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Do male “long-distance calls” function in mate defense? A comparative study of long-distance calls in primates

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Abstract Long-distance calls produced by males are common among vertebrate species. Several hypotheses have been proposed to explain features of male long-distance calls and their phylogenetic distribution in primates, but the putative functions of male long-distance calls have yet to be tested comprehensively. We used phylogenetic comparative methods to investigate hypotheses for the function of male long-distance calls. We focused on the mate defense hypothesis, which states that male long-distance calls function in intra-sexual competition for mates, but we also examined factors involving resource defense, mate attraction, and habitat. Phylogenetic reconstruction of male long-distance calls in 158 primate species indicates that the presence of male long-distance calls is the ancestral state. The carrying distance of male long-distance calls is correlated with the size of the home range, which is consistent with the role of male long-distance calls in defending mates, attracting mates, and defending resources. However, measures of male intra-sexual competition were not associated with the evolution of male long-distance calls. Evolutionary transitions were only partly correlated with factors related to mate attraction. Instead, the strongest correlates of male long-distance calls were activity period, body mass, home range, habitat and some measures of resource defense. Our results are consistent with long-distance call production as a costly signal, but detailed

study within species is required to assess these costs and the functions of long-distance calls in individual cases. Electronic Supplementary Material is available if you access this article at <http://dx.doi.org/10.1007/>.

Keywords Comparative study · Intra-sexual competition · Long-distance call · Primates · Vocalization

Introduction

In many primate species, males produce vocalizations that are considered long-distance calls (Waser 1977; Cheney 1987; Hohmann and Fruth 1995). The term long-distance call, also known as long or loud call, refers to the distance over which such calls carry. Thus long distance calls have the potential to function in extra-group communication among males, particularly in territorial spacing involving mate defense (Waser 1977; Sekulic 1982; Oates and Troco 1983; Whitehead 1987; Halloy and Kleiman 1994; Cowlshaw 1996; Steenbeek et al. 1999; Oates et al. 2000). This putative function is supported by the observation that long-distance calls frequently are contagious, in that calling by one male stimulates other males to counter-call (Whitehead 1987; Tenaza 1989; Steenbeek et al. 1999). Moreover, long-distance calls may be more common in males than females, which is consistent with a mate defense hypothesis because males are thought to compete for mates while females compete mainly for resources (Emlen and Oring 1977; Nunn 1999). Non-primate animals also exhibit long-distance vocalizations that may have similar functions, including birds and frogs, although different functions may predominate in different clades (Harrington and Mech 1978; Clutton-Brock and Albon 1979; Ryan 1985; McComb et al. 1994; Leonard and Horn 1995).

Although circumstantial evidence suggests that male long-distance calls function in mate defense, alternative hypotheses exist, and these alternatives are not mutually exclusive of the “mate defense hypothesis.” Two alternative hypotheses are most commonly considered. First,

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male long-distance calls may play a role in attracting mates (Waser 1977; Mitani 1985a; Steenbeek et al. 1999). This “mate attraction hypothesis” can explain counter-calling, because other males would benefit from attracting females that are searching for a mate. The mate attraction hypothesis clearly plays a role in some vertebrates, including frogs (Ryan 1985) and birds (Searcy and Andersson 1986). A second hypothesis for male long-distance calls involves resource defense (Sekulic 1982; Tenaza 1989; Mitani 1990; Wich et al. 2002a). This “resource defense hypothesis” might be expected to operate in mating systems characterized by resource defense polygyny, in which males defend resources needed by females (Clutton-Brock 1989; Fashing 2001). Resource defense also may play a prominent role in monogamous mating systems, if males defend resources used by females to invest in their offspring.

