3.5	60	40		Fenton *et al*., 1983	
	6	67	37	37	Fenton and Bell, 1981	
	0.5–2.5	82	40	45	Fenton and Bell, 1979	
M. daubentonii	3.11	79	33		Jones and Rayner, 1988	Oral
	2–5	95	35		Miller and Degn, 1981	
	5	90–95	25.5		Kalko and Schnitzler, 1989	
	2.91	81.4	29.4	46.2	Vaughan *et al*., 1997	
M. evotis	2.71	71	37	51	Faure and Barclay, 1994	Oral
	1–3		40		Thomas *et al*., 1987	
	2	105	40		Fenton *et al*., 1983	
	3	97	54	63	Fenton and Bell, 1981	
	1.14	71.22	37	50.78	Faure *et al*., 1990	
M. lucifugus	3–7		40		Thomas *et al*., 1987	Oral
	2.5	62	41		Fenton *et al*., 1983	
	5	78	38	45	Fenton and Bell, 1981	
	1–3	78	40	45	Fenton and Bell, 1979	
		79.2	33.5	45.3	Herd and Fenton, 1983	
	3	85	42		Barclay, 1984	
	2.5	93.2	39.6	44.2	Fenton and Fullard, 1979	
	2.3	78	39		Griffin, 1958	
M. myotis	3–4	100	40		Habersetzer and Vogler, 1983	Oral
M. mystancinus	2.23	80.3	32.5	47.5	Vaughan *et al*., 1997	Oral
M. sodalis	3	75	41	75	Fenton and Bell, 1981	Oral

TABLE 1. Continued

Genus/Species	Duration (ms)	Highest Frequency (kHz)	Lowest Frequency (kHz)	Frequency with Max. Energy (kHz)	Reference	Emission Source
M. thysanodes	8	49	31	34	Fenton and Bell, 1981	Oral
M. vivesi	3	45	20		Suthers, 1967	Oral
	2.5	36	20		Griffin, 1958	
M. volans	3–7		35		Thomas *et al*., 1987	Oral
	4–5	40–35	30		Fenton *et al*., 1983	
	10	89	40	46	Fenton and Bell, 1981	
	1–5	89	42	46	Fenton and Bell, 1979	
Pipistrellus hesperus	4	91	53	62	Fenton and Bell, 1981	Oral
P. nanus	1–6	90	60		Fenton and Thomas, 1980	Oral
	4	90	62	70	Fenton and Bell, 1981	
	1.2	126.4	75.4	82.2	Fenton and Fullard, 1979	
	5	90	62		Aldridge and Rautenbach, 1987	
	1.8–7.5	82.1–90	42.4–67.4	43.4–71.1	Taylor, 1999	
P. pipistrellus		100	50		Miller and Degn, 1981	Oral
sensu lato	2.7–2.9	115–118	43		Waters and Jones, 1995	
	2	90	45		Pye, 1966*b*	
	3	120	55	100–60	Surlykke and Miller, 1985	
P. rueppelli	8	70	40	45	Fenton and Bell, 1981	Oral
	4	70	40		Aldridge and Rautenbach, 1981	
Scotophilus nigrita		55	28		Fenton, 1985	Oral
	15	55	28	30	Fenton and Bell, 1981	
Molossidae						
Chaerephon ansorgei		28	16		Fenton, 1985	Oral
	15	28	16	17.8	Fenton and Bell, 1981	
	15	28	16	18	Taylor, 1999	
Molossus ater	5	40–45	25–30		Pye, 1966*b*	Oral
Nyctinomops macrotis	20	30	17	21	Fenton and Bell, 1981	Oral
	10	40		40	Simmons *et al*., 1978	
Otomops martiensseni		17	10	13	Fenton, 1985	Oral
	5–57.3	29.5	10–24.9	13–26.0	Taylor, 1999	
	5	17	10	10	Fenton and Bell, 1981	
Tadarida aegyptiaca	15	26	15	18	Fenton and Bell, 1981	Oral
	7–15	23.2–26	15–18.7	18–20	Taylor, 1999	

