Chapter 7
The Vocal Repertoire of Tibetan Macaques (*Macaca thibetana*) and Congeneric Comparisons

Sofia K. Blue

7.1 Introduction

The vocal repertoires of mammals usually consist of a fixed number of calls, some of which are closely linked to particular contexts. Though not to the same extent as humans, other mammals have been documented to emit highly modifiable calls with a cognitively rich set of meanings (Seyfarth and Cheney 2010). Fixed vocal production coupled with modifiable context emission and comprehension may have been homologous traits present in our prelinguistic ancestor, since they appear to be present in a wide array of taxonomic groups. Seyfarth and Cheney (2012) suggest that the common ancestor of Old World monkeys, apes, and humans had limited vocal production and open-ended comprehension, and by making comparisons with our closest living relatives, we can further illustrate the implications of theories concerning language evolution.

Our limitless repertoire of sound combinations and capacity for vocal learning is unmatched in the animal kingdom. To date, songbirds have been the focus of vocal learning studies in non-human animals, and evidence in mammals has been restricted to species of cetaceans, pinnipeds, elephants, and bats (Lattenkamp and Vernes 2018). Surprisingly, our closest living relatives, the non-human primates, are deficient in their ability to learn new vocalizations. This inability may be a result of a lack of neuronal potential required for vocal learning although the vocal tract is speech-ready (Fitch et al. 2016). Vocal production is, for the most part, highly constrained in non-human animals, and mammalian repertoires usually consist of a variety of grunts, threatening vocalizations, alarm calls, and screams (Seyfarth and Cheney 2012). Comparing the diverse array of vocal repertoires and communication across taxa is one way to identify the selective pressures behind vocal complexity

S. K. Blue (✉)

Primate Behavior and Ecology Program, Department of Anthropology and Museum Studies, Central Washington University, Ellensburg, WA, USA
e-mail: Sofia.Bernstein@cwu.edu

and the biological underpinnings of language-specific traits. Finding an appropriate measure of vocal complexity, however, is challenging when there are no standard methods for quantifying, classifying, or describing vocal repertoires.

7.2 Measuring Vocal Complexity

7.2.1 Vocal Repertoire Size

Although communication is undoubtedly multimodal in nature, across the modalities the number of distinct signals or signaling units can be used as a representative of communicative complexity (Peckre et al. 2019). For studies investigating the modality of acoustic communication, one possible metric of vocal complexity is repertoire size. Repertoire size is defined by the number of call types produced by a species or population (Peckre et al. 2019). Therefore, repertoire size is a strictly numeric measure unable to provide any information concerning the function or usage of the calls that constitute them. Variable data collection methods among studies constrain the ability to make exact comparisons across species and genera, further limiting the informative value of repertoire size alone. In addition, comparing repertoire size leaves out the identification of species-specific calls that may have evolved.

Hohmann (1991) carried out a comparative analysis of the vocal repertoires of four species of Old World monkey (*Macaca radiata*, *Macaca silenus*, *Presbytis johnii*, *Presbytis entellus*). For the species under Hohmann's (1991) investigation, previous reports of their vocalizations were very fragmented. To bypass this challenge and make accurate comparisons, Hohmann (1991) recorded calls from these four species and used the same methods to analyze the call recordings. Even though this study involved an intensive classification of the vocal repertoire of four different species, emphasis was placed on comparisons of the frequencies of call type emission and vocal activity among sex/age classes, rather than identifying species-specific calls or call usage. Therefore, the extent to which vocal complexity among the four species was investigated is limited.

7.2.2 Identifying Homologous and Derived Calls

Gustison et al. (2012) proposed that the identification of homologous (acoustically similar calls shared between species) and derived vocalizations (acoustically unique to a species) among closely related species can be used as a measure of vocal complexity. By focusing on the identification of acoustically homologous calls (Hohmann 1991; Gustison et al. 2012) and identifying species-specific derived calls, researchers are not constrained by the variable methods used across studies to classify vocal repertoires. Furthermore, comparing homologous and derived

vocalizations among closely related species is essential in the identification of phylogenetic, social, and ecological factors influencing varying degrees of vocal complexity.

To date, few studies in non-human primates have approached investigations on vocal complexity through the identification of derived calls. Kudo (1987) compared the vocal behavior of mandrills (*Mandrillus sphinx*) to savannah baboons (*Papio* spp.) and geladas (*Theropithecus gelada*) and found that differences among the three species' vocal behavior were due to the ecological pressures associated with the attenuation of sound in forest versus savannah habitats. More recently, Gustison et al. (2012) identified the homologous and derived vocalizations in two closely related species, geladas and chacma baboons (*Papio ursinus*). In this comparison, derived vocalizations were uttered in social and reproductive contexts unique to a species, suggesting that differences in sociality and reproductive ecology were the driving factors in the evolution of these species-specific vocalizations.

7.3   Understanding the Evolution of Vocal Complexity

To understand the evolution of vocal complexity, it is necessary to make comparisons across closely related species. Although broader interspecies comparisons do exist and reveal some interesting patterns (McComb and Semple 2005), in-depth investigations among closely related species allow researchers to tease apart which factors have driven the evolution of communication (Bouchet et al. 2013). Macaques may be an ideal genus for investigations of vocal complexity because of several characteristics. Vocalizations in the *Macaca* genus have garnered a considerable amount of attention over the years, and the literature is rich enough to make detailed comparisons across many species. In addition, the genus is the most geographically widespread and behaviorally diverse genus of non-human primate because macaques display a high range of interspecific variation and inhabit the greatest range of habitats (Thierry et al. 2000). By documenting the diversity across the macaques through a comparative perspective and the identification of derived calls, I can investigate how potential selective pressures, like phylogeny, sociality, and ecology, shape which calls are conserved or vary in the vocal repertoires of the genus.

The effects of phylogeny, sociality, and ecology are essential in the explorations on the evolution of vocal complexity (Freeberg et al. 2012). Phylogeny may act as a starting point for mapping the evolutionary convergence of vocal characters. For example, complex oropendola bird songs are conserved and relatively invariant among the three genera (Price and Lanyon 2002), and primate vocalizations appear to be largely genetically predetermined (Newman and Symes 1982). It is widely accepted in the literature that sociality may be an essential driving factor in species with high degrees of vocal complexity (Blumstein and Armitage 1997; Wilkinson 2003; Freeberg 2006; Furrer and Manser 2009). In their investigation on Tonkean macaques (*Macaca tonkeana*), Masataka and Thierry (1993) concluded that sociality

determines the vocal repertoire of a species as strongly as phylogenetic constraints. Lastly, since macaques inhabit a wide range of habitats, interspecific variation in vocal repertoires may be the result of these ecological differences (Masataka and Thierry 1993). It is likely, however, that any one of these factors is insufficient to explain vocal diversity and that a complex interplay of phylogenetic, social, and ecological factors influences degrees of vocal complexity.