Several field studies have addressed possible functions of long-distance calls in one or a few species of primates (see references above and Brown 1989), but few comparative studies have examined general patterns among long-distance calls and socio-ecological variables across a wide array of species (e.g., Hohmann and Fruth 1995; Mitani and Stuht 1998; Nunn 2000). In this paper, we examine the macroevolutionary correlates of long-distance calls produced by male primates. The aim of our paper is to identify the function of male long-distance calls and to test the generality of patterns across primate species. We focus on tests of hypotheses relevant to the mate defense hypothesis, as this appears to be the most general explanation for male long-distance calling. Because this hypothesis and its main alternatives focus on inter-group conflict, we used the operational definition that long-distance calls result in counter-calling by extra-group males (Nunn 2000), as this definition only assumes extra-group communication without assigning a particular function beforehand. In addition, however, long-distance calls may function to reduce predation (Cheney and Wrangham 1987; Gautier-Hion and Tutin 1988; Cordeiro 1992) or to facilitate subgroup re-aggregation (Waser 1977; Wrangham 1977).

Methods

Information on the presence of long-distance calls was obtained from an unpublished comparative database (Nunn 2000) and updated using the published literature and personal communications from field biologists. These and all other unpublished data used in this paper are available upon request (See also <http://faculty.virginia.edu/charlienunn> and Electronic Supplementary Material).

Our focus is on extra-group conflict, which we define to include conflict between males resident in different bisexual groups (inter-group conflict) as well as conflict between resident males and potential immigrants (e.g., from all-male bands). We obtained information on long-distance calls by males and females, using sources that provided information on counter-calling by same-sexed individuals outside the group. A species was classified as not producing such calls if either of two conditions were met: (1) long-distance calls were not reported, or (2) it was stated that counter-calling to long-distance calls did not occur. Using this definition excludes vocalizations that function purely for within-group communication or as alarm calls. For example, wahoo calls in baboons (*Papio* spp.) generally function as alarm calls and within-group communication (Hall and DeVore 1965; Buskirk et al. 1974, except in *Papio papio*; Byrne 1981). Among vervets (*Cercopithecus aethiops*), calls produced during inter-group encounters, like the wrt and chutter, are not audible over long distances, and counter-calling from extra-group males is not mentioned explicitly (Struhsaker 1967).

We conducted two main sets of tests. First, we focused on the scaling of carrying distance with home range size and body mass. If male long-distance calls function in communication with extra-group males, then we expect that the association between long-distance call carrying distance and home range size should exhibit a positive relationship. An association between carrying distance and home range size has been documented previously, but results were based on a very small sample (Brown 1989). We obtained data on carrying distance, measured as the maximum distance at which a long-distance call is audible to observers, from the published literature and experts on vocal communication for particular species (references provided below). These measurements have often been estimated subjectively, introducing measurement error into the estimates of carrying distance. However, we have no reason to believe that this measurement error biases the analysis. Thus, measurement error is likely to reduce the strength of patterns rather than create spurious relationships (Clutton-Brock and Harvey 1984). Estimates of measurement error currently are unavailable for most estimates of carrying distance, making it impossible to implement more recent comparative methods that can take this error into account in comparative analyses (Martins and Hansen 1997).

The second set of tests examined the macroevolutionary correlates of male long-distance calls and was used to evaluate the validity and generality of the mate defense hypothesis and its main alternatives. Under the mate defense hypothesis, the strength of male intra-sexual conflict is the primary predictor variable for the presence of long-distance calls. Directly testing this association is complicated by the fact that most species of primates exhibit some level of male competition, but reports often are qualitative rather than quantitative, and the data are rarely comparable across multiple species. Thus, we tested whether male long-distance calls are correlated with morphological measures of male intra-sexual competition, including relative male canine size, body size dimorphism and the socioeconomic sex ratio (the ratio of adult females to adult males) (Table 1). Relative male canine size was taken from Plavcan et al. (1995), body mass dimorphism from Smith and Jungers (1997) while the socioeconomic sex ratio was based on values for male and female numbers in the group from Nunn and Barton (2000).

