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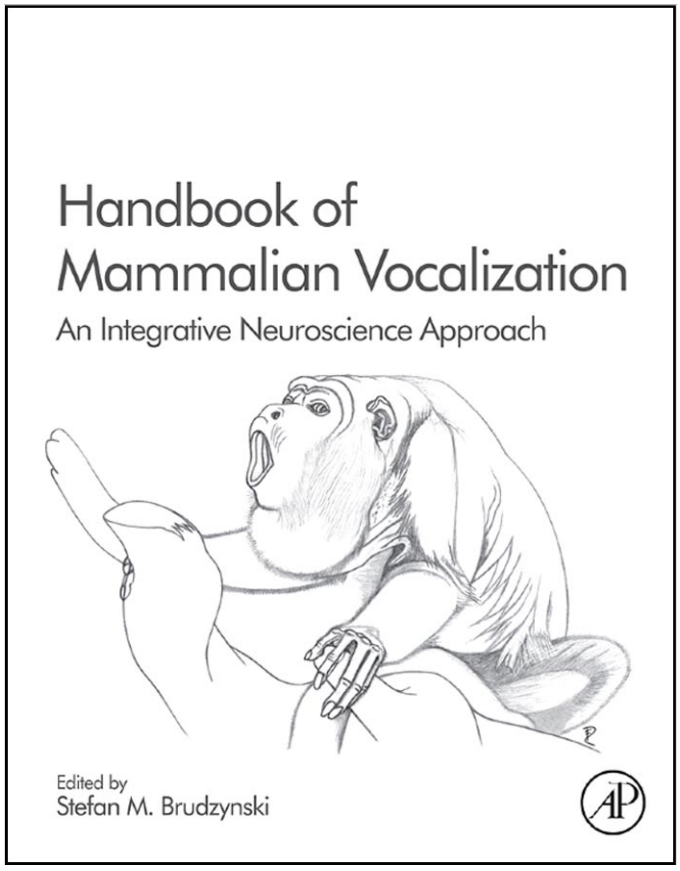

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CHAPTER 11.4

Recognition of individuals within the social group: signature vocalizations

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Abstract: Signature vocalizations contain sufficiently unique spectral and/or temporal identity to allow conspecifics to differentiate between individuals. Experimental assessment of signature content relies on: (1) accurate discrimination of vocalizations according to individual callers using human observers and statistical methods; (2) playback experiments with conspecifics in captivity or in the wild. Signature vocalizations are often acquired through social and vocal learning. Functions for such signals include individual recognition (e.g., between parents and offspring, mating pairs, territorial rivals) and the mediation of social interactions. Signature cues are likely to be subtle, and their analysis is likely to benefit from the use of new data collection technologies and human speech recognition techniques.

Keywords: signature vocalizations; vocal learning; signature whistles; playback experiments; individual recognition; playback

I. Introduction

Animals can use a variety of sensory modalities, including visual, olfactory and auditory cues, to communicate information about individual identity. These signals contain signature content when their inter-individual variability exceeds their intra-individual variability. Olfactory signals often require conspecifics to approach the site where a scent is left and they tend to be carried by wind or air currents. Visual signals can be obscured by physical obstacles or darkness and can be attenuated in marine habitats. Acoustic methods of encoding individual identity, however, do not have these disadvantages and offer animals the opportunity to communicate rapidly and coordinate behavior and interaction over a range of distances. Such individually-distinctive signals are called signature vocalizations. Certain animals incorporate additional spectral or temporal cues into their calls to supply sufficient acoustic variation to allow differentiation between individuals.

This chapter is divided into three main sections. The first section will focus on what constitutes a signature vocalization; namely, the different acoustic features that might endow a signal with signature information, how these signals are defined experimentally and how they are acquired by an animal and subsequently developed. The second part is concerned with the functional aspects of signature signals and how the consequence of individual recognition may impact both affiliative and aversive social interactions. Finally, recommendations for future research are offered.