In this contribution, I explore vocal homologs and derived calls in the *Macaca* genus through the:

1. Identification of the main categories of call production
2. Selection of call types from each category of call production to compare across the genus
3. Identification of homologs based on acoustic characteristics
4. Identification of species-specific derived calls and main differences across the genus
5. Comparisons with the Tibetan macaque vocal repertoire
6. Exploration of phylogenetic, social, and ecological factors that may influence homologous and derived calls

7.4 Methods

7.4.1 Categories of Call Production

Two previous studies designated categories for comparison across different species of Old World monkeys (*M. radiata*, *M. silenus*, *P. johnii*, *P. entellus*: Hohmann 1991; *Papio ursinus*, *T. gelada*, Gustison et al. 2012). I followed Gustison et al. (2012) and identified calls in macaques within three main categories and included the subcategories differentiated for each: allospecific (*alarm* and *food calls*), social (long-distance and close-range calls (competitive, distress, and contact)), and other (see Fig. 7.1). Allospecific calls are elicited by external stimuli and include *alarm* and *food calls*. The majority of vocalizations in mammals are emitted during social interactions with conspecifics (Gustison et al. 2012). Such social calls are further categorized into two subclasses: long-distance and close-range calls. For close-range calls, a further subdivision is necessary; so I classified close-range calls into three additional subcategories to cover the many different contexts in which these calls are emitted: contact, competition, and distress. The last category, other, includes calls that are not strictly emitted in a particular context or the context is unknown.
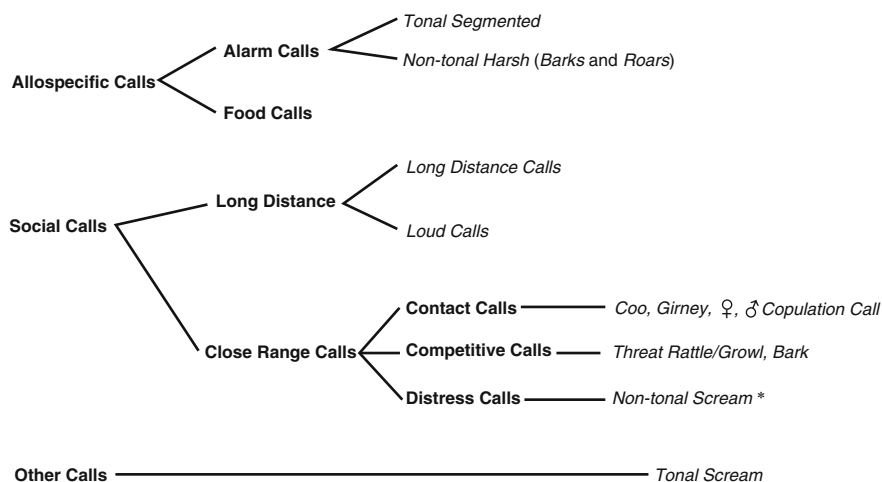
Fig. 7.1 Call categories and call types investigated in the genus *Macaca*. The main categories and subcategories are in bold, and calls in italics indicate the call types chosen for homologous and derived comparisons. (*) Non-tonal screams are not strictly distress calls since they are also emitted in feeding contexts

7.4.2 Exploring Vocal Homologs and Derived Calls in the Genus **Macaca**

The homologous call types investigated come from a review of the macaque literature and the identification of calls that were similar in acoustic structure alone, even if they were designated different names in the literature or were emitted in different contexts. Derived calls are defined as acoustically unique to a species and were also identified via visual inspection of spectrograms. Similar to my previous study (Bernstein et al. 2016), I followed Rowell and Hinde (1962) and first identified calls as either clear or harsh. Clear calls are tonal with energy concentrated in harmonic frequency bands, while harsh calls are atonal and acoustically unstructured with underlying harmonic frequency bands obscured by broadband noise and a distribution of energy across a wide frequency spectrum (Palombit 1992; Rowell and Hinde 1962). Once calls were classified as either clear or harsh, I then focused on temporal and frequency characteristics to identify homologous calls. These characteristics included the presence or absence of harmonic frequency bands, the modulation of frequency bands, spectral shifts (e.g., abrupt changes like the presence of a fast-rise transient from high pitch to low pitch), the concentration of spectral energy, whether or not calls were attached to or superimposed onto a noisy portion, and the duration of the call.

In order to make comparisons in the macaque genus, I used reports from which the entire repertoire was systematically investigated and excluded investigations that described only particular call types. This method is similar to the one adopted by McComb and Semple (2005) in their investigation of the coevolution of vocal

communication and repertoire size as a measure of vocal complexity. To date there are repertoire studies from 11 different macaque species, including my study on Tibetan macaques (Tibetan macaques, *Macaca thibetana*, Bernstein et al. 2016; Formosan macaques, *M. cyclopis*, Hsu et al. 2005; Barbary macaques, *M. sylvanus*, Hammerschmidt and Fischer 1998; Tonkean macaques, *M. tonkeana*, Masataka and Thierry 1993; long-tailed macaques, *M. fascicularis*, Palombit 1992; bonnet macaques, *M. radiata*, Hohmann 1989; lion-tailed macaques, *M. silenus*, Hohmann and Herzog 1985; Sugiyama 1968; stump-tailed macaques, *M. arctoides*, Lillehei and Snowdon 1978; Japanese macaques, *M. fuscata*, Green 1975; Itani 1963; rhesus macaques, *M. mulatta*, Rowell 1962; Rowell and Hinde 1962). Comparison of call emission frequency and in which contexts calls were uttered was analyzed when the results were available across the published repertoires in the genus.

7.4.3 Comparisons with Tibetan Macaques and Phylogenetic, Social, and Ecological Factors

I included a wider array of species for comparisons with the Tibetan macaque vocal repertoire based on phylogenetic closeness, even if their repertoires have not been systematically analyzed and reported. I made this attempt to incorporate studies on specific calls for a more robust comparison with particular Tibetan macaque calls that were not included in the genus comparison. I chose interspecific call types based on their acoustic similarity and not context (for context comparisons, see Table 7.2).