Table 1 Predicted effects of socio-ecological variables on male long-distance calls

Hypothesis	Correlates of male long-distance calls
Mate defense hypothesis	Positive association expected between presence of long-distance calls and (1) body mass dimorphism, (2) relative male canine size, and (3) socioeconomic sex ratio
Mate-attraction hypothesis	Long-distance calls should be correlated with female transfer
Resource defense	Male long-distance calling should be associated with territoriality and higher D-index.

We generated further predictions to examine alternative hypotheses.

1. The mate-attraction hypothesis predicts that male long-distance calls are correlated with female transfer between groups, as female attraction to males from other groups is only effective if females can enter the group. Information on female dispersal was updated from Nunn and van Schaik (2000) using the published literature and personal communications.
2. Males also may give long-distance calls if they function in resource defense, but under this hypothesis, females should also produce calls; in fact, the distribution of calling between the sexes should be female-biased, because females are expected to show increased participation in territorial defense of food resources (Emlen and Oring 1977). Data on territoriality were obtained primarily from major review sources, including Mitani and Rodman (1979), Cheney (1987), Grant et al. (1992) and Lowen and Dunbar (1994).
3. The resource defense hypothesis also predicts that the presence of male long-distance calls is associated with a higher defensibility of the home range, which we assayed using the D-index (an index indicating the defensibility of an area based on daily travel distance and home range size, Mitani and Rodman 1979; values were calculated from an unpublished comparative database on primate day range length and home range size, updated from Nunn and van Schaik 2001).

A final hypothesis was not considered above but may explain some of the variance in patterns of long-distance calling across species. It has been hypothesized that long-distance calls are more likely to have evolved in areas where visual displays have little function in communication (i.e. tropical rain forests and other densely wooded habitats; Waser and Waser 1977; DeVore 1979) or where long-distance calls cannot be propagated over large distances due to acoustic properties of the habitat such as in savanna environment (Waser and Brown 1986). Thus, long-distance calls should be less common in savanna-dwelling species, as compared to species living in forested habitats. Information on habitat characteristics was taken from Nunn and van Schaik (2001). In this test, arboreal species were excluded from the dataset and comparison was made between terrestrial species living in wooded versus open habitats. By focusing on terrestrial species, we controlled for the correlated effects of home range size, group size and body mass, which tend to be smaller in arboreal species (Clutton-Brock and Harvey 1977; Nunn and van Schaik 2001).

Phylogenetic comparative methods

We used methods based on independent contrasts (Felsenstein 1985) and the concentrated changes test (Maddison 1990) to test hypotheses in an explicitly phylogenetic framework (Harvey and Pagel 1991; Nunn and Barton 2001). Independent contrasts are calculated as differences between species or higher nodes. As species differences, these contrasts represent evolutionary change since pairs of taxa last shared a common ancestor. Contrasts therefore test whether evolutionary change in one trait is correlated with change in another trait. They also are useful for examining a combination of continuous and discrete characters, such as the presence of long-distance calls, using the "BRUNCH" algorithm in the computer program CAIC (Purvis and Rambaut 1995). Analyses were based on Purvis' (1995) composite estimate of primate phylogeny. Previous research has revealed that log-transformed data and branch lengths best meet the assumptions for the variables considered here, and so these transformations were used (Garland et al. 1992). We also examined outliers and in some cases repeated tests without these data points, which helps to meet the assumptions of independent contrasts and deals with inflated type I error rates under an alternative model of trait evolution (Price 1997; Harvey and Rambaut 2000; Nunn and Barton 2001).

The concentrated changes test examines the correlation among discrete traits (Maddison 1990). It tests whether a character state in some hypothesized dependent trait is correlated with a particu-

lar character state in an independent trait. We used the computer program MacClade version 4.0 (Maddison and Maddison 1992) to implement the concentrated changes test. Polytomies in the primate phylogeny (Purvis 1995) were randomly resolved prior to running the test, and we based our statistical results on 1,000 simulations. We also used MacClade to trace characters, e.g., for calculating the numbers of gains and losses. To examine the effects of different random resolutions and the assumptions of parsimony, we repeated analyses using four different randomly resolved trees and the ACCTRAN and DELTRAN reconstruction algorithms (Maddison and Maddison 1992).