medial edges of nostrils; (i) distance from notch of pinna to lateral edge of nostril on the same side; (j) pinna length from notch to tip of pinna; (k) greatest width across pinna either laid out on a flat surface or, if curvature is too great, folded at the curvature with the two separate widths added together; (l) length of tragus from inferior margin at the tragus/pinna juncture perpendicular to tip; (m) greatest width of tragus and perpendicular to length; (n) length of anti-tragus from inferior margin at the anti-tragus/pinna juncture perpendicular to tip; (o) greatest width of anti-tragus perpendicular to length; (p) distance between meatuses from left to right external auditory canals; (q) breadth across outermost edges of left and right free standing pinnae; (r) distance between innermost edges of left and right free standing pinnae; (s) number of raised transverse ridges present on inner curve of pinna; (t) spacing of ridges is the distance averaged from 3 inter-ridge measurements between ridges on inner curve of pinna; (u) angle of pinna to head taken on lateral side of head with protractor aligned with anterior ventral margin of the mandible, centered at notch of pinna and follows line of free-standing pinna through the tip; (v) total length of noseleaf from ventral surface of the continuous horseshoe to dorsal tip of spear or lancet; (w) horseshoe length from ventral surface of the continuous horseshoe to the continuous dorsal top of horseshoe; (x) greatest width of horseshoe and perpendicular to length; (y) spear or lancet length from base, near an imaginary line between the two nostrils, to tip; (z) greatest spear or lancet width and perpendicular to length.

We documented from the literature the following search call parameters: duration, highest and lowest frequency, and frequency with maximum energy (Table 1). When two sources for a species' search call were located, we averaged the search calls together. When three or more search call sources were located, we compared the calls for consistency and extreme values were discarded before the call data were averaged. Recordings we used span the 45-year history of echolocation data, and we took recording differences into account when the available call data was averaged. In addition, we noted emission source for each family (Pedersen, 1993).

We used bivariate plots and regression analysis (STATVIEW) to detect patterns within our data and compared regression lines with Student's *t*-test. As in Freeman (1984, 1988) we used the sum of the natural logs of length, width, and height of head to estimate head volume and thus, size of bat. Natural logs of all but one (angle of pinna) facial measurements were regressed against this composite size character (SIZE) to determine whether facial measurements were correlated. Duration is not correlated with SIZE. We regressed the measurements of facial features and duration directly. Since all frequency parameters are correlated with SIZE, we calculated the residuals from these regressions and regressed the residuals against the measurements of facial features. Because we made multiple comparisons of these emission parameters to our measurements of facial features, the *P*-value used for statistical significance has to be reduced from 0.05 to 0.0005 based on the formula, $0.95 = (1 - \alpha)^n$, where $n = 104$ and is the number of regressions run.

RESULTS

Our attempts to find significant correlations between our measurements of facial features and call parameters were weak to unsatisfactory once the factor of size was accounted for. At this stringent value of $\alpha = 0.0005$, perhaps it is not surprising that we found no significant relationships. However, when we relaxed α to 0.05, we still failed to find any significant relationships. This demonstrates that the lack of significance was not simply a function of adjustment of a attributable to multiple comparisons but to a lack of strong relationship between facial features and call parameters.

The relationship between frequency with maximum energy and the composite size character is significantly different between nasal and oral emitting bats. Nasal emitting bats have higher frequencies with maximum energy for their head volume (SIZE) than oral emitting bats as seen in their different slopes (Fig. 2A). Overall, bats with higher frequencies with maximum energy have smaller head volumes. Although not significant, nasal emitting bats in this study tend to have longer, narrower heads (below the line) than oral emitting bats (above the line; Fig. 2B). Three nasal emitting phyllostomids (*Sphaeronycteris toxophyllum, Centurio senex, Phyllostomus hastatus*) are exceptions. The relationship between the distance from nostril to eye, which we designate as muzzle length, versus head length is significantly different between oral and nasal emitting bats such that nasal emitting bats have longer overall head lengths but shorter muzzle lengths (Fig. 2C).