After I identified the homologous and derived calls in the genus, I explored potential phylogenetic, social, and ecological factors. Depending on the source and the type of genetic study, the phylogenetic classification of macaques can vary. One of the most recent studies by Li et al. (2009) investigated the phylogeny of the macaques based on Alu elements. I used their classification for the comparisons investigated here (for each species' designation in the phylogeny, see Table 7.1). For the social component, I compared the contexts of emission and, if available, the rate at which the call types are emitted in a species' repertoire. In addition, I used reviews of the *Macaca* genus (Thierry et al. 1996, 2000; van Schaik et al. 1999; Maestripieri and Roney 2005; Pradhan et al. 2006) and the life history traits provided by Singh and Sinha (2004) to explore social and ecological factors.

Table 7.1 Shared call types in the macaque genus

Group	Species	Call types											
		Coo	Threat rattle/ growl	Non-tonal scream	Girney	Tonal scream	Squeak	Food call	Alarm call	♀ Cop call	♂ Cop call	Bark	Loud call
Sylvanus	*sylvanus*	x[a]	–	x	–	x	x	–	NT	x	–	x	–
Silenus	*silenus*	x	x	x	x	x	x	–	NT	x	x	–	x
	nemestrina	x	x	x	–	–	x	–	NT	x	–	x	–
	tonkeana	x	x	x	x	x	x	–	TS	x	–	x	x
Sinica	*radiata*	x	x	x	x	x	x	–	TS	x	x	x	x
	thibetana	x	x	x	–	x	x	–	TS	x	x	x	x
	arctoides	x	x	x	x	x	x	–	NT	x	x	x	x
Fascicularis	*fascicularis*	x	x	x	–	x	x	–	NT, TS	x	x	x	–
	fuscata	x	x	x	x	x	x	–	TS	x	–	–	x
	mulatta	x	x	x	x	x	x	x	TS	–	x	x	–
	cyclopis	x	x	x	x	x	x	x	TS	x	x	x	–

An x indicates that the call type is present in the repertoire of that species

NT non-tonal harsh alarm calls including barks and roars, *TS* tonal segmented alarm calls

[a]*M. sylvanus* have a limited use of coo calls in their repertoire (Bruce and Estep 1992)

7.5 Results

### 7.5.1 Homologous and Derived Calls in the Genus

I selected call types from the three main categories (allospecific, social, and other) of call production across the genus. I identified the following as the shared calls in the 11 macaque species investigated: *coo*, *threat rattle/growl*, *non-tonal scream*, *girney/ greeting call*, *tonal scream*, *squeak*, *food call*, *alarm call* (*non-tonal harsh* and *tonal segmented* types), *female* and *male copulation call*, *bark*, and *loud call* (Table 7.1). The main category allospecific calls includes the *tonal segmented* and *non-tonal harsh alarm calls* and the *food call*. *Threat rattle/growl*, *bark*, *non-tonal scream*, *coo*, *girney*, *female* and *male copulation call*, *long distance*, and *loud call* are in the social category, and the *tonal screams* are in the other category since they are emitted in feeding and distress contexts (for subcategories, see Fig. 7.1).

For the 11 species investigated, I identified 9 derived calls based solely on acoustic structure: the *krahoo* (*M. fascicularis*); *food yell*, *atonal greeting*, and *tonal girney* (*M. cyclopis*); *warble*, *harmonic arch*, *chirp*, and *male copulation scream* (*M. mulatta*); *male copulation grunt* (*M. arctoides*); *tonal estrus call* (*M. fuscata*); and *female copulation call* (*M. thibetana*).

The main differences found in the homologous calls concerned the frequency of emission and the range of call types within a specific context. For example, *M. arctoides* have a limited use of *coo* calls with considerably more harsh, noisy calls in a purely graded signal system (Bruce and Estep 1992). *Macaca tonkeana* and *M. cyclopis* macaques have a wider range of agonistic and *girney/greeting* calls, respectively, that is unparalleled in the rest of the genus (Masataka and Thierry 1993; Hsu et al. 2005).

7.5.2 Comparisons with the Vocal Repertoire of Tibetan Macaques

The Tibetan macaque vocal repertoire consists of five clear calls (*coo*, *squawk*, *leap coo*, *weeping*, *modulated tonal scream*) and seven harsh calls (*squeal*, *noisy scream*, *growl*, *bark*, *compound squeak*, *pant*, *female copulation call*) (for a quantitative analysis of the vocal repertoire, see Bernstein et al. (2016); see Fig. 7.2). In order to make congeneric comparisons with the Tibetan macaque vocal repertoire, I included a wider array of species based on phylogenetic closeness, even if their repertoires have not been systematically analyzed and reported. I made this attempt to incorporate studies on specific calls for a more robust comparison with particular Tibetan macaque calls that were not included in the genus comparison above (i.e., *squawk*, *squeal*, *leap coo*, *weeping*, and *pant*). I chose interspecific call types based on their acoustic similarity and not context (for context comparisons see Table 7.2).
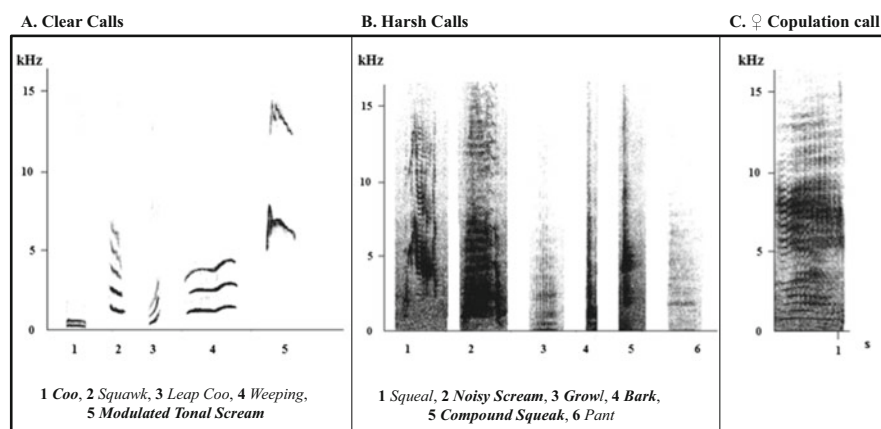
Fig. 7.2 Adapted from Bernstein et al. (2016). Calls in **bold** are homologous calls shared with the rest of the genus. (**a**) Representative spectrograms of the clear calls in the repertoire (**b**) Representative spectrograms of the harsh calls in the repertoire (**c**) Representative spectrogram of the female copulation call