When testing particular directional predictions, as outlined above, we used one-tailed statistical tests with the significance level set to 0.05. One-tailed tests have the advantage of increasing statistical power (Cohen 1988; Sokal and Rohlf 1995) and are therefore appropriate when directional, a priori predictions are made and the statistical power cannot be increased by further sampling (a situation common to comparative biology).

Results

General patterns

Information on the presence or absence of male long-distance calling in primates was available for 158 species. First, we examined the phylogenetic distribution of male long-distance calls. Using MacClade (Maddison and Maddison 1992), we found that the presence of male long-distance calls is most likely to be the ancestral state (Fig. 1). Thus, assuming that gains and losses are equally likely, and focusing on unambiguous transitions, long-distance calls were lost 15–16 times during primate evolution, with 2 subsequent reversals depending on resolutions of polytomous nodes. These numbers are unlikely to be exact, given the variety of assumptions involved in reconstructing gains and losses phylogenetically (e.g., Omland 1997; Cunningham et al. 1998). The critical issue for testing the hypotheses that follow, however, concerns the ancestral state and the polarity of trait change in the primate lineages. Based on the distribution of calls across extant primates, we assume that the presence of long-distance calls is the ancestral state for primates. Thus, our phylogenetic tests examine the factors that lead to losses of male long-distance calls rather than gains.

Prior to testing the hypotheses, we examined the general correlates of long-distance calls and their patterns across species. This is an important step to identify potentially confounding variables and avoid spurious relationships. In our dataset long-distance calls were more common in males than females; in fact, there were no species in which females were classified as exhibiting long-distance calls without males also having long-distance calls (Table 2). With regard to ecological factors, long-distance calls were approximately equally common in simple tabulations of diurnal and nocturnal species (Table 3). However, incorporation of phylogenetic information using the concentrated changes test revealed an association between activity period and losses of long-distance calls, with long-distance call losses concentrated significantly on branches characterized by nocturnal

