A COMPARATIVE ANALYSIS OF PASSERINE MOBBING CALLS

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ABSTRACT.—We examined the acoustic structure of mobbing calls of 52 species of passerines representing an array of taxa. Marler suggested that calls given during mobbing have characteristics enhancing locatability that include abrupt onsets and a wide frequency range. Only about one-half of the species we studied produced calls during mobbing that had these characteristics. However, clicks (probably produced by bill snapping) sometimes were given during dives at predators. Vocalizations given during mobbing were quite diverse in acoustic structure. Two trends were noted: phylogenetic patterns; and possible convergence in certain species engaged in interspecific flocking. *Received 4 May 1995, accepted 7 September 1995.*

ATTENTION CONCERNING the evolution of avian vocalizations has focused on song (e.g. Kroodsma and Miller 1982). However, nonsong vocalizations may offer even better possibilities for understanding the evolution of acoustic structure. Marler (1957) pointed out that some avian vocalizations such as song showed marked specific distinctiveness, while others lacked these features and often were similar among unrelated species, indicating the influence of different selection pressures on diverse vocal categories. Marler (1955, 1957) and Marler and Hamilton (1966) pioneered studies of evolutionary forces shaping acoustic structure of avian calls, and it is surprising that little research has followed this lead.

Our comparative study focused on the acoustic structure of sounds given during mobbing. A variety of behavior patterns with different structures and functions may be elicited by predators, including distraction displays ("broken wing") near the nest or young, "distress" calls by captured individuals, and "alerting" calls when a predator is sighted. The term "alarm" is sometimes used in the literature, but its meaning is ambiguous and could include several categories of vocalizations. Klump and Shalter (1984), recognizing the need for distinguishing among categories of antipredator behavior, provided a comprehensive classification. The distinguishing feature of mobbing vocalizations is that they are given while approaching the predator, with the callers frequently changing positions (Klump and Shalter 1984). Proposed functions of mobbing are numerous (reviewed by Curio 1978), but the "move-on hypothesis," stressing the role of the

harassment in causing the predator to leave the vicinity, has a considerable amount of empirical support (Curio 1978, 1994).

In a seminal work, Marler (1955) demonstrated the antithetical acoustic structure of two types of vocalizations elicited by predators. Calls given when a hawk is flying overhead often are high pitched, cover a narrow frequency range, and lack abrupt onsets or terminations, while those given during mobbing cover a wide frequency range and show abrupt onsets. Calls in the first category may have features making them difficult to localize, while mobbing calls have features enhancing locatability (Marler 1955, 1959, Marler and Hamilton 1966), and may facilitate the recruitment of other individuals (Marler 1959). While few experimental studies demonstrate detectability of calls by the species emitting them, the "churr" mobbing call of the Great Tit (*Parus major*) has frequency characteristics within the best detectability range for the species and transmits over longer distances than the species' seeet calls given to a flying hawk (Klump and Shalter 1984). When birds mob a predator, they call and their actions often are very conspicuous, including approaching and retreating. If the main function of mobbing is to induce the predator to move on, the participation of numerous individuals engaged in harassing the predator would be advantageous. Sonograms of the mobbing calls of seven species of British passerines representing several different families are remarkably similar (Marler 1959:fig. 16), suggesting convergent evolution.

We examine both the structure of mobbing calls and a number of different hypotheses con-

cerning their evolution: (1) Do mobbing calls of passerines belonging to a wide variety of taxa confirm Marler's predictions of convergent acoustic structure in diverse taxa? Convergence would be indicated by abrupt onsets (clicklike patterns) and a wide frequency range (Marler 1959, Marler and Hamilton 1966). It is not clear whether these attributes must always co-occur for ease of localization. By definition, a click covers a wide frequency range and has a sharp onset, but a call could cover a wide frequency range and not be a click. In other words, some calls might have one feature that would supposedly enhance locatability, but not necessarily both. While mobbing calls are often clicks (Marler 1959), their most important feature is a wide frequency range, and the sounds of different species may show considerable variation in other attributes while exhibiting this salient feature (Marler and Hamilton 1966). We examine Marler's hypothesis not only by analysis of the characteristics of mobbing calls, but also by comparison of this category of calls with passerine nestling calls, where different selection pressures are presumably operating (Popp and Ficken 1991). (2) Are there also phylogenetic trends in the acoustic structure of the calls? Are these phylogenetic patterns superimposed on the predicted structural convergence due to selection for certain types of acoustic structure? (3) Does the acoustic structure of mobbing calls provide insights concerning the functions of mobbing? Features promoting locatability might support the move-on hypothesis, indicating the main function is recruitment of other individuals in harassing the predator. However, are additional selection pressures operating? (4) While call similarity among unrelated taxa could be due to natural selection favoring a narrow range of "best" acoustic design for mobbing effectiveness, could convergent evolution of calls of unrelated taxa in some cases be due to direct selection to facilitate interspecific communication?

We recorded calls in a variety of situations including natural mobbing of predators (and a few nest-hole competitors), presentation of owl mounts, and playbacks, as well as calls induced by our presence near nests. Recordings were made during both the breeding and nonbreeding seasons. We probably have not sampled the entire repertoire of mobbing calls from certain species, and different predators might elicit calls in some species that differ from those we re-

corded. The expectation is, however, that with a large and diverse assemblage of species sampled, trends will allow tentative conclusions. We hope that the findings will encourage further study of a complex phenomenon.