Overall, the acoustic structure and context of emission was similar among the species investigated. A few main differences in context were a result of the group composition and various species-specific behaviors present in the congeneric species, but not in Tibetan macaques. For example, all of the infants died during my study on the vocal repertoire of Tibetan macaques, and therefore information about the calls associated with mother-infant interactions are limited (Bernstein et al. 2016). Also, an absence of calls from infants leaves out one vital age class that is necessary for a more complete comparison across species. Additionally, Tibetan macaques are one of two macaque species that show bridging behavior where two adults simultaneously lift an infant (Ogawa 1995, this volume). Bridging may be another context associated with infants where individuals emit calls that I was unable to observe.

Also, within the context of mating, female Tibetan macaques do not show any behaviors indicative of estrus (Li et al. 2005) and do not emit an estrous call. My study took place in the Valley of the Wild Monkeys, China, a site where the provisioned macaque groups that inhabit the mountainous sparsely covered terrain have been protected from hunting and trapping since the 1940s (Wada et al. 1987). During my observations, the Tibetan macaques did not emit an *alarm* or *food call*. Although Tibetan macaques were observed to emit *loud calls* that propagated over a large distance, these calls were clustered in the noisy scream category.

The female Tibetan macaque *copulation call* was the only call in my previous study that was a derived vocalization distinct from what has been reported in the rest of the genus (Bernstein et al. 2016). Usually, female macaques emit soft grunts during copulations. The Tibetan macaque females also emit quiet calls, but their acoustic structure does not involve biphasic "inhale-exhale" components, and they are instead shrill, undulating calls that are not always given in phrases. In

Table 7.2 Tibetan macaque vocal repertoire and congeneric comparisons

	Species	Call type	Context
Coo			*Foraging*, *provisioning*, *group movements*, *cohesion*, *dispersal*
	M. radiata	Contact whoo	Similar
	M. cyclopis	Contact coo	Similar
	M. sinica	Hum	Similar
	M. fuscata	Class II coo	Similar
	M. mulatta	Clear call	**Shut out**[a]
	M. fascicularis	Coo	Similar
	M. arctoides	Coo	Similar
	M. silenus	Whoo call	Similar
	M. sylvanus	Coo	**Limited use**[a]
Squawk			*♂ copulation call*, *dispersal*, *food begging*, *arrival of tourists*
	M. fuscata	Class IV high squawk	**Defensive submissive**[a]
	M. cyclopis	Squawk	**Defensive submissive**[a]
Squeal			*Submissive agonistic context*, *displacement by humans*
	M. radiata	Squeal	**Rejection of infants by mother, juvenile mobbing of adults**[a]
	M. cyclopis	Squeal	**Infant separation**[a]
	M. fuscata	Class VI squeal	**Estrus solicitation, infant separation**[a]
	M. silenus	Shriek	Submissive agonistic interactions
Noisy scream			*Agonistic*, *submissive intragroup/interspecies*, *provisioning*, *dispersal*
	M. cyclopis	Non-tonal scream	Similar
	M. radiata	Non-tonal scream	Intergroup interactions, **infant weaning**[a]
	M. mulatta	Non-tonal scream	Similar
	M. nemestrina	Agonistic scream	Similar
	M. cyclopis	Food yell	Similar
	M. sinica	Food yell	**Foraging discovery new food source**[a]
	M. fascicularis	Wraagh	Similar

(continued)

Table 7.2 (continued)

	Species	Call type	Context
Growl			*Agonistic*, *submissive intragroup/interspecies*, *provisioning*, *male-male mounts provisioning/ foraging*, *male-male mounts*
	M. cyclopis	Threat rattle	Similar
	M. radiata	Threat rattle	**Group movement**[a]
	M. silenus	Rattle	Similar
	M. fascicularis	Harr	**Juveniles threatened, during play**[a]
	M. fuscata	Class X gruff	**During threats and standoffs**[a]
Bark			*Intragroup/interspecies agonistic*, *provisioning*, *movements*, *weaning*
	M. radiata	Bark	Similar
	M. nemestrina	Bark	Similar
	M. tonkeana	Bark	Similar
	M. mulatta	Bark	Similar
	M. arctoides	Bark	Similar
	M. cyclopis	Bark	Similar
	M. fuscata	Bark	**Alarm response to dogs, snakes, raptors**[a]
Compound squeak			*Intragroup/interspecies agonistic context*, *weaning*
	M. cyclopis	Compound squeak	Similar
Leap Coo			Adults, *provisioning*, *foraging*, *group movements*, *arrival of tourists*; juveniles, *weaning*
	M. nemestrina	Leap coo	**During juvenile excitement**[a]
Weeping			*Rejection and weaning of juveniles*
	M. cyclopis	Weeping	Similar
	M. silenus	Weeping	Similar
	M. radiata	Pulse whoo	Similar
	M. sinica	Infant separation call	Similar
Modulated tonal scream			*Harassment of copulations, intragroup/interspecies agonistic context, provisioning, rejection and weaning of juveniles*
	M. sylvanus	Mod. tonal scream	**Forced separation from mother**[a]
	M. cyclopis	Tonal squeak	Similar
	M. radiata	Squeak	Similar
	M. fuscata	Squeak	♀ **homosexual solicitations**[a]

(continued)

Table 7.2 (continued)

	Species	Call type	Context
Pant			*Harassment of copulations*, intragroup/interspe-cies agonistic context
	M. mulatta	Pant threat	Similar