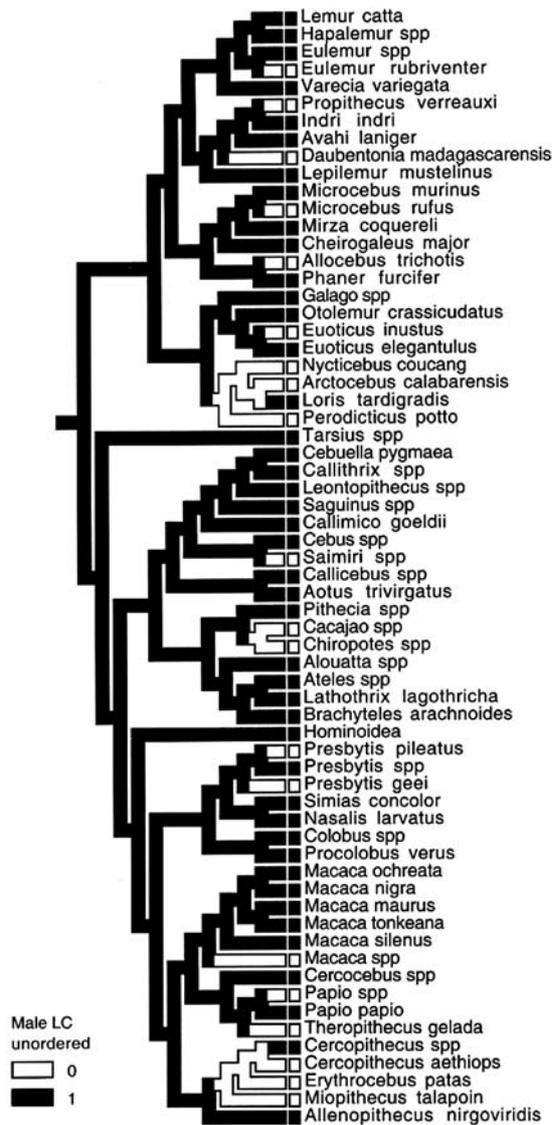


Fig. 1 The absence (0) and presence (1) of male long-distance calls (*Male LC*) mapped onto the Purvis phylogeny (1995). See Purvis (1995) for support indices for particular nodes on this supertree. Species in the same genus that had the same value for male long-distance calls were combined to reduce the size of the printed tree. Therefore only a limited number of species are presented in this figure

activity period ($P=0.03-0.04$, based on alternative resolutions of primate phylogeny). This result is largely due to the nocturnal prosimians in which several long-distance call losses occur. Looking across species, long-distance calls are more common in arboreal taxa (Table 3). The concentrated changes test, however, revealed no significant correlation with substrate use and long-distance call production ($P=0.20-0.28$ based on alternative resolutions of primate phylogeny).

Body mass is a covariate in many comparative studies of primates (Clutton-Brock and Harvey 1977), and it is possible that the presence of long-distance calls also correlates with body mass. We found that larger-bodied pri-

Table 2 Number of species in which males and females produce long-distance calls. Data are available for fewer than the 158 species reported in the text because information was missing on female long-distance calls for two of these species

	Females: no calls	Females: long-distance calls
Males: no calls	34	0
Males: long-distance calls	54	68

Table 3 Number and percentage of species with male long-distance calls for different ecological variables. Data are based on 158 species. Numbers refer to absolute number of species exhibiting criteria for having long-distance calls (see Materials and methods), with numbers in parentheses indicating the percentage of species in that category that exhibit calls. Data from Nunn and van Schaik (2001)

	Male LC
Diurnal	107 (79.9)
Nocturnal	16 (69.6)
Terrestrial	13 (50.0)
Arboreal	111 (84.1)

mates are less likely to produce long-distance calls and this result approaches significance in phylogenetic tests. Thus, 11 out of 17 contrasts in male body mass were negative over evolutionary transitions to long-distance calls ($t_{16}=-1.93$, $P=0.07$). We discuss the implications of this result in what follows.

Long-distance call carrying distance and home range size

All of the hypothesized functions of long-distance calls (mate defense, resource defense, mate attraction) predict that carrying call distance of male long-distance calls should be related to the size of the home range. When focusing on species that were classified as having long-distance calls, we found a significant, positive relationship between carrying distance and home range size using species values ($F_{1,41}=6.89$, $P=0.006$, one-tailed) and independent contrasts ($b=0.20$, $F_{1,36}=5.34$, $P=0.013$, one-tailed; Table 4). The significant result in contrasts analysis, however, relies on removal of three obvious outliers (involving *Colobus polykomos* vs *C. guereza*, *Macaca nigra* vs *M. maurus*, and *Aotus trivirgatus* vs *Callicebus moloch* + *personatus*). These outliers are mainly on the tips of the primate phylogeny and therefore are likely to reflect the error inherent in estimating carrying call distance and branch lengths rather than confounding variables that also create outliers in contrasts analysis (see Nunn and Barton 2000, 2001).