Most of the facial characteristics we measured are significantly ($P < 0.05$) correlated with SIZE. Facial features not correlated with SIZE are: greatest width of antitragus, number of transverse ridges on the pinna, spacing of ridges on the pinna, angle of pinna to head, horseshoe length, and spear length. Because of strong correlations between most facial measurements and SIZE and the different correlations between frequency with maximum energy versus SIZE for nasal and oral emitting bats (Fig. 2A), the relationship between facial measurements and frequency with maximum energy is obscured. No significant correlations exist between facial measurements and the residuals from the frequency with maximum energy and SIZE for each emission source. Likewise, two facial features not correlated with SIZE — angle of

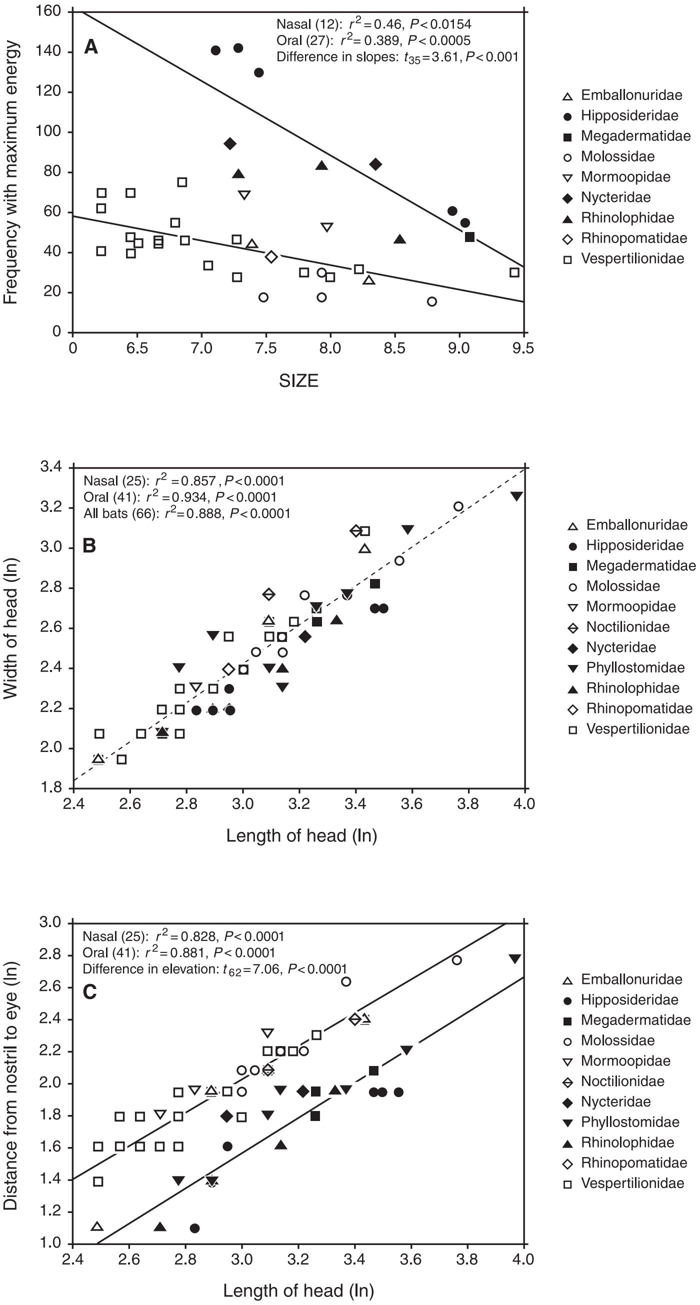

FIG. 2. Bivariate plots of echolocation frequency and morphological relationships between oral (open symbols) and nasal (filled symbols) emitting families of bats in our study. Sample size is in parenthesis. (A) Nasal emitters have a significantly higher frequency with maximum energy versus SIZE than oral emitters. (B) Oral emitting bats above the line have wider heads than nasal emitters for the same given length. The dashed regression line for all bats shows that three phyllostomids (*Sphaeronycteris toxophyllum*, *Centurio senex*, and *Phyllostomus hastatus* in order from left to right) have wider heads for their length than other nasal emitters. (C) Nasal emitting bats have a significantly shorter muzzle (distance from nostril to eye) than oral emitting bats for the same head length

free-standing pinna to the head and number of ridges on the pinna — show no correlation with frequency with maximum energy.