II. What is a signature vocalization?

II.A. Features that embed signature content

Two general sets of acoustic properties might be used by an animal to encode signature information. Firstly, spectral features can differ between individuals, including such basic features as a call's fundamental frequency and harmonics. A variety of species of birds and mammals produce contact calls that can be differentiated spectrally, including pairs of orange-fronted parakeets (*Aratinga canicularis*) from the Guanacaste province of Costa Rica (Fig. 1a) (Cortopassi and Bradbury, 2000) and mother–pup pairs of South American fur seals

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(*Arctocephalus australis*, Phillips and Stirling, 2000), Galapagos fur seals (*Arctocephalus galapagoensis*) and Galapagos sea lions (*Zalophus californianus wollebaeki*, Trillmich, 1981). Features of spectral variability, such as relative harmonic energies and the mean, modulation and sonographic shape of the fundamental frequency, are used in different combinations by individuals of numerous species to encode

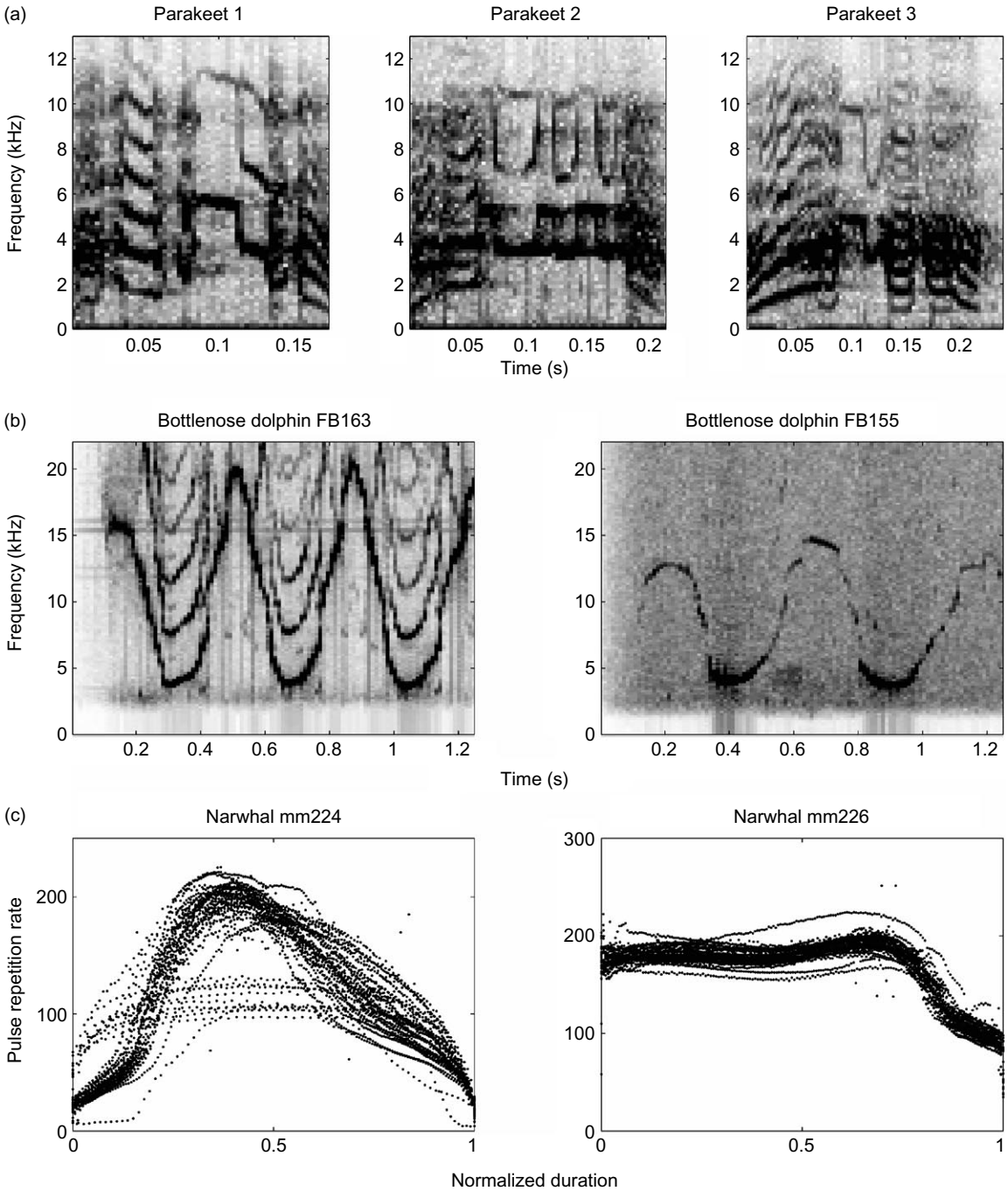

Fig. 1. Examples of signature vocalizations. (a) Orange-fronted parakeet contact calls, courtesy of J.W. Bradbury. Each subplot corresponds to a different individual (labeled 1–3 here). (b) Signature whistles of female bottlenose dolphin individuals FB163 and FB5, courtesy of L.S. Sayigh. (c) Pulse repetition rates of combined tonal/pulsed signals for individual narwhals mm224 and mm226, respectively, reprinted courtesy of the Journal of the Acoustical Society of America.

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signature information (e.g., squeaks of adult timber wolves (*Canis lupus*, Goldman et al., 1995); calls of subantarctic fur seal pups (*Arctocephalus tropicalis*, Charrier et al., 2002); signature whistles of bottlenose dolphins (Fig. 1b) (*Tursiops truncatus*, Caldwell and Caldwell, 1965; Janik et al., 2006)).

Secondly, temporal elements can contain signature information. For example, the sonar signals of big brown bats (*Eptesicus fuscus*) and the isolation calls of pallid bats (*Antrozous pallidus*) showed individual differences in the duration and temporal arrangement of certain frequency elements, respectively (Masters et al., 1995; Brown, 1976). In another example, the relative timing and repetition rate of the pulses of combined tonal/pulsed signals of two Arctic narwhals (*Monodon monoceros*) off Baffin Island, Canada, showed individual variation suitable for individual signatures (Fig. 1c) (Shapiro, 2006).