Another way to test for an association is to examine whether increases in home range size are correlated with increases in long-distance call carrying distance in a non-parametric test. This test makes no assumptions regarding branch lengths and evolutionary model, but simply tests whether the direction of change in the two traits

Table 4 Home-range size and carrying distance of long-distance call. Home range data are from Nunn and Barton (2000), unless otherwise indicated. When data were available from more than one source we used mean values. Most studies provide few details on how carrying distance was determined

Species	Home-range (ha)	Distance call (m)	Source for distance call
<i>Alouatta palliata</i>	43.5	1,250	Baldwin and Baldwin 1976; Whitehead 1987
<i>Alouatta seniculus</i>	12.1	1,000	Vercauteren Drubbel and Gautier 1993
<i>Aotus trivirgatus</i>	7.1	50	Robinson et al. 1987
<i>Callicebus moloch</i>	5.7	1,000	Kinzey 1997
<i>Callicebus personatus</i>	4.7	1,000	Kinzey 1997
<i>Callithrix jacchus</i>	13.3	200	Epple 1968
<i>Cercocebus albigena</i>	270.7	1,150	Chalmers 1968; Waser 1977; Brown 1986
<i>Cercocebus aterrimus</i>	59	750	Horn 1987; Estes 1991
<i>Cercocebus galeritus</i>	40.7	600	Quris 1980
<i>Cercocebus torquatus</i>	250	1,000	Estes 1991
<i>Cercopithecus campbelli</i>	21.5	500	Zuberbühler, personal communication
<i>Cercopithecus diana</i>	105.5	800	Zuberbühler, personal communication
<i>Cercopithecus mitis</i>	83.8	685	Waser and Waser 1977; Brown 1986
<i>Colobus badius</i>	57.5	250	Korstjens, unpublished data
<i>Colobus guereza</i>	12.6	750	Marler 1972
<i>Colobus polykomos</i>	36	500	Korstjens, unpublished data
<i>Eulemur mongoz</i> ^a	2.9	100	Curtis, personal communication
<i>Galagoides demidoff</i>	0.9	100	Charles-Dominique 1974
<i>Gorilla gorilla</i>	2,544.5	1,600	Schaller 1963
<i>Hylobates agilis</i>	27	1,000	Gittins and Raemaekers 1980
<i>Hylobates klossi</i>	21.5	625	Tenaza 1975
<i>Hylobates lar</i>	34.2	1,100	Raemaekers and Raemaekers 1984
<i>Hylobates moloch</i> ^b	17	1,000	Kappeler 1984
<i>Hylobates muelleri</i> ^c	36	1,100	Mitani 1985b
<i>Hylobates syndactylus</i>	26.5	3,000	Chivers 1976
<i>Indri indri</i>	22.5	2,000	Pollock 1986
<i>Lemur catta</i>	14.4	1,000	Jolly 1966
<i>Macaca maurus</i>	25	150	Muroyama and Thierry 1998
<i>Macaca nigra</i> ^d	260	300	N. Bynum, personal communication
<i>Macaca silenus</i>	50.7	650	Hohmann 1991; Green 1981
<i>Pan paniscus</i>	3,475	500	Hohmann and Fruth 1995
<i>Pan troglodytes</i>	1,786.8	900	Waser and Waser 1977
<i>Papio papio</i>	1,295	2,500	Byrne 1981
<i>Pongo pygmaeus</i>	2,250	900	MacKinnon 1974; Mitani 1985a
<i>Presbytis comata</i> ^e	38	800	Ruhiyat 1983
<i>Presbytis johnii</i>	161.6	450	Poirier 1968
<i>Presbytis potenziani</i>	22	1,000	Tilson and Tenaza 1976
<i>Presbytis thomasi</i> ^f	37.7	700	S. Wich, unpublished data
<i>Procolobus verus</i>	26.5	150	Korstjens, unpublished data
<i>Saguinus fuscicollis</i>	34.3	200	T. Windfelder, personal communication
<i>Saguinus imperator</i> ^g	30	200	T. Windfelder, personal communication
<i>Simias concolor</i>	14.4	500	Tenaza 1989
<i>Tarsius spectrum</i>	1	400	Gursky 2000

^a Curtis and Zaramody 1998; ^{b,c} Leighton 1987; ^d Kinnaird and O'Brien 2000; ^e Ruhiyat 1983; ^f Assink and van Dijk 1990; ^g Terborgh 1983

are correlated. Results support the prediction: among the 40 positive contrasts in home range size, 30 show expected increases in carrying call distance, giving a significant result in a sign test ($P < 0.005$, one-tailed).