METHODS

We recorded birds at several sites, both during the breeding and nonbreeding seasons, and in response to a variety of stimuli (Table 1). In all cases, the birds' responses met our criterion of mobbing (i.e. an approach toward the stimulus, usually within about 10 m and often closer). In a few cases, especially with owl playback, several species participated in the same mobbing event. Individuals were not color-banded, but in many cases recordings were obtained from three or more individuals.

We used a Sony Professional Walkman cassette tape recorder and a Nakamichi directional microphone except for calls obtained at nests where a Realistic ultra-thin microphone was placed within 1 m of the nest. Sonograms were produced using a Kay Digital 7800 Sona-graph at the 150 Hz band width setting (to provide a compromise for temporal and frequency measurements). Measurements were made from sonograms using a ruler. We then obtained measurements of the following variables on five calls for each species and calculated mean values: (1) maximum frequency (kHz); (2) minimum frequency; (3) frequency range (maximum–minimum frequency); and (4) call durations (measurements given for individual units, although some were given in series of repetitions).

In addition to measurements, calls were categorized by their general configuration on sonograms, a reflection of both temporal and frequency aspects (Table 2). This analysis was done blindly, as the categorizer did not have information on the identity of the species. The categories are somewhat arbitrary, but supplement the data obtained from measurements in giving an overall view of what species share certain call similarities. The following categories were used: (I) *Thin vertical line.* These are very short-duration sounds covering a wide frequency range. Some sound like a click, others like a sharp chip. (II) *Thick vertical bar.* These calls are similar to the previous category, but are longer in duration and the quality differs. They often have a harsh sound and do not sound like clicks. (III) *Horizontal band.* These calls are longer in duration than those in the previous two categories. The frequency range varies. In some cases, only a single band is given, but in others, stacks of bands occur (i.e. Black-capped Chickadee). (IV) *Chevron.* Calls are usually of short duration and have a chevron shape, with an ascending frequency, a peak, and a descending frequency. (V) *Diverse group.* All of these calls are acoustically more complex than those in other categories, although they do not necessarily share common patterns.

TABLE 1. Characteristics of mobbing calls. For species with two kinds of calls, shorter call given first.

Species	Site[a]	Con-text[b]	Frequency (kHz)			Duration (s)
			Highest	Lowest	Range	
Tyrannidae						
Willow Flycatcher (*Empidonax traillii*)	W	HN	6.16	2.17	3.99	0.020
Say's Phoebe (*Sayornis saya*)	A	HN	5.35	2.15	3.20	1.092
Dusky-capped Flycatcher (*Myiarchus tuberculifer*)	A	PT	3.10	2.21	0.89	0.162
Ash-throated Flycatcher (*M. cinerascens*)	A	FT	5.10	2.70	2.40	0.073
Great Crested Flycatcher (*M. crinitus*)	W	CT	5.45	1.88	3.56	0.238
Sulphur-bellied Flycatcher (*Myiodynastes luteiventris*)	A	O[1]	6.85	1.91	4.94	0.008
			8.26	2.35	5.91	0.350
Eastern Kingbird (*Tyrannus tyrannus*)	W	HN	7.67	5.05	2.63	0.113
Hirundinidae						
Tree Swallow (*Tachycineta bicolor*)	W	HN	5.69	3.00	2.69	0.010
			5.44	3.58	1.86	0.133
Bank Swallow (*Riparia riparia*)	W	HN	7.97	0.24	7.73	0.008
			5.46	2.53	2.93	0.092
Barn Swallow (*Hirundo rustica*)	W	HN	5.92	3.97	1.95	0.170
Corvidae						
Steller's Jay (*Cyanocitta stelleri*)	A	O[2]	5.53	3.18	2.35	0.589
American Crow (*Corvus brachyrhynchos*)	W	O[3]	3.81	1.22	1.53	1.817
Paridae						
Black-capped Chickadee (*Parus atricapillus*)	A	CT	5.18	2.97	2.21	0.124
Mexican Chickadee (*P. sclateri*)	W	PT	7.66	3.34	4.33	0.008
Bridled Titmouse (*P. wollweberi*)	W	HN	7.08	2.59	4.49	0.028
Aegithalidae						
Bushtit (*Psaltriparus minimus*)	A	PT	7.53	4.92	2.61	0.081
Sittidae						
Red-breasted Nuthatch (*Sitta canadensis*)	A	PT	4.89	3.95	0.94	0.030
White-breasted Nuthatch (*S. carolinensis*)	A	PT	3.30	1.86	1.44	0.036
Pygmy Nuthatch (*S. pygmaea*)	A	PT	4.07	3.21	0.86	0.031
Certhiidae						
Brown Creeper (*Certhia americana*)	A	PT	8.06	6.97	1.09	0.143
Troglodytidae						
Bewick's Wren (*Thryomanes bewickii*)	A	HN	6.23	2.67	3.55	0.026
House Wren (*Troglodytes aedon*)	W	HN	6.89	3.30	3.58	0.023
Muscicapidae						
Golden-crowned Kinglet (*Regulus satrapa*)	A	PT	8.46	7.44	1.02	0.114
Ruby-crowned Kinglet (*R. calendula*)	A	PT	7.48	2.84	4.65	0.017
Eastern Bluebird (*Sialia sialis*)	W	HN	5.95	2.04	3.90	0.017
			3.02	2.38	0.65	0.120
Hermit Thrush (*Catharus guttatus*)	A	PT	4.58	2.03	2.55	0.029
			4.48	2.08	2.40	0.143
Wood Thrush (*Hylocichla mustelina*)	W	HN	6.03	2.69	3.34	0.016
American Robin (*Turdus migratorius*)	W	HN	3.55	1.43	2.12	0.060
Mimidae						
Gray Catbird (*Dumetella carolinensis*)	W	HN	3.12	1.24	1.88	0.029
			6.10	2.35	3.75	0.458
Brown Thrasher (*Toxostoma rufum*)	W	HN	7.45	3.22	4.23	0.048
Vireonidae						
Solitary Vireo (*Vireo solitarius*)	A	O[4]	5.93	2.58	3.35	0.159
Hutton's Vireo (*V. huttoni*)	A	O[4]	5.75	2.73	3.02	0.289
Warbling Vireo (*V. gilvus*)	—	O[5]	6.56	3.20	3.36	0.250
Red-eyed Vireo (*V. olivaceus*)	—	O[5]	5.06	2.55	2.51	0.218