II.B. Experimental determination of signature vocalizations

Two general stages are commonly followed to demonstrate that a particular signal constitutes a signature vocalization. Because it is often straightforward to identify vocalizations of individual animals in captivity, the first step of recordings often occurs in the laboratory. Once the individual recordings are acquired, it is necessary to determine whether there is a sufficient combination of inter-individual variability and intra-individual consistency to sort the signals according to the individual animals that produced them. One common approach is to ask a group of naïve human observers to categorize a set of signals, usually by sorting spectrograms visually into different classes (e.g., Janik, 1999). This technique is straightforward and useful as a first approach, since human classifiers have good skills in matching patterns and evaluating signals in a general way. These results can indicate whether more advanced analyses are likely to be fruitful. However, the use of human subjects can be time-consuming and may not reveal the precise acoustic features used to discriminate individuals.

Several analytical approaches have been developed, most of which require extracting a set of temporal and spectral features from all or part of the signal to classify the calls. Such approaches tend to require an *a priori* assessment of which characteristics to compare across a set of signals. Tonal signals are often represented as contour traces to facilitate comparison. It is straightforward to measure such parameters as a contour's initial, final, mean, minimum and maximum frequencies, temporal duration and the degree of its frequency modulation. In addition, the relative energies between different harmonics can be determined from the original recording. A signal composed of discrete pulses might be characterized by its duration, number of pulses and average inter-pulse interval (or, inversely, the pulse repetition rate). Once these features have been extracted from vocalizations produced by known individuals, statistical methods can be used to assess the significance of inter-individual differences (Falls, 1982; Sokal and Rohlf, 1995).