Context of emission for Tibetan macaques in *italics*
Comparisons made from acoustic spectra and context of emission provided in previous reports of macaque vocal repertoires (Tibetan macaques, *Macaca thibetana*, Bernstein et al. 2016; Formosan macaques, *Macaca cyclopis*, Hsu et al. 2005; Barbary macaques, *M. sylvanus*, Hammerschmidt and Fischer 1998; Tonkean macaques, *M. tonkeana*, Masataka and Thierry 1993; long-tailed macaques, *M. fascicularis*, Palombit 1992; bonnet macaques, *M. radiata*, Hohmann 1989; lion-tailed macaques, *M. silenus*, Hohmann and Herzog 1985; Sugiyama 1968; stump-tailed macaques, *M. arctoides*, Lillehei and Snowdon 1978; Japanese macaques, *M. fuscata*, Green 1975; Itani 1963; rhesus macaques, *M. mulatta*, Rowell 1962; Rowell and Hinde 1962)
[a]Tibetan macaques do not emit the homologous call in the **bold** context reported in the comparison species

comparison to the rest of the macaque genus, *female copulation call* rate was low and resembled that of *M. tonkeana* and *M. fuscata* (Masataka and Thierry 1993; Hohmann 1989; Oda and Masataka 1992; see Table 7.3). Similar to *M. radiata*, a closely related species in the same lineage, females do not emit an *estrous call* and *copulation calls* are the only auditory cue females emit in a copulation context. Males did emit *copulation calls* as well, but at a much higher frequency. Harassment of copulatory dyads is evident in Tibetan macaques, involves a wider range of age/sex classes than what is reported for most other members of the genus, and appears to be associated with the number of females in the audience.

7.5.3   Potential Effects of Phylogeny, Sociality, and Ecology

Phylogenetic Factors In the macaque species whose repertoires have been system-atically analyzed and reported, there are two main types of acoustically structured *alarm calls*: *non-tonal barks* and *roars* (NT) or *tonal segmented* (TS) calls. Hohmann (1989) proposed that the type of *alarm call* (NT or TS) present in the repertoire of a macaque species is mostly conserved within phylogenetic groups (NT, *sylvanus* and *silenus*; TS, *sinica* and *fascicularis*). This pattern holds true for the *silenus*, *sinica*, and *fascicularis* groups (see Table 7.1). Indeed, species in the *silenus* group (*M. nemestrina* and *M. silenus*) have *non-tonal alarm calls* (Caldecott 1986; Hohmann and Herzog 1985). The only two terrestrial species of macaque with a purely graded signal system, *M. sylvanus* of the *sylvanus* lineage and *M. arctoides* of the *sinica* group, also have *non-tonal alarm calls* (Fischer and Hammerschmidt 2002; Chevalier-Skolnikoff 1974). The only exception in the *silenus* group, *M. tonkeana*, emits *tonal segmented alarm calls*. This pattern, where the acoustic structure of an *alarm call* is conserved within phylogenetic groups, is found in

Table 7.3 Copulation calls in *Macaca* and life history traits

Phylogenetic group	Species	♂ Copulation call	♀ Copulation call	Traits					
				Mount pattern	Seasonality	Number of males	♀♂ Ratio	Sexual dimorphism	Sex skin
Sylvanus	M. sylvanus	–	x	SME	2	4.7	1.1	0.37	Yes
Silenus	M. silenus	x	x	MME	1	1.6	9.9	0.38	Yes
	M. nemestrina	–	x	MME	0–1	2.4	6.3	0.54	Yes
	M. tonkeana	–	x	MME	0–1	2	3.4	0.5	Yes
Sinica	M. radiata	x	x	SME	2	7.3	1.7	0.54	No
	M thibetana	x	**Shrill**	SME	2	5.5	1.9	0.36	Little
	M. arctoides	**Grunt**	x	SME	1	?	1.32	0.37	No
Fascicularis	M. fascicularis	x	x	SME	1	4.7	4.8	0.41	Little
	M. fuscata	–	x, **Tonal estrus**	MME	2	3.4	1.3	0.32	Little
	M. mulatta	**Scream**	–	MME	2	4.5	2.9	0.22	Little
	M. cyclopis	x	x	MME	2	1.8	1	0.2	Little

Compilation from van Schaik et al. (1999), Maestripieri and Roney (2005), and Pradhan et al. (2006)

An x indicates the call is present in the repertoire of the species

Calls in **bold** are species-specific derived calls

Breeding seasonality: 0, 33% of births in 3-month period; 1, between 33% and 67%; 2, 67% in 3-month period (van Schaik et al. 1999)

sympatric species from different phylogenetic groups that may be prey to the same predators (*M. silenus* and *M. radiata*, Hohmann 1989).

Fooden (1976) sorted the macaque lineages based on the reproductive anatomy of males and females. Although his study relied only on behavioral and anatomical features, his classification is still mostly accurate even with more sophisticated genetic analyses. The evolution of different reproductive anatomy likely stemmed from each lineage going through a genetic bottleneck (Tosi et al. 2003). The three species that emit derived *copulation calls* (*M. thibetana*, *M. mulatta*, *M. arctoides*) are more closely related than they initially appear. Recent studies in the whole genome sequencing of Tibetan macaques have found that they are most closely related to Chinese rhesus macaques despite having been reported in different lineages (Fan et al. 2014). Analyses of mitochondrial loci in the macaque genus show stump-tailed macaques to potentially be a hybrid of proto-*M. thibetana* (Tosi et al. 2003).

Social Factors Most of the derived calls in the macaque genus are related to the context of mating, in particular, *female* and *male copulation calls*. Throughout the genus, males typically produce squeak-like *copulation calls*, while females emit grunts characterized by an "inhale-exhale element" (Pradhan et al. 2006). However, a few species stray from these genus characteristic calls and emit acoustically distinct calls associated with copulations. Two species emit acoustically distinct *male copulation calls*: *M. mulatta copulation screams* (Hauser 1993) and *M. arctoides copulation grunts* (Bauers 1993). Japanese macaques are the only macaque species that have studies reporting a distinct *estrous call* from the *female copulation call* (Oda and Masataka 1992), and my previous study reports an acoustically distinct shrill *female copulation call* in Tibetan macaques (Bernstein et al. 2016). All of these species that emit acoustically distinct calls in the context of copulations are seasonal breeders, have promiscuous mating systems, all exhibit the interruption of copulations by conspecifics, and have similar adult female-to-male ratios (1.3:2.9, Singh and Sinha 2004; Pradhan et al. 2006).

A large number of call types in the context of agonistic interactions is a characteristic of *M. tonkeana*. This species has high degrees of tolerance, small rank differences, a high frequency of conciliatory patterns, small interindividual distances, and a high rate of bidirectional agonistic interactions (Masataka and Thierry 1993). Context-dependent differences were also found in the derived *girney/greeting calls* of *M. cyclopis*. All of the *girney/greeting calls* were paired with particular contexts and age/sex classes, with acoustic structure changing according to the recipient of the *girney/greeting call* (Hsu et al. 2005).