TABLE 1. Continued.

| Species | Site[a] | Con-text[b] | Frequency (kHz) | | | Duration (s) |
			Highest	Lowest	Range	
Emberizidae						
Yellow Warbler (*Dendroica petechia*)	W	HN	7.39	3.74	3.64	0.016
Black-throated Gray Warbler (*D. nigrescens*)	A	PT	7.11	3.60	3.52	0.008
Grace's Warbler (*D. graciae*)	A	PT	7.05	3.97	3.08	0.008
American Redstart (*Setophaga ruticilla*)	W	HN	8.21	4.00	4.21	0.016
Common Yellowthroat (*Geothlypis trichas*)	W	HN	7.47	3.82	3.65	0.031
Red-faced Warbler (*Cardellina rubrifrons*)	A	PT	6.64	3.60	3.05	0.011
Painted Redstart (*Myioborus pictus*)	A	HN	6.28	2.88	3.40	0.248
Olive Warbler (*Peucedramus taeniatus*)	A	PT	3.66	2.77	0.89	0.114
Northern Cardinal (*Cardinalis cardinalis*)	W	HN	7.39	5.67	1.72	0.031
Indigo Bunting (*Passerina cyanea*)	W	GM	8.14	4.94	3.20	0.051
Chipping Sparrow (*Spizella passerina*)	W	HN	11.10	7.48	6.62	0.041
Field Sparrow (*S. pusilla*)	W	HN	12.28	5.06	7.21	0.056
Savannah Sparrow (*Passerculus sandwichensis*)	W	GM	7.99	4.50	3.50	0.008
Song Sparrow (*Melospiza melodia*)	W	HN	4.44	3.42	1.02	0.039
Yellow-eyed Junco (*Junco phaeonotus*)	A	PT	7.31	5.05	2.27	0.016
Red-winged Blackbird (*Agelaius phoeniceus*)	W	HN	5.37	2.63	2.74	0.023
Eastern Meadowlark (*Sturnella magna*)	W	GM	5.35	3.39	1.96	0.087
Common Grackle (*Quiscalus quiscula*)	W	HN	3.77	1.81	1.96	0.034

[a] (W) Wisconsin; (A) Arizona.

[b] (GM) Great Horned Owl (*Bubo virginianus*) plastic model; (PT) playback of Northern Pygmy-Owl (*Glaucidium gnoma*) calls; (FT) playback of Flammulated Owl (*Otis flammeolus*) calls; (CT) playback of Black-capped Chickadee mobbing calls; and (HN) human near nest with young. Other (O) contexts, which included interactions with: (1) Acorn Woodpeckers (*Melanerpes formicivorus*); (2) Cooper's Hawk (*Accipiter cooperi*); (3) Osprey (*Pandion haliaetus*); and (4) Gray-breasted Jays (*Aphelocoma ultramarina*) near nest; as well as (5) sonograms based on recordings from "A Field Guide to Bird Songs," Houghton Mifflin Co.

RESULTS

We examine our data in relation to the hypothesis stated earlier concerning the acoustic structure of avian mobbing calls. Sonograms are given in Figure 1. In some cases we include two calls for a single species when the sounds are quite different. The sample includes 52 passerine species: 7 suboscines (Tyrannidae); and 45 oscines from a variety of different families. The largest sample (18 species) is of members of the Emberizidae.

General acoustic patterns.—The sonograms (Fig. 1), call measurements (Table 1), and categorizations (Table 2) indicate considerable diversity of acoustic structure. Twenty-nine species or 55.8% of the total species ($n = 52$) have at least one mobbing call in their repertoire that falls into categories I and II (thin vertical lines and thick vertical bars). However, if clicks used in attack dives are excluded, only 48.1% of species are in these categories. Thus, about one-half the species do not give brief, wide-frequency-band calls in mobbing. Marler (1955) used the "chink" of the Chaffinch (*Fringilla coelebs*) as an exemplar of a mobbing call demonstrating features of lo-

catability. This call has a frequency range of about 3 kHz. Calls of the seven species in Marler (1959) are of short duration. Five species cover at least 7 kHz, with two covering a narrower frequency range of about 3 kHz. If we use 3 kHz as the minimum frequency range for a criterion of a wide frequency range, 21 of 29 calls (72.4%) in our categories I and II would be included.