An alternative explanation is that body mass explains the significant association between home range size and carrying call distance, because body mass and home range size show a strong association in our dataset (independent contrasts: $b = 0.93$, $F_{1,35} = 7.72$, $P = 0.009$; see also Nunn and Barton 2001). In fact, when body mass is entered as an independent variable in a multiple regression model with home range size in analysis of independent contrasts, only mass is a significant predictor of carrying distance (mass: $b = 0.64$, $F_{1,34} = 15.7$, $P = 0.0004$; home range: $b = 0.14$, $F_{1,34} = 1.48$, $P = 0.23$). The strong association between body mass and home range size may make it difficult to assess the independent effects of each of these variables in a multiple regression model (i.e., col-

linearity). In addition, body mass is likely to be measured with less error than home range size; thus, body mass may explain more variation in carrying call distance.

Regardless of the underlying causality, these results suggest a mechanism accounting for losses of long-distance calls over evolutionary transitions to increased body mass. Large-bodied species require larger home ranges (Milton and May 1976; Nunn and Barton 2000), and it may be too energetically costly to produce a call that covers the diameter of a large home range, even in large-bodied species. Two lines of evidence support this proposal. First, not all species produce calls that are audible over one home range diameter. Of the 43 species for which data were available, only 18 have long-distance calls that carry more than one home range diameter, and only eight of these species produce long-distance calls that are audible over more than two home range di-

Table 5 Measures of male intra-sexual competition and male long-distance calls. No results significantly different from 0

	Body mass dimorphism		Relative male canine size		Socionomic sex ratio	
	Number of contrasts positive	<i>t</i> -statistic	Number of contrasts positive	<i>t</i> -statistic	Number of contrasts positive	<i>t</i> -statistic
All species	10/16	1.43	4/10	-0.54	5/10	-0.36
Single-male only	1/6	-2.34	1/3	0.47	1/3	0.49

ameters. Second, the presence of male long-distance calls is negatively related to home range size. Thus, among 14 evolutionary transitions to long-distance calls, 13 corresponded with negative contrasts in home range size ($t_{13}=-4.16$, $P=0.001$).

Correlates of male long-distance calls

Mate defense hypothesis

If male long-distance calls function in mate defense, then reductions in male intra-sexual aggression should be associated with losses of male long-distance calls. Using data on body mass dimorphism, relative male canine dimorphism, and socionomic sex ratios, however, we found no support for this prediction (Table 5). This analysis may confound competition within groups and competition between groups, because long-distance calling might be expected between groups while either form of competition may lead to dimorphism. Thus, we also examined these patterns after excluding all species characterized as polygynandrous (to exclude competition for females within the group). However, the results remain non-significant (Table 5).

Mate-attraction hypothesis

To examine the hypothesis that long-distance calls function in mate-attraction, we determined whether losses of male long-distance calls were concentrated on branches characterized by female philopatry. The data (Table 6) indicate that a high percentage of species in which females transfer have male long-distance calls (88.7%), whereas in species without female transfer this percentage is lower (60.0%). However, this difference is not consistently significant in the concentrated changes test. Depending on the resolution of primate phylogeny the number of losses of male long-distance calls in species where females are philopatric varies from five to seven with *P*-values ranging from $P=0.02$ to 0.1.

Resource defense hypothesis

Territorial defense of resources may also explain the distribution of long-distance calls across primate species. There is a general trend for non-territorial species of pri-

Table 6 Number and percentage of species with male long-distance calls in relation to female transfer

	Male LC
Female transfer	55 (88.7)
No female transfer	24 (60.0)

Table 7 Number and percentage of species with male long-distance calls in relation with territoriality measures

	Male LC
Territorial	64 (92.8)
Non territorial	19 (50.0)
D-index >1	47 (81.0)
D-index <1	17 (70.8)

mates to lose long-distance calls, but the association is not perfect (see Table 7).