Ecological Factors Overall, *loud calls* adhere to the bioacoustic requirements for long-distance propagation of sound (e.g., the repetition of units and phrases, no intergradations to other vocal patterns, a stereotyped structure, a large range of frequencies, and a concentration of energy on the lower frequencies; Hohmann and Herzog 1985). *Loud calls* are harsh calls where the fundamental frequency is in the lower frequency range. However, only some species show a large range of frequencies and utter *loud calls* that are composed of both tonal and non-tonal harsh

units. Three macaque species utter *loud calls* that are acoustically distinct from the rest of the genus and are composed of tonal and harsh units in a wider range of frequencies (*M. silenus*, *loud call*, Hohmann and Herzog 1985; *M. fascicularis*, *krahoo*, Palombit 1992; *M. tonkeana*, *loud call*, Masataka and Thierry 1993). Also, for all three species, only males have been reported to emit these *loud calls*. The *loud calls* of *M. silenus* are mixed units with a noise-like inhalation phase followed by a tonal exhalation (Hohmann and Herzog 1985), the *krahoo* of *M. fascicularis* is distinct for its harsh "*kra*" syllable at the beginning of the call (Palombit 1992), and *M. tonkeana*'s *loud call* is characterized by a distinct flag and mast with a sharp upward and downward frequency modulation (Masataka and Thierry 1993). All three species live in rainforest habitats and are mostly arboreal.

Food calls are common in the genus, but so far only two species have been reported to give acoustically distinct calls strictly emitted in food-related contexts. *M. mulatta warbles*, *harmonic arches*, and *chirps* are acoustically distinct calls made exclusively in a food context (Hauser and Marler 1993). *M. cyclopis* emit *food yells* similar to the *M. sinica food call*, but are acoustically distinct (Hsu et al. 2005). Reports from these two species are from provisioned groups living in human habitations or captivity.

7.6 Discussion

Mammalian vocalizations consist mainly of grunts, harsh non-tonal threatening vocalizations, and the sometimes tonal alarm calls and screams (Seyfarth and Cheney 2012). Indeed, the macaque genus shared these basic vocalizations (e.g., grunts, *girneys*, *estrus calls*, *female copulation calls*; harsh non-tonal calls, *barks*, *growls*; *tonal alarm calls*; screams, *shrieks*, *tonal*, *non-tonal screams*) but also emitted additional tonal calls (e.g., *coos*, *squawks*, and *male copulation calls*). Overall, macaque repertoires can be described as a graded signal system with intergradations between calls, and the contexts of emission for shared calls were consistent.

Although primate vocalizations appear to be largely genetically predetermined (Newman and Symes 1982), there are differences in the flexibility and conservation of the call types investigated. The flexibility observed in the derived vocalizations seems to be a by-product of the characteristics of the contexts in which calls are emitted or species-specific features. The most salient difference found in my congeneric comparison were the calls emitted in the copulation context. Three species emit derived *copulation calls* (*M. thibetana female copulation call*, *M. mulatta male copulation scream*, *M. arctoides male copulation grunt*). These species that emit *copulation calls* uncharacteristic of the genus have species-specific features in their copulation styles.

7.6.1 The Tibetan Macaque Vocal Repertoire

In sum, the Tibetan macaque vocal repertoire was generally comparable to that of other macaque species. The context of emission was also similar across species, but with a few key differences. For example, my previous study could not investigate the vocalizations of infants because of a 100% mortality rate during the 2014 mating season (Bernstein et al. 2016). Future studies on the vocalizations of infants and infant-related contexts may find that Tibetan macaques do emit calls not previously described in the analysis of the repertoire. The main differences found between Tibetan macaques and the rest of the genus may not only be a result of a missing age class but also the method used to quantify the repertoire and species-specific aspects of their social behavior.

An absence of a *food call* or *alarm call* may be the result of site management. These call types may not be absent. It is possible that I simply did not observe them over the course of my study or that provisioning and predators being hunted out of the area have removed these contexts that would elicit calls they may have present in their repertoire. Although Tibetan macaques do emit calls that propagate over a large distance, they were not a distinct call type like the *loud calls* described for other species. Most of the species that emit *loud calls* live in rainforest habitats where certain acoustic requirements are necessary for sound propagation. Tibetan macaques inhabit mountainous terrain with sparse tree coverage, where the propagation of their calls is not limited by a densely covered forest (Xia et al. 2010). My quantitative method of relying solely on acoustic characters to define distinct call types may have clustered calls identified separately in other studies into more overarching categories. The same could be true for *greeting calls*. In some cases, variants of the *coo* call are considered as a separate category, but for my study, individual classification of *coo* call variants was not warranted.

The unique copulatory behavior of Tibetan macaques may be one reason an acoustically distinct female call was selected for. Also within the context of mating, female Tibetan macaques do not show any behaviors indicative of estrus (Li et al. 2005), and therefore, it is not surprising that their concealed ovulation would yield the absence of an *estrous call*. The similarity between *M. thibetana*, *M. tonkeana*, and *M. fuscata* in terms of a low *female copulation call* rate may imply a cost-benefit strategy that differs between the sexes. All of these species are seasonal breeders, living in multi-male, multi-female groups, and exhibit high rates of copulation interruptions (see Table 7.3). *Macaca tonkeana* and *M. fuscata copulation call* emission rate may also be low because females additionally produce *estrous calls* to solicit males. These species may have evolved an alternate strategy of mating promiscuously and a low call rate to reduce female competition. My preliminary investigation on the association between *female copulation call* rate and harassment of copulatory dyads does indicate that harassment increases with the number of females in the audience.

However, the presence of both *male* and *female copulation calls* might indicate that part of their function is to synchronize male and female mating behavior,

especially in seasonally breeding species. Additionally, for males, it might not be so costly to call as it is for females. Adult females harass copulations, sneak copulate with lower-ranking males, and mate promiscuously with males outside of their consortship. In primates, there are very few studies that have investigated a cost-benefit analysis of signaling in the mating context (Hauser 1993). Future studies should investigate the costs and benefits of producing *copulation calls* along with emission rate and how intra- and intersexual selection plays a role in the mating strategies and auditory sexual signals of males and females.