The calls included in categories III, IV and V are even more diverse in acoustic structure than those in I and II. Of 29 calls in these categories, 8 (33.3%) covered a wide frequency range by our criterion. These calls usually lacked abrupt onsets.

Although Marler (1955) predicted a wide frequency range and short duration, no predictions were made about the absolute nature of highest or lowest frequency. However, a wide frequency range would lead to the expectation of a high maximum frequency and a relatively low minimum frequency. Considerable variation occurs in all aspects of frequency (Table 1). The maximum frequencies of the Field Sparrow and Chipping Sparrow are above 10 kHz, while those of most other species are much lower. The

TABLE 2. Categorization of mobbing calls. For species having more than one type of call, shorter call designated as 1 and longer as 2 (in parentheses).

I. Thin vertical line.—Eastern Bluebird (1), Tree Swallow (1), American Redstart, Yellow Warbler, Grace's Warbler, Sulphur-bellied Flycatcher (1), Red-faced Warbler, Black-throated Gray Warbler, Yellow-eyed Junco, Savannah Sparrow, Indigo Bunting, Bank Swallow (1)

II. Thick vertical bar.—Willow Flycatcher, Wood Thrush, Ruby-crowned Kinglet, Common Yellowthroat, Brown Thrasher, Red-winged Blackbird, Hermit Thrush (1), Bewick's Wren, Ash-throated Flycatcher, Common Grackle, Gray Catbird (1), Bridled Titmouse, Northern Cardinal, House Wren, Mexican Chickadee, Field Sparrow, Chipping Sparrow

III. Horizontal band.—Gray Catbird (2), Steller's Jay, American Crow, Warbling Vireo, Red-eyed Vireo, Hutton's Vireo, Solitary Vireo, Black-capped Chickadee, Olive Warbler, Eastern Bluebird (2)

IV. Chevron.—Song Sparrow, White-breasted Nuthatch, American Robin, Pygmy Nuthatch, Red-breasted Nuthatch, Dusky-capped Flycatcher

V. Diverse group.—All more complex than other groups: Bank Swallow (2), Eastern Meadowlark, Brown Creeper, Golden-crowned Kinglet, Tree Swallow (2), Eastern Kingbird, Barn Swallow, Painted Redstart, Great Crested Flycatcher, Say's Phoebe, Hermit Thrush (2), Bushtit, Sulphur-bellied Flycatcher (2)

lowest frequency also varies. Some sounds are extremely brief clicks, while others are very long (e.g. some corvids). However, duration and absolute-frequency parameters may not be as important for the postulated quality of locatability as the other qualities (i.e. rapidity of onset and frequency range).

Call repetitions.—Calls of some species usually occur in a series. These repetitive calls are shown as doublets in Figure 1, although they were parts of longer series. For example, Bridled Titmice produced strings of 20 or more note repetitions. Rapidly repeated calls tend to be of short duration, but some species such as wood-warblers that have short chips usually give only singlets.

Species with more than one type of mobbing call.— We undoubtedly did not sample the total mobbing-call repertoires of many of these species. Some species have more than one type of mobbing call. Sometimes the differences between calls are relatively minor (see dd and ee for Hermit Thrush in Fig. 1). In other cases, however, the differences are more dramatic (e.g. hh and ii for Gray Catbird). American Crows have a complex graded series of mobbing calls, var-

iants occurring in different contexts and presumably encoding somewhat different messages (Brown 1985).

Some species have both short clicklike sounds and longer calls. We were unable to determine the specific contexts of both calls in all cases, but a trend is clear. In all swallows studied, Sulphur-bellied Flycatchers, and Eastern Bluebirds, the click was given during a dive on the predator. The other calls of these species are not given in attack, but in approaches and harassment. For example M.S.F. observed several Purple Martins (*Progne subis*; no recordings obtained) approach a perched Sharp-shinned Hawk (*Accipiter striatus*). On initial approach, typical swallow "gurgling" sounds were made, but a click occurred in a dive on the hawk.

Phylogenetic trends.—The sonograms in Figure 1 are arranged according to families and are in *AOU Check-list* (1983) order. Here we produce an overall appraisal of the similarities and differences of certain groups. In some cases, a sufficient number of representatives from within a family is available for comparisons; in other cases, the number of species sampled is too small.