The coefficient of variation (i.e., the ratio between the standard deviation and the mean) of each feature is often also computed. Its value should be greater between than within individuals if the selected vocalizations are to qualify as potential signature signals (Lengagne, 2001; Charrier et al., 2002). Discriminant function analysis (Jones et al., 1993) and principal coordinates analysis (Cortopassi and Bradbury, 2000) have also been successfully applied to differentiate among the signals produced by multiple individuals. Other, nonparametric approaches can also be useful. For example, Shapiro (2006) applied a modified cross-correlation metric to compare the whistles produced by two narwhals.

The second essential step is a playback experiment to test whether conspecifics can discern between vocalizations produced by different individuals. Once demonstrated, the manipulation or removal of certain acoustic features in a playback can then indicate which parameters in the signal contain the relevant signature information for other conspecifics. For example, Charrier et al. (2001) used playback experiments to demonstrate that subantarctic fur seal pups on Amsterdam Island in the Indian Ocean responded to the calls of any female a few hours after birth. Within 2–5 days, however, this response became specific only to the vocalizations of their own mother. The pups stopped responding to other similarly-aged, possibly familiar reproductive females from the same study colony (Charrier, personal communication). Subsequent experimental manipulations of the maternal vocal signals showed that the pups relied on the harmonic structure and the initial ascending frequency modulation to recognize their mothers, but did not use amplitude modulation (Charrier et al., 2003). Charrier et al. (2002) also studied the question from the mothers' perspective and found that mothers used the fundamental frequency and the next two harmonics of their pup calls to recognize the pup successfully.

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Similar results confirming individual discrimination based on signature vocalizations were obtained from bottlenose dolphins (Sayigh et al., 1998, discussed in greater detail below). Results of these studies go beyond the recognition of familiar or unfamiliar signals (e.g., Bee and Gerhardt, 2002) which can arise from simple habituation. Instead, they provide evidence for individual recognition capabilities among conspecifics, a demanding discrimination task.

II.C. Ontogeny of signature vocalizations

The development and acquisition of a signature vocalization can reveal how animals learn and at least some of the salient features of an animal's acoustic and/or social environment. Numerous terrestrial mammals can distinguish among vocalizations of individuals because of the unique physical differences characterizing their vocal tracts (see Tyack, 2000; and also Frey and Gebler, Chapter 10.3 in this volume). Such morphological differences represent inherited physical features, which cannot be learned. They likely account for certain aspects of the individually characteristic signals in some species. Often, however, animals can control the articulation and modulation of these signals to further modify certain acoustic features.

In a variety of species, animals acquire signature vocalizations through learning. Although physical constraints limit the temporal and spectral space in which the signature vocalization can be generated, learning allows an animal to differentiate and mimic species-specific acoustic patterns that it perceives in its environment. Vocal learning, a form of production learning in which signals are rendered more or less similar to those produced by other conspecific, heterospecific or synthetic sound models (Janik and Slater, 1997, 2000), can explain the ontogeny of a signature vocalization. Bottlenose dolphins provide an example. Early observations suggested that bottlenose dolphins produce signature whistles (Caldwell and Caldwell, 1965) and that the structure of these whistles may be influenced by their acoustic environment. Tyack (1986) reported that two captive animals produced their own signature whistles most of the time and sometimes produced the whistle of the other companion dolphin, suggesting that they could mimic one another. Demonstrations of vocal imitation in bottlenose dolphins (Richards et al., 1984) and observations of matching artificial flat tone whistles (Miksis et al., 2002) support the conclusion that these animals are capable of vocal learning. The studies on signature whistle ontogeny collectively reinforce the notion that bottlenose dolphins use vocal learning to imitate or sometimes eschew an acoustic model.

In some situations, an individual animal learns from itself. Human beings (*Homo sapiens*) are the most striking mammalian example of this phenomenon and show numerous parallels with vocal development among songbirds (Doupe and Kuhl, 1999). These similarities include learning difficult vocalizations early in life, using specialized brain structures to help integrate motor and auditory processes, possessing intrinsic perception and learning mechanisms, relying on acoustic models, and practicing through listening to themselves (i.e., auditory feedback).

III. Functional aspects of signature vocalizations

It is important to address the various functions of signature vocalizations to understand how these signals operate in both captive and natural settings.