7.6.2 Phylogenetic, Social, and Ecological Factors Influencing Macaque Vocal Repertoires

The type of *alarm call* was conserved within phylogenetic groups (*non-tonal*, *sylvanus* and *silenus*; *tonal segmented*, *sinica* and *fascicularis*) and followed the designation described by Hohmann (1989) with a few exceptions. *Macaca sylvanus* and *M. arctoides*, the exceptions in the *sinica* group, would be expected to have *non-tonal harsh alarm calls* since their repertoires consist of mostly harsh calls and their placement in the phylogeny of macaques is contested (*M. arctoides*, Li et al. 2009). *Macaca tonkeana*, the only exception in the *tonkeana* group, emit *tonal segmented alarm calls*, which may be the result of this species having a wide array of tonal calls in their repertoire (Masataka and Thierry 1993). In conclusion *alarm calls* are one salient example of a vocalization type that is mediated by phylogeny and a repertoire's acoustic structure, which is largely genetically predetermined (Newman and Symes 1982).

The species that emit derived species-specific *copulation calls* are all closely related. Phylogenetic and social factors associated with reproduction may be the selective factors under which derived calls have evolved in these three species. Future studies are needed to investigate the *copulation calls* of females in more detail, to understand their effect as an auditory sexual signal, and to make more in-depth comparisons of their acoustic structure with the rest of the genus.

Certain aspects of *M. tonkeana* social behavior may drive the need for a larger number of agonistic vocalizations (Masataka and Thierry 1993). The high degree of variability in the frequency of the acoustic structure of *girney/greeting calls* in *M. cyclopis* could also be a result of sociality since they were heavily context dependent. Some of these acoustically distinct *girney/greeting calls* are different from what has been reported in the rest of the genus and could be considered as derived calls.

Factors that influence call production and the extent to which a sound travels can sometimes be enhanced or restricted based on the type of environment that a species inhabits. The environment can affect the context in which a call is given, or change the motivational threshold to call (Green 1981). Macaques inhabit the widest range of habitats; therefore, environmental factors may drive the differences seen among

the repertoires of various macaque species. The *loud calls* of *M. silenus* and *M. tonkeana*, and the *krahoo* of *M. fascicularis*, are acoustically distinct from the rest of the genus. Their *loud calls* are made up of tonal and harsh units in a wider range of frequencies, and their arboreal lifestyle and rainforest habitat may have selected for a call with an acoustic structure that enables the propagation of sound in a dense forest.

The acoustically distinct *warbles*, *harmonic arches*, and *chirps* of *M. mulatta* and the *food yells* of *M. cyclopis* and *M. sinica* are allospecific *food calls* emitted by species from provisioned groups living in human habitations or captivity. These allospecific calls are related to the quantity or quality of a food source (Gustison et al. 2012), and provisioning heightens these characteristics in a given environment. *Food calls* and *alarm calls* are special in that they both are emitted in response to non-conspecifics and they combine call elements to procure new meanings. Therefore, it is possible that other species that do not emit a food-specific call still have the basic acoustic requirements needed to flexibly alter the acoustic structure of a call to convey a food context-specific meaning.

7.7 Conclusions

The main differences in the genus are in the calls associated with copulation. Macaques are the most behaviorally diverse and widespread primate genus, yet reproductive features appear to be the most important discriminating factor among species. This may explain the flexibility of derived call types observed in the *copulation calls* of males and females. However, particularly for this genus, it is difficult to tease apart the effects of phylogeny and behavior on reproduction. Instead, a complex interplay of phylogenetic and social features of a species' reproduction drives the evolution of derived calls in the context of copulations. In conclusion, it is not likely that any particular factor is mutually exclusive. Instead, a complex interplay of phylogenetic, social, and ecological factors may shape the development of derived calls and the preservation of homologous calls across the macaque genus.

References

Bauers KA (1993) A functional analysis of staccato grunt vocalizations in the stumptailed macaque (*Macaca arctoides*). Ethology 94:147–161

Bernstein SK, Sheeran LK, Wagner RS, Li J, Koda H (2016) The vocal repertoire of Tibetan macaques (*Macaca thibetana*): a quantitative classification. Am J Primatol 78:937–949

Blumstein DT, Armitage KB (1997) Does sociality drive the evolution of communicative complexity? A comparative test with ground-dwelling sciurid alarm calls. Am Nat 150:179–200

Bouchet H, Blois-Heulin C, Lemasson A (2013) Social complexity parallels vocal complexity: a comparison of three non-human primate species. Front Psychol 4:390

Bruce KE, Estep DQ (1992) Interruption of and harassment during copulation by stumptail macaques, *Macaca arctoides*. Anim Behav 44:1029–1044

Caldecott JO (1986) Mating patterns, societies and the ecogeography of macaques. Anim Behav 34:208–220

Chevalier-Skolnikoff S (1974) Male-female, female-female, and male-male sexual behavior in the Stumptail Monkey, with special attention to the female orgasm. Arch Sex Behav 3:95–116

Fan Z, Zhao G, Li P et al (2014) Whole-genome sequencing of Tibetan macaque (*Macaca thibetana*) provides new insight into the macaque evolutionary history. Mol Biol Evol 31:1475–1489

Fischer J, Hammerschmidt K (2002) An overview of the Barbary macaque, *Macaca sylvanus*, vocal repertoire. Folia Primatol 73:32–45

Fitch WT, de Boer B, Mathur N, Ghazanfar AA (2016) Monkey vocal tracts are speech-ready. Sci Adv 2:1–7

Fooden J (1976) Provisional classification and key to living species of macaques (Primates: *Macaca*). Folia Primatol 25:225–236

Freeberg TM (2006) Social complexity can drive vocal complexity: group size influences vocal information in Carolina chickadees. Psychol Sci 17:557–561

Freeberg TM, Dunbar RIM, Ord TJ (2012) Social complexity as a proximate and ultimate factor in communicative complexity. Philos Trans R Soc Lond Ser B Biol Sci 367:1785–1801

Furrer RD, Manser MB (2009) The evolution of urgency-based and functionally referential alarm calls in ground-dwelling species. Am Nat 173:400–410

Green S (1975) Variation in vocal pattern with social situation in the Japanese monkey (*Macaca fuscata*): a field study. In: Rosenblum A (ed) Primate behavior: developments in field and laboratory research. Academic, New York, pp 1–102

Green S (1981) Sex differences and age graduations in vocalizations of Japanese and liontailed monkeys (*Macaca fuscata* and *Macaca silenus*). Am Zool 21:165–183