The only suboscines for which we had re-

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Fig. 1. Sonograms of mobbing calls: (a) Willow Flycatcher; (b) Say's Phoebe; (c) Dusky-capped Flycather; (d) Ash-throated Flycatcher; (e) Great Crested Flycatcher; (f and g) Sulphur-bellied Flycather; (h) Eastern Kingbird; (i and j) Tree Swallow; (k and l) Bank Swallow; (m) Barn Swallow; (n) Steller's Jay; (o) American Crow; (p) Black-capped Chickadee; (q) Mexican Chickadee; (r) Bridled Titmouch; (s) Bushtit; (t) Red-breasted Nuthatch; (u) White-breasted Nuthatch; (v) Pygmy Nuthatch; (w) Brown Creeper; (x) Bewick's Wren; (y) House Wren; (z) Golden-crowned Kinglet; (aa) Ruby-crowned Kinglet; (bb and cc) Eastern Bluebird; (dd and ee) Hermit Thrush; (ff) Wood Thrush; (gg) American Robin; (hh and ii) Gray Catbird; (jj) Brown Thrasher;
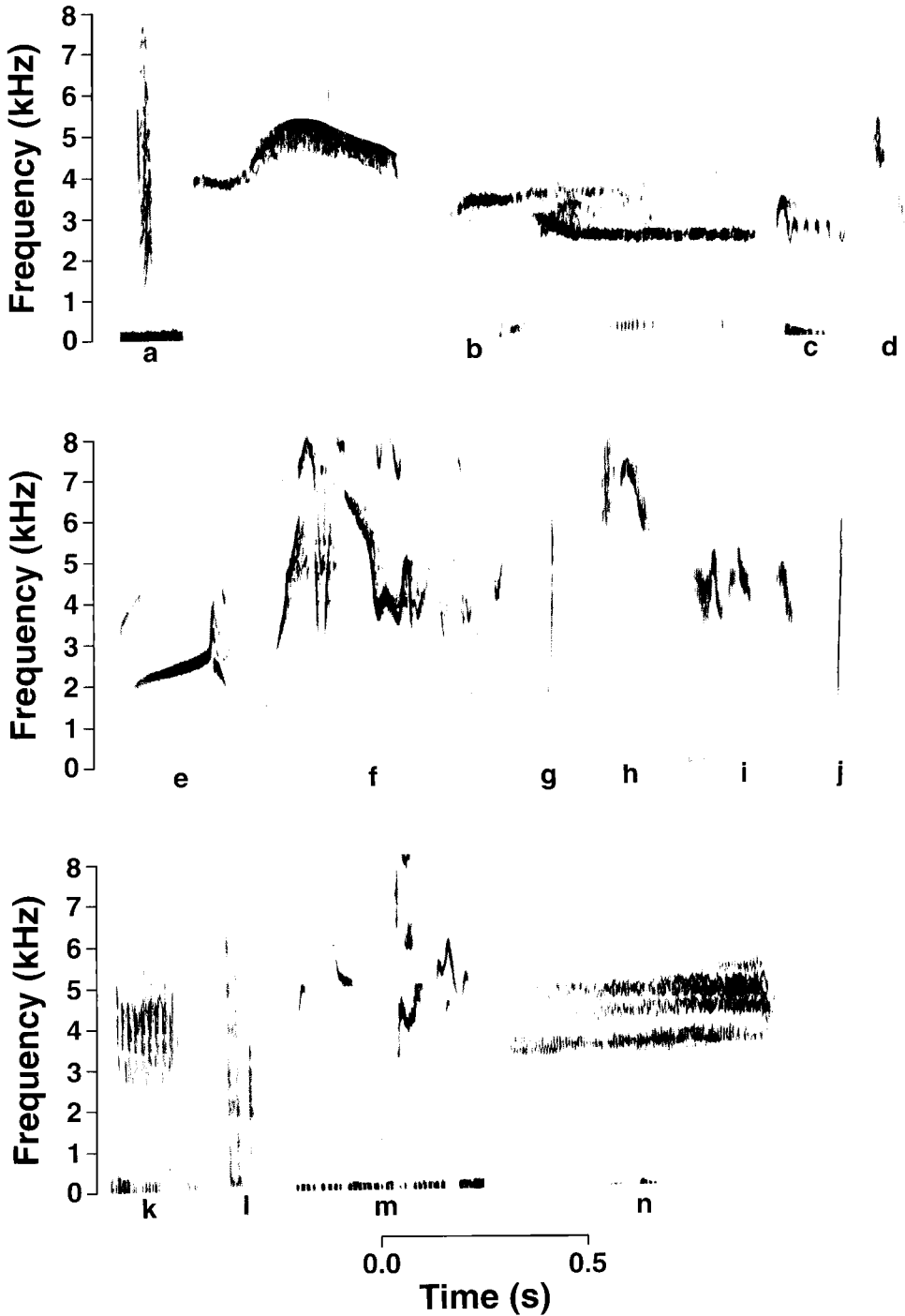
(kk) Solitary Vireo; (ll) Hutton's Vireo; (mm) Warbling Vireo; (nn) Red-eyed Vireo; (oo) Yellow Warbler; (pp) Black-throated Gray Warbler; (qq) Grace's Warbler; (rr) American Redstart; (ss) Common Yellowthroat; (tt) Red-faced Warbler; (uu) Painted Redstart; (vv) Olive Warbler; (ww) Northern Cardinal; (xx) Indigo Bunting; (yy) Chipping Sparrow; (zz) Field Sparrow; (A) Savanah Sparrow; (B) Song Sparrow; (C) Yellow-eyed Junco; (D) Red-winged Blackbird; (E) Eastern Meadowlark; (F) Common Grackle. A 0.0- to 0.5-s scale used for all calls, except for yy and zz, which have 0.00- to 0.25-s scale.
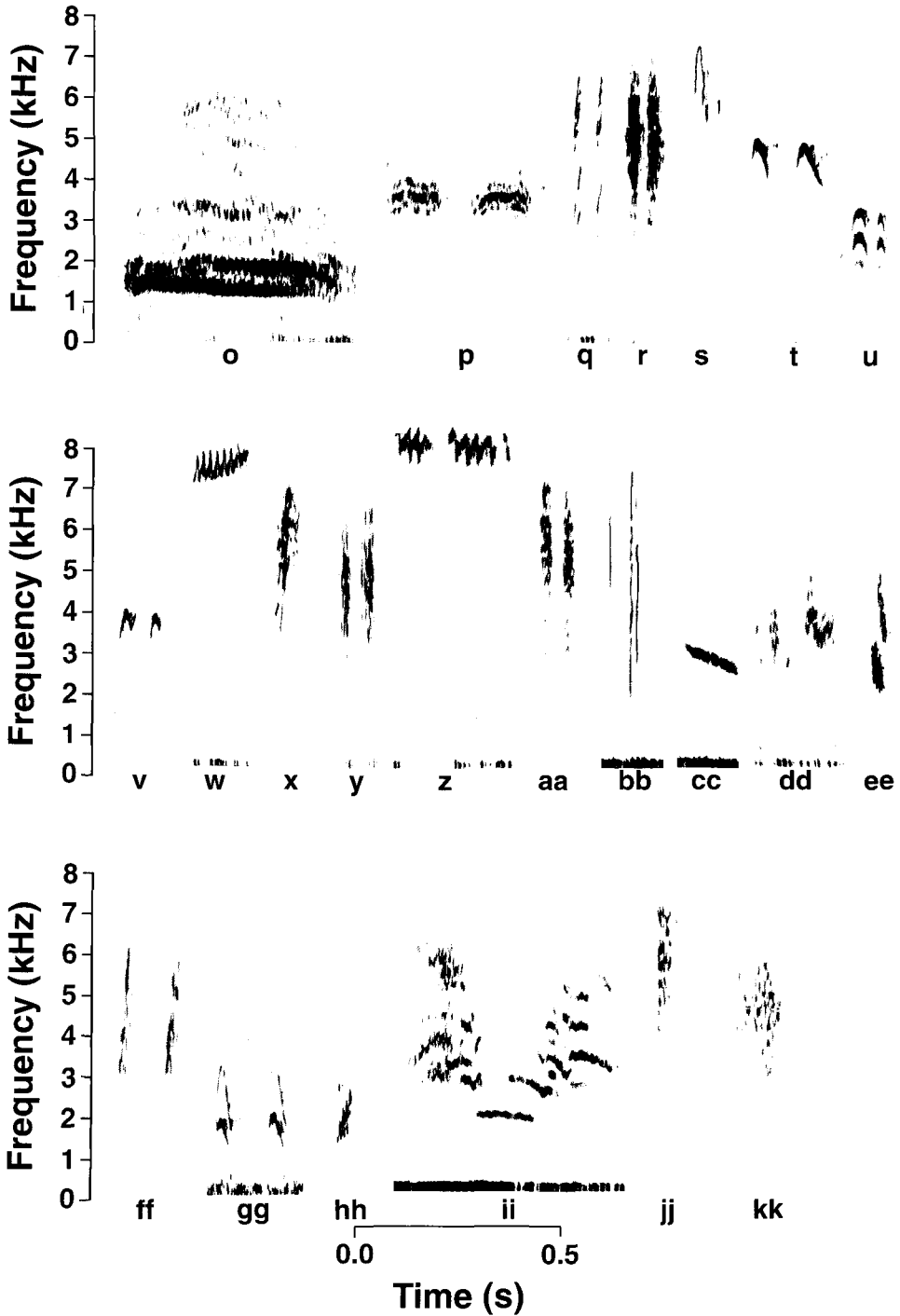
Fig. 1 (continued).