DISCUSSION

The relationship between frequency with maximum energy versus SIZE is such that nasal emitting bats have higher frequencies with maximum energy given their head volume (SIZE) than oral emitting bats (Fig. 2A). Although we followed Pedersen's (1993) description of emission sources for families, not all families or species of bats are easily placed into a category. Phyllostomids are generally accepted as nasal emitters, but *Desmodus rotundus* has been listed as an oral emitter (Schmidt, 1988). Some oral emitting bats, such as *Corynorhinus townsendii* and *Barbastella barbastellus*, have been shown to emit echolocation calls effectively through the nostrils (Griffin, 1958; Rydell and Bogdanowicz, 1997) while the nasal emitting bat, *Carollia perspicillata,* can emit echolocation calls orally (Griffin and Novick, 1955).

Frequency with maximum energy which occurs in the outward pulse of a call has been considered one of the most consistent echolocation call parameters and one of the most critical (Fullard *et al.*, 1991). Unfortunately, it is also one of the least reported parameters. However, frequency with maximum energy is qualitatively different in frequency modulated (FM) calls versus constant frequency (CF) calls. In the latter there is only pure tone (very narrow band of frequency also called constant frequency) and a resistance to time overlap in pulse and echo. There is a frequency for the outward pulse and an upward Doppler shift in that frequency in the returning echo. Doppler shifting can occur in CF/FM bats as well. This is not the case in FM calls, which have a broader band of frequencies and rely on time overlap of frequencies to distinguish pulse from echo (Fenton *et al.*, 1995). We do not have frequencies with maximum energy for phyllostomids or noctilionids from the literature (Table 1). Phyllostomids are low intensity callers and are difficult to record. Frequency with maximum energy has been shown to correspond with the frequency of best hearing in species with FM calls and CF/FM calls (Schnitzler and Henson, 1980; Neuweiler, 1984; Neuweiler *et al.*, 1984). Neuweiler *et al.* (1987) demonstrated that *Rhinolophus rouxi*, a bat that compensates for Doppler-shift, can alter the frequency with maximum energy. Differences between echolocation call parameters of nasal and oral emitting bats have not been thoroughly examined. Although nasal emitting bats have higher frequencies with maximum energy and generally higher spectral call parameters than oral emitting bats, different call types are used by both nasal and oral emitters. Constant frequency calls and CF/FM calls are widespread and show little taxonomic significance (Pye, 1973). Multiharmonic FM sweeps are used for nearly every microchiropteran diet, including insects, blood, vertebrate prey, nectar, pollen and fruit but not fish, and all frequency patterns are used to catch insects (Pye, 1980).

Mass is an especially important factor among flying animals. In bats overall body mass is negatively correlated with frequency parameters, both across and within families, so that smaller bats generally have higher frequency calls (Heller and Helversen, 1989; Jones and Rayner, 1991; Bogdanowicz *et al.*, 1999; Jones, 1999). No overall difference in body mass between oral and nasal emitters has been reported.