III.A. Parent–offspring recognition

Recognition between parents and offspring is one of the primary functions of some signature vocalizations (Falls, 1982). It appears to drive signature vocalizations in numerous gregarious species of birds and mammals. Most studies on this topic have been conducted on bird species. As the signature vocalizations in birds are likely similar to those in mammals, a broad comparative perspective is useful. Colonial species generally encounter selective pressure for parents and offspring to recognize one another in a flurry of other individuals, a situation that is important but less confusing among non-colonial species. In birds, swallows demonstrate parent–offspring recognition convincingly. Parents and young of colonial species such as bank (*Riparia riparia*) and cliff swallows (*Hirundo pyrrhonota*) both produce and recognize signature vocalizations (Beecher et al., 1981, 1985; Sieber, 1985; Stoddard and Beecher, 1983), which ensures parental care is directed toward the correct offspring. In addition, some bat species live in very large colonies where recognition of individuals within the social group, particularly infants, is vital for their survival (Boughman, 1997; Bohn et al., 2007; Kazial et al., 2008). On the other hand, among non-colonial barn (*Hirundo rustica*) and tree swallows (*Tachycineta bicolor*) and solitary rough-winged

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swallows (*Stelgidopteryx ruficollis*), recognition between parents and offspring is weaker or absent altogether (Beecher, 1981; Medvin and Beecher, 1986; Leonard et al., 1997). In these non-colonial species, parents and offspring can locate one another more easily using location cues, since fewer conspecifics are nearby.

As expected, parent–offspring vocal recognition is common among colonial penguin species. The complexity of their signature vocalizations varies, however, according to whether the penguins do or do not build nests. Since nests provide a helpful visual landmark for individuals attempting to locate one another, the signature content of parental calls of certain nest-building species tends to be simpler. For example, Adélie (*Pygoscelis adeliae*) and gentoo (*P. papua*) penguins rely primarily on the basic feature of pitch of the vocalization to distinguish individuals (Jouventin and Aubin, 2002). In contrast, non-nest-building species such as king and emperor penguins must rely more heavily on acoustic discrimination and their resulting two-voice signature systems are more complex (Robisson, 1990; Jouventin et al., 1999; Aubin et al., 2000; Lengagne et al., 2000, 2001).

Although learning can require a long period of time, sometimes the survival needs can facilitate a quick and early learning. For example, as described above, fur seal pups learn to recognize their mothers' voices within 2–5 days after birth (Charrier et al., 2001). The reason for this early and fast learning is related to the fact that fur seal mothers must go to sea to feed and to build sufficient nutrient reserves for lactation while their newborn pups remain ashore. Because the mother must reunite with her pup once she returns to land, the two animals need to recognize each other in a crowd of conspecifics. The situation leads to both the pup and the mother acquiring vocal signatures (Charrier et al., 2002, 2003). The timing of this recognition always occurs before the mother's departure (2–10 days following birth). The importance of such recognition is evidenced by the fairly widespread synchrony between when parents and offspring first separate and the development of the capacity to recognize one another (Falls, 1982).

III.B. Individual recognition among adults

Within the context of acoustic communication, Falls (1982) pointed out that individual variation, or the differences in the vocal signals between individuals, form a precondition for individual recognition by using these acoustic cues to discriminate between conspecifics. Such recognition can arise in both affiliative and aversive (e.g., aggressive) situations.

Mate recognition is one of the contexts in which animals need to identify each other reliably, a scenario that can benefit from employing signature vocalizations. Mated pairs of colonial seabird species, for example, can encounter the same difficulties of locating one another in large, noisy colonies as the parents and offspring of the species described earlier. For instance, Manx shearwaters (*Puffinus puffinus*) entered their burrows at night when visual landmarks were less helpful. Males arrived at a burrow first and responded generically to the sounds of any vocalizing females that arrived later in the season. Playback experiments demonstrated that the female was the member of the pair bond that discriminated among the male calls to locate her mate and the appropriate burrow (Brooke, 1978).