cordings were seven species of flycatchers. Considerable diversity occurs within members of the group. Calls of some species are acoustically simple; others (especially those of Sulphur-bel- lied Flycatcher and Say's Phoebe) are complex with notes of varied structures. The oscines show diversity as well, and similarities that are probably due to common ancestry are apparent only
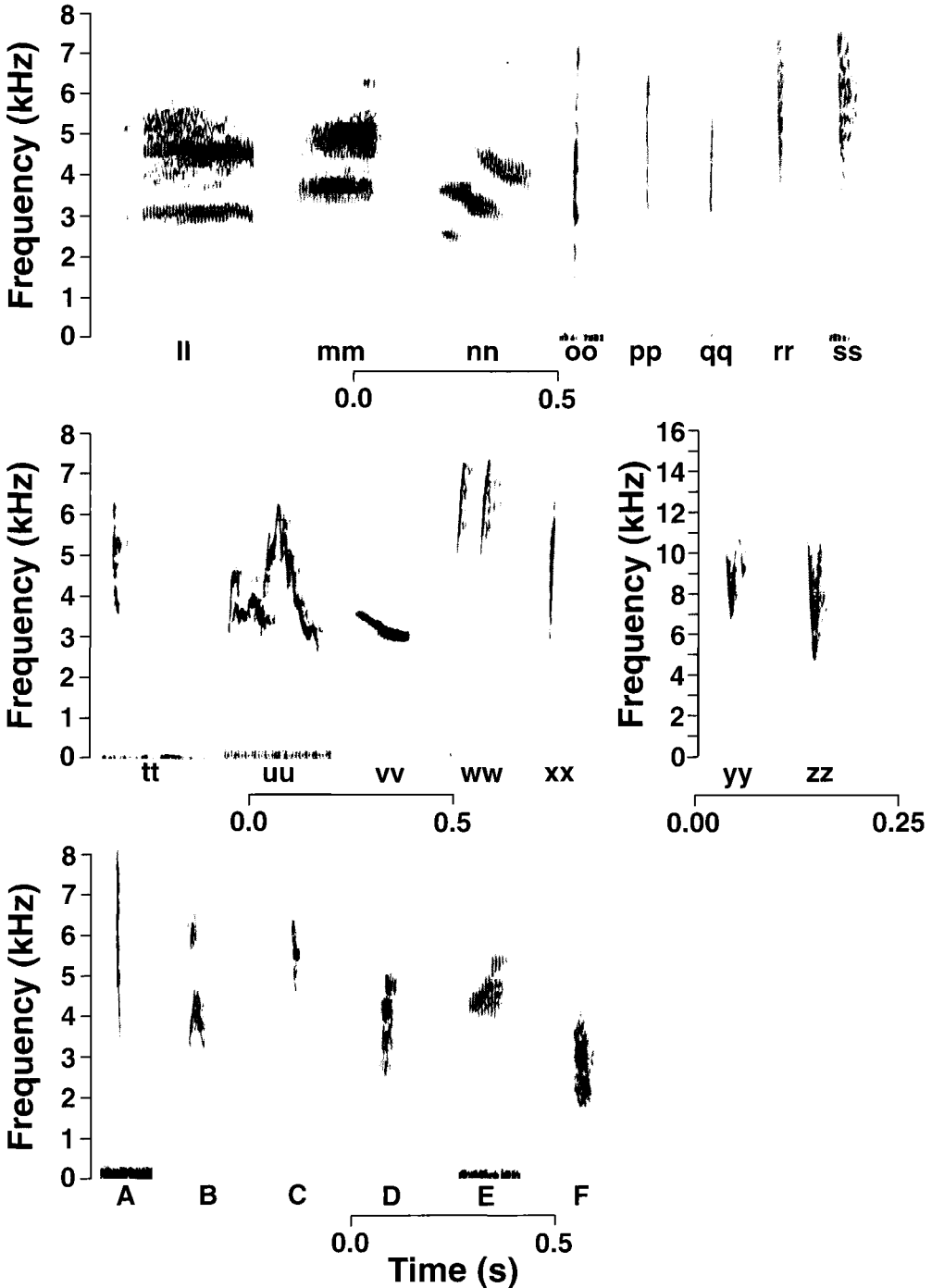
Fig. 1 (continued).