Our study confirms differences in head shapes and sizes as well as differences in frequencies with maximum energy between nasal and oral emitters. For bats studied here, nasal emitting species tend to have longer, narrower heads than oral emitters, although this trend does not include three phyllostomids (Fig. 2B). Fenton (1989) finds that among animal-eating bats in general, four nasal emitting families have proportionally longer heads than three oral emitting families. This is not true for the oral emitting molossids, with longer than expected heads, and the nasal emitting hipposiderids, with shorter than expected heads. Freeman (2000) suggests that within the morphospace of strictly insectivorous, non-phyllostomid families of bats the problem of durophagy (eating hard-shelled prey) has been solved in different ways by oral and nasal emitting bats. Nasal emitting bats that eat hard items have narrower, longer heads with vertically tall mandibular rami and tall sagittal crests while oral emitting bats have shorter, wider heads. However, the absolute shortest, widest skulls and the longest, narrowest skulls are found among the diverse phyllostomids (Freeman, 1998). Interestingly, phyllostomids, despite great morphological variation in trophic structure, all have similar echolocation calls (Gould, 1977; Belwood, 1988).

Further, we can confirm that nasal emitting bats have shorter muzzles relative to head length than oral emitting bats. This means a shorter portion of a longer head is occupied by the length from the eye to the nostril of nasal emitters (Fig. 2C). Freeman (2000) suggests that nasal emitters need a certain length of nasal capsule for a properly functioning emission of echolocation calls through the nose instead of through the mouth, but we cannot confirm that idea here.

The wide array of notable and bizarre facial features within Chiroptera has raised questions regarding their function in echolocation (Griffin, 1958). Our study found no significant correlations between facial features and the residuals from the frequency with maximum energy and skull size for each emission source. However, facial features such as noseleaves enable bats to send narrower bands of emissions while large pinnae enable bats to have better directionality of hearing than would be expected from such small emitting and receiving structures as is the case with bat heads (Au, 1993). One of the most obvious facial differences between nasal and oral emitters is that nasal emitters have some type of noseleaf. No study has quantified the difference between the function of a noseleaf and nostrils as opposed to the function of lips and mouth in echolocation emission. In phyllostomid bats, the noseleaf has a wide range of sizes, but there is correspondingly little variation in echolocation calls (Belwood, 1988; Bogdanowicz *et al.*, 1997). Within the Rhinolophidae and Hipposideridae, after controlling for size of bat, noseleaf width was found to be correlated with frequency of strongest amplitude (Robinson, 1996; see also Bogdanowicz, 1992).

Sounds returning to the bat are collected and funneled by the external pinnae (Au, 1993; Obrist, 1995). Obrist *et al.* (1993) found no significant correlations between pinnal measurements and echolocation parameters across families. Obligatory carnivorous bats, all nasal emitters, were found to have larger ear areas than oral emitting animalivorous bats (Freeman, 1984). Henson (1970), after reviewing several studies on the role of the pinnae in bats, concluded that the pinnae's main function was to increase the directionality of the sound reception system. The need for directionality of sound reception increases with increasing frequency (Obrist *et al.*, 1993). Ears set more caudally on the head and partially facing laterally (outward) aide in the collection of faint high or low frequency echoes (Fenton, 1984; Freeman, 1984; Bruns *et al.*, 1989; Obrist *et al.*, 1993). The ridges on the inner surface of the pinna are thought to reflect sound that then enters the ear canal after the original echo and could help the bat determine the vertical direction of the sound source (Lawrence and Simmons, 1982).

Numerous factors may interact with a mammal's echolocation system. For bats, some of these factors are: the characteristics of the auditory system, overall size, skull and tooth morphology, wing morphology and flight speed, foraging habitat, prey and prey availability, and facial morphology (Fenton, 1985; Aldridge and Rautenbach, 1987; Fullard *et al.*, 1991; Pedersen, 1993; Kalko, 1995; Bogdanowicz *et al.*, 1999; Jones, 1999).

There is considerable difference in frequencies of sound used by species of bats. There is a general relationship between size and frequency of sound and size of bat. However, the relationship between size and frequency is different for nasal and oral emitters. Finally, there is the obvious difference that nasal emitters have noseleaves and oral emitters do not. However, beyond these obvious relationships we can find no strong correlations between the facial features we measured and frequencies used for echolocation by bats. Although we found little evidence for form following function, this is potentially a rich area of research particularly with more sophisticated technology and quantification of echolocation strategies employed by bats.

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