Gustison ML, le Roux A, Bergman TJ (2012) Derived vocalizations of geladas (*Theropithecus gelada*) and the evolution of vocal complexity in primates. Philos Trans R Soc Lond B Biol Sci 367:1847–1859

Hammerschmidt K, Fischer J (1998) The vocal repertoire of Barbary macaques: A quantitative analysis of a graded signal system. Ethology 104:203–216

Hauser MD (1993) Rhesus monkey copulation calls: honest signals for female choice? Proc Biol Sci 254(1340):93–96

Hauser MD, Marler P (1993) Food-associated calls in rhesus macaques (*Macaca mulatta*): I. Socioecological factors. Behav Ecol 4:194–205

Hohmann GM (1989) Vocal communication of wild bonnet macaques (*Macaca radiata*). Primates 30:325–345

Hohmann GM (1991) Comparative analyses of age-specific and sex-specific patterns of vocal behavior in 4 species of old-world monkeys. Folia Primatol 56:133–156

Hohmann GM, Herzog MO (1985) Vocal communication in lion-tailed macaques (*Macaca silenus*). Folia Primatol 45:148–178

Hsu MJ, Chen LM, Agoramoorthy G (2005) The vocal repertoire of Formosan macaques, *Macaca cyclopis*: acoustic structure and behavioral context. Zool Stud 44:275–294

Itani J (1963) Vocal communication of the wild Japanese monkey. Primates 4:11–67

Kudo H (1987) The study of vocal communication of wild mandrills in Cameroon in relation to their social structure. Primates 28:289–308

Lattenkamp EZ, Vernes SC (2018) Vocal learning: a language-relevant trait in need of a broad cross-species approach. Curr Opin Behav Sci 21:209–215

Li JH, Yin HB, Wang QS (2005) Seasonality of reproduction and sexual activity in female Tibetan macaques *Macaca thibetana* at Huangshan, China. Acta Zool Sin 51:365–375

Li J, Han K, Xing J et al (2009) Phylogeny of the macaques (Cercopithecidae: *Macaca*) based on *Alu* elements. Gene 448:242–249

Lillehei RA, Snowdon CT (1978) Individual and situational differences in the vocalizations of young stumptail macaques. Behaviour 65:270–281

Maestripieri DM, Roney JR (2005) Primate copulation calls and postcopulatory female choice. Behav Ecol 16:106–113

Masataka N, Thierry B (1993) Vocal communication of Tonkean macaques in confined environments. Primates 34:169–180

McComb K, Semple S (2005) Coevolution of vocal communication and sociality in primates. Biol Lett 1:381–385

Newman JD, Symes D (1982) Inheritance and experience in the acquisition of primate acoustic behavior. In: Snowdon CT, Brown CH, Petersen MR (eds) Primate communication. Cambridge University Press, New York, pp 59–70

Oda R, Masataka N (1992) Functional significance of female Japanese macaque copulatory calls. Folia Primatol 58:146–149

Ogawa H (1995) Bridging behavior and other affiliative interactions among male Tibetan macaques (*Macaca thibetana*). Int J Primatol 16:707–729

Palombit RA (1992) A preliminary study of vocal communication in wild long-tailed macaques (*Macaca fascicularis*). I. Vocal repertoire and call emission. Int J Primatol 13:143–182

Peckre L, Kappeler PM, Fichtel C (2019) Clarifying and expanding the social complexity hypothesis for communicative complexity. Behav Ecol Sociobiol 73(1):11

Pradhan GR, Engelhardt A, van Schaik CP, Maestripieri D (2006) The evolution of female copulation calls in primates: a review and a new model. Behav Ecol Sociobiol 59:333–343

Price JJ, Lanyon SM (2002) Patterns of song evolution and sexual selection in the oropendolas and caciques. Behav Ecol 15:485–497

Rowell TE (1962) Agonistic noises of the rhesus monkey (*Macaca mulatta*). Symp Zool Soc Lond 8:91–96

Rowell TE, Hinde RA (1962) Vocal communication by rhesus monkey (*Macaca mulatta*). Proc Zool Soc Lond 128:279–294

Seyfarth RM, Cheney DL (2010) Production, usage, and comprehension in animal vocalizations. Brain Lang 115:92–100

Seyfarth RM, Cheney DL (2012) Primate social cognition as a precursor to language. In: Gibson K, Tallerman M (eds) Oxford handbook of language evolution. Oxford University Press, Oxford, pp 59–70

Singh M, Sinha A (2004) Life history traits: ecological adaptations or phylogenetic relics? In: Thierry B, Singh M, Kaumanns W (eds) Macaque societies: a model for the study of social organization. Cambridge University Press, Cambridge, pp 80–83

Sugiyama Y (1968) The ecology of the liontailed macaque (*Macaca silenus* Linnaeus): a pilot study. J Bombay Nat Hist Soc 65:283–293

Thierry B, Heistermann M, Aujard F et al (1996) Long-term data on basic reproductive parameters and evaluation of endocrine, morphological, and behavioral measures of monitoring reproductive status in a group of semi-free ranging Tonkean macaques (*Macaca tonkeana*). Am J Primatol 39:47–62

Thierry B, Iwaniuk AN, Pellis SM (2000) The influence of phylogeny on the social behaviour of macaques (primates: Cercopithecidae, genus *Macaca*). Ethology 106:713–728

Tosi AJ, Morales JC, Melnick DJ (2003) Paternal, maternal, and biparental molecular markers provide unique windows onto the evolutionary history of macaque monkeys. Evolution 57:1419–1435

van Schaik CP, van Noordwijk M, Nunn CL (1999) Sex and social evolution in primates. In: Lee PC (ed) Comparative primate socioecology. Cambridge University Press, Cambridge, pp 204–240

Wada K, Xiong CP, Wang QS (1987) On the distribution of Tibetan and rhesus monkeys in Southern Anhui province, China. Acta Theriol Sin 7:148–176

Wilkinson GS (2003) Social and vocal complexity in bats. In: de Waal FBM, Tyack PL (eds) Animal social complexity: Intelligence, culture, and individualized societies. Harvard University Press, Cambridge, MA, pp 322–341

Xia DP, Li JH, Zhu Y, Sun BH, Sheeran LK, Matheson MD (2010) Seasonal variation and synchronization of sexual behaviors in free-ranging male Tibetan macaques (*Macaca thibetana*) at Huangshan, China. Zool Res 5:509–515