in certain groups. The two corvid species produce similar long-banded calls. The three nuthatches basically have chevron-shaped calls, with species differences in the details. Calls of four species of vireos were analyzed (two from recordings described as "scold" calls). Despite obvious species differences, calls of three species are very much alike, with the other species

(Solitary Vireo) showing some structural resemblance. All basically produce a harsh snarl.

The family for which we have the largest number of representatives is the Emberizidae. Formerly, this family was split into a number of different families, some of which are now relegated to subfamily status (AOU 1983). Most wood-warblers (Parulinae) and sparrows (Emberizinae) have mobbing calls that are very similar, typically a short chip covering a wide frequency range. Among the wood-warblers, however, two notable exceptions occur: the Painted Redstart, and the Olive Warbler. The Painted Redstart probably has closest affinities with Central and South American congeners (no other representatives in our sample). The call of the Olive Warbler is very different from that of other members of the Parulinae. In fact, a remarkable resemblance occurs between its call (Fig. 1w) and that of the Eastern Bluebird (Fig. 1bb). The resemblance is unlikely to be convergent because this kind of slurred whistle was not found in any other species sampled. The phylogenetic relationship of the Olive Warbler is uncertain, and its closest relatives may be the Muscicapidae to which bluebirds also belong, rather than the wood-warblers (AOU 1983). General similarities are shared among the other emberizids, except the buzzy call of the meadowlark is markedly different from the others.

A few groups are very heterogeneous. For example, the species of the Muscicapidae are very different from each other. The mobbing calls of the three parids are different despite the general acoustic similarity and apparent homologies of many calls within *Parus* (Hailman and Ficken in press).

DISCUSSION

Acoustic structure.—Acoustic structures of mobbing calls of different passerine species are diverse, contrary to predictions of convergent evolution. In this relatively large comparative study, we found that fewer than 50% of species' calls conformed to Marler's prediction of sharp onsets and wide frequency ranges. While some call convergence may occur, probably related to ease of locatability as postulated by Marler (1955), other selection pressures shape mobbing calls in some species. Phylogenetic constraints operate in some groups and, in the absence of selection for specific distinctiveness (Marler

1957), ancestral patterns may be retained. In special cases, selection for heterospecific communication in mixed-species flocks may lead to convergence.