Vocalizations are used by some mammalian species for advertising and maintaining their territories (e.g., in elephants, see Garstang, Chapter 3.2 in this volume). Among certain species of songbirds, males also sing to each other to maintain and defend their territories. These contexts serve an aggressive function. The responses to an intruding male with unfamiliar song may result from a simple discrimination between known neighbors and unknown strangers (e.g., indigo buntings (*Passerina cyanea*), Emlen, 1971; little owls (*Athene noctua*), Hardouin et al., 2006), a dichotomous classification system that does not demand individual recognition. Sometimes, however, individuals respond vocally (i.e., aggressively) to the song of a familiar neighbor if that song originates from a different and unexpected location (e.g., white-throated sparrows (*Zonotrichia albicollis*) (Falls and Brooks, 1975); hooded (*Wilsonia citrina*) and Kentucky warblers (*Oporornis formosus*) (Godard and Wiley, 1995). This suggests that for some species, birds are not simply habituating to the songs produced repeatedly by their neighbors. Rather, they might be recognizing conspecifics insofar as they associate particular songs with specific individuals whose geographical distribution generally remains fixed. More work is required to rigorously demonstrate individual recognition, but such a scenario would help these animals conserve their energy resources by targeting their vocal behavior at, and establishing their territories in response to, intruders or new arrivals in specific defensive contexts.

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III.C. Mediating social interactions

Signature vocalizations can greatly facilitate social interactions between animals where individual-specific relationships (evidenced by distinctive behavioral responses to different conspecifics) are important. Bottlenose dolphins provide a useful case study in this regard, since their social and vocal behavior has been studied extensively in both the laboratory and the wild. Their social structure is characterized by a fission–fusion dynamic, a situation in which animals fluidly and repeatedly associate with, separate from, and rejoin one another (Wells et al., 1987). This fluidity of social structure, coupled with individual-specific relationships in which dolphins treat different animals as distinct entities, provides a scenario for which their individually characteristic signature whistles are well-suited (Tyack and Sayigh, 1997).

In Sarasota, Florida, temporarily restrained mother bottlenose dolphins and their independent offspring responded more strongly to one another's signature whistles than to those of other individuals of the same age (Sayigh et al., 1998). The results of this work demonstrate that signature whistles are likely used for individual recognition and they might play a role in reuniting mothers with their calves when they separate from one another. Similarly, free-ranging adult, allied male dolphins produced their signature whistles most frequently when they separated voluntarily from their partners and least frequently when they were swimming together (Watwood et al., 2005). In addition, temporarily restrained allied males that were separated involuntarily from one another produced more signature whistles than during periods when they were swimming freely (Watwood et al., 2005). These findings suggest that allied male dolphins, while separated, might also use signature whistles as contact calls to help them find one another and stay in contact.

In addition to the vocal learning described above, bottlenose dolphins are capable of vocal labeling (Richards et al., 1984) in which a vocalization is used to identify an object or individual acoustically. This has particularly interesting implications when animals become separated. Janik and Slater (1998) studied the social context of whistle usage of a group of four bottlenose dolphins (including one juvenile, one sub-adult and two adult animals) at a captive facility consisting of two connected pools of unequal size. Whenever an individual voluntarily left the group by swimming to the smaller pool apart from the remaining animals, it produced its signature whistle at a much higher rate than when all four dolphins swam together in the main pool. These results suggested that the animals were using their signature whistles to facilitate group cohesion (Janik and Slater, 1998). Because group composition is likely to change in the wild, a common group call would be insufficient to maintain this cohesion. Rather, given the vocal mimicry abilities of these animals (see Richards et al., 1984; Tyack, 1986; Miksis et al., 2002), they could accommodate an individual arriving at, or departing from, the group by simply learning its signature whistle. Taken together, these studies provide evidence that bottlenose dolphins (at least in captivity) produce their own signature whistles in certain contexts but are also capable of copying the signature whistles of their companions in other situations.