Problems occur in a large-scale comparative approach such as ours. In most cases, the total acoustic repertoire for these species is unknown, and some calls may be nonspecific, occurring in a wide variety of situations. For example, the "tp" of the Eastern Phoebe (*Sayornis phoebe*) occurs in many situations including mobbing, and the "twh-t" is also given in mobbing and many other contexts characterized by indecisive behavior (Smith 1977). An interesting question would be whether trends in message specifications are different in flycatchers and oscines. Another unanswered question concerns whether special calls, not given in other contexts, occur in mobbing. For the wood-warblers, the same calls seem to occur in mild alarm and, therefore, are not specific to mobbing (M.S.F. pers. obs.). This trend may be true for other species. If many calls encode general messages, little interspecific call convergence would be expected, perhaps explaining our findings for only a slight trend for calls with abrupt onsets and wide frequency range.

Some of the species studied form mixed-species flocks. Possibly, some resemblances among distantly related species may be related to selection for interspecific communication as suggested by Moynihan (1962). For example, Brown Creepers and Golden-crowned Kinglets are frequent flock associates (M.S.F. pers. obs.) and give calls during mobbing that are strikingly similar. Convergence may result from selection for interspecific communication rather than for calls that are easily locatable. In fact, if flock associates are usually in close proximity during most activities, locatability would probably not be important. The unusual nature of the very-high-pitched buzzy calls of the Golden-crowned Kinglet and Brown Creeper supports the idea of call convergence related to mixed-species flocking. Perhaps the striking differences between the mobbing calls of the congeneric Ruby-crowned and Golden-crowned kinglets are due to selection for convergence with different flock associates.

Mobbing calls of the two species of chickadees for which we have information (Mexican and Black-capped chickadees) are quite different, probably due to a usage shift despite the

overall similarity of the repertoires of the two species. During close approaches to a potential predator, Black-capped Chickadees usually give Chick-a-dee calls consisting of strings of *D* notes, sometimes but not always, preceded by introductory notes (*A, B,* or *C;* see Hailman et al. 1985). However, Mexican Chickadees give strings of *C* notes when actually harassing the predator, the *A* and *D* notes and combinations thereof being used more often during the initial approach (Ficken et al. 1994). Both chickadees have *A, B, C,* and *D* note types that seem homologous (the *B* is very rare in Mexican Chickadee), but usage differs and the calls given during the closest approach to a predator are different in the two congeners.

Function.—In some cases two types of sounds are given, with a click occurring during a dive, while a totally different sound is made during approach and mobbing while perched. The two sounds probably have very different functions and are directed at a different set of individuals. The calls given on approach may be directed at conspecifics, or even heterospecifics in cases of mixed flocks, and aid in recruitment of others. In contrast, the click is probably directed at the predator rather than a conspecific, and may have an acoustic design that startles and possibly distracts the predator. Both types of calls could induce predators to leave the vicinity (supporting the move-on hypothesis of mobbing), one through recruitment and subsequent harassment, and the other due to an attack. As Leger and Carroll (1981) pointed out the "smooth upswept vocalization" given in dives by the Phainopepla (*Phainopepla nitens*) is very unlike the harsh repetitive mobbing calls of many species, but attack calls would not be expected to possess features that aid in localization.

In contrast to other sounds made during mobbing, clicks seem to be nonvocal and probably produced by mandible snapping. These snaps or clicks are made only by a few species. All the species noted clicking feed on flying insects, and such mandible snapping is probably a common part of their prey-capture behavior that has become ritualized as attack behavior. Perhaps other species, lacking the preadaptation of this feeding response were unable to evolve similar sounds.

Comparison with nestling calls.—In addition to assessing similarities and differences among mobbing calls of diverse taxa, another approach to the problem of whether convergent evolution is occurring in mobbing calls is to compare them with the results of a comparative study of nestling calls. Contrary to expectations, calls of nestlings were not related to obvious features, such as open versus cavity nesting, or locatability (Popp and Ficken 1991). Rather, phylogenetic constraints were of major importance, as well as the relationship of nestling calls as precursors of some fledgling and adult calls. A comparison of the sonograms of nesting calls of 71 species of passerines with our sample of mobbing calls indicates greater diversity in acoustic structure of nestling calls. Nestling calls included the following categories: repeated, tonal, complex, multiple banded, arched and noisy. This classification was not appropriate for mobbing calls, many of which have sharp onsets and cover a wide frequency range. These findings suggest some convergence due to selection for locatability in mobbing calls, but not nestling calls.

General conclusions.—Our findings lend only weak support to the suggestion (Marler 1959, Marler and Hamilton 1966) that mobbing calls have acoustic design features for ease of location that include abrupt onsets and wide frequency bands. Support for Marler's view comes from analysis of experimental results showing that broad-band signals are more easily locatable than narrow band signals (Klump and Shalter 1984). However, our results indicate that selection pressures other than locatability may be operative.

Despite some of the obvious sources of error in a broad study of mobbing calls such as ours, the general validity of the comparative approach is substantiated. Examination of a diverse assemblage of both closely and distantly related species helps provide insights concerning the selective pressures shaping call structure. Also needed are intensive repertoire analyses of single species; such studies would allow analysis of the fine-grained aspects of message categorizations in antipredator calls.

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