An example of such whistle copying may have been observed in the Moray Firth, Scotland, where whistles were localized to the free-ranging bottlenose dolphins (Janik, 2000). For each pair of consecutive whistles, both the distance between their localized origins and the inter-whistle time interval were computed. If a dolphin could not have traveled this distance within the calculated time interval when swimming at its maximum speed, the two whistles were considered to have been produced by different individuals. Among 176 such whistle interactions between dolphins, 39 (22%) involved matched exchanges of the same whistle between different individuals separated by up to 579 m ($\bar{x}$ = 179 m). These matched interactions may have functioned as a mechanism for animals to address one another, indicate alliance membership, or coordinate interactions over large distances (Janik, 2000). This may have been a demonstration of signature whistles being produced and then copied, although additional work on identifying the whistler and the social and behavioral context is required.

In summary, bottlenose dolphin fission–fusion social structure is characterized by individual specific social relationships that benefit from an ability to detect and recognize individuals by their signature whistles. The production of these individually specific vocal signals is not uncommon among other species that share a similarly fluid social dynamic in environments that are at least occasionally visually occluded. Furthermore, signature vocalizations often accompany situations where: (1) individual contact between animals is biologically important (e.g., parents and offspring, mated pairs, social allies, or aggressors); and (2) separation due to visual barriers or confusion among numerous conspecifics is present.

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IV. Future directions

A couple of areas of research related to signature vocalizations stand out as especially promising for future work.

The signature vocalizations described in this chapter often differ from one another in a somewhat obvious manner. However, it is likely that animals are capable of distinguishing each other using far more subtle acoustic cues than those we have described. Only recently, for example, the stereotyped calls of resident, fish-eating killer whales (*Orcinus orca*) off the coast of Vancouver Island, Canada, were shown to contain sex-specific spectral features relating to the relative energy levels of different harmonics (Miller et al., 2007). A towed hydrophone array (Miller and Tyack, 1998) allowed the determination of which killer whale was vocalizing, a technical advancement that greatly facilitated the collection of the data. Data collection technologies, which also include digital archival tags (e.g., Johnson and Tyack, 2003) and both terrestrial and marine recorder arrays (e.g., Miller et al., 2004; Mennill and Vehrencamp, 2008), will improve the reliability of assigning vocalization sequences to the individuals producing them. The application of these technologies towards deepening our understanding of how and why individual animals produce and use signature vocalizations in the wild should be encouraged.

A second area for future work should involve investigation of the detailed acoustic features that animals are using to identify one another. Animals use a rich array of feature detectors to detect signals buried in background noise. This problem is especially important in colonial situations, in which, with the increasing number of individuals, the noise generally occupies a nearly identical temporal and spectral bandwidth as the signal being sought. However, even young animals overcome the masking easily and probably rely on subtle features to make the discrimination possible. In addition, many terrestrial species rely on the morphological differences of the vocal tract and/or vocal production organ to differentiate between speakers (see Tyack, 2000). This has been harder to assess for marine mammals. All of the members of a killer whale acoustic clan, for example, produce a common set of stereotyped vocalizations that are difficult for humans to discriminate.

It is possible, however, that these animals are embedding barely noticeable (to us) signature information into their vocalizations that a more detailed investigation might detect. For human speech recognition, extensive research has been conducted by analyzing voices of human speakers and comparing subtle features of their verbal utterances (e.g., Reynolds, 1995). One approach worth exploring involves taking the techniques that have been developed to differentiate between human speakers and using them to classify similar-sounding animal vocalizations according to the individuals that produced them. This may lead to the discovery of additional features that animals use to encode their individual identity acoustically.

V. Conclusions

Signature vocalizations are attributes of individual animals containing spectral and temporal acoustic features that allow conspecifics to perform individual recognition. Signature information is best demonstrated by coupling computer- or human-based classification schemes in the laboratory with playback experiments in the wild. The ability to recognize other individuals offers an adaptive advantage in such situations as parents searching for their young, social companions attempting to reestablish contact and male aggressors asserting their territorial claims. Signature vocalizations also offer a way for researchers to single out both relevant social partnerships in the midst of a gregarious colony and meaningful encounters in the mist of a communicative flurry.

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