Among the primates in our dataset, long-distance calling is reconstructed as ancestral, and most losses of male long-distance calls occur on branches characterized by losses of territoriality. Using MacClade, we reconstructed 9–11 losses of male long-distance calls among species with information on territoriality. Depending on the resolution of the polytomies, we found that 7–9 losses of male long-distance calls were concentrated on branches in which territoriality was lost as well. The concentrated changes test showed that this association was significant ($P<0.005$ for all resolutions).

We also examined the patterns using the defensibility index (D-index, Mitani and Rodman 1979) to determine if animals that inhabit more defensible home ranges tend to be more likely to exhibit long-distance calls by males. There was no clear pattern for the D-index to decrease over evolutionary transitions in male long-distance calls (4 of 9 contrasts were negative, $t_8=-0.27$, $P=0.4$, one-tailed). To assess the quality of our data, we tested whether territoriality relates to the D-index and found significant support for this predicted association (12 of 12 contrasts in D-index were positive over transitions in territoriality; $t_{11}=3.48$, $P=0.003$, one-tailed). Body mass was negatively related to the D-index ($b=-0.48$, $F_{1,62}=31.69$, $P<0.001$), and body mass declined significantly over evolutionary transitions in territoriality (of the 16 transitions, 8 produced negative body mass contrasts: $t_{15}=-2.29$, $P=0.036$). These results provide further evidence consistent with the hypothesis that the defensi-

bility of primate home ranges decreases with body mass, potentially explaining the negative association between mass and the presence of male long-distance calls.

As a final test for the possible correlation between male long-distance calls and the D-index, species were classified as having a D-index <1 or >1 (following Mitani and Rodman 1979). The concentrated changes test indicates that male long-distance call losses were not likely to have occurred on branches of the tree characterized by a low D-index (*P*-values range from 0.32 to 0.34 on alternative resolutions of the tree).

These results are therefore contradictory: analysis of territoriality showed an association with male long-distance calling, but the D-index did not, despite a high concordance between the D-index and our measures of territoriality. Moreover, some species also run counter to expectations, since some species have long-distance calls but are not territorial (e.g. *Pongo pygmaeus* and *Eulemur fulvus*) or are territorial but lack long-distance calls (e.g., *Eulemur rubriventer* and *Propithecus verreauxi*). These exceptions provide further evidence that factors other than resource defense play a role in explaining variation in long-distance calling across species.

Habitat use

The data indicate that long-distance calls are indeed more common in species that live in forested habitats. Among terrestrial species, none of those living in open (non-wooded) areas produced long-distance calls, whereas in 13 (68.4%) of the terrestrial species living in wooded areas, males produce long-distance calls. Although male long-distance calls also were lost in species living in wooded areas, there were more losses in species living in open habitats (concentrated changes test: $P=0.03-0.04$ bases on four random resolutions of polytomies). Moreover, gains were concentrated among species living in wooded areas (e.g., the Guinea baboon, *Papio papio*).

Discussion

Phylogenetic reconstruction indicates that the presence of male long-distance calls is the ancestral state for primates. Among extant species, long-distance calls more commonly characterize males than females. The major factors that explain this diversity are activity period, body mass, habitat, and home range size. We also found a strong association between home range size and long-distance-call carrying distance. Surprisingly, we found evidence for the mate attraction and resource defense hypotheses in some tests, yet no support for the more widely accepted hypothesis that long-distance calls function in mate defense. Recently, Fashing (2001) argued that resource defense polygyny may be an overlooked factor in primate social evolution. Although our results fail to support this function of male territoriality as a general phenomenon in primates, they further highlight the need to investigate such factors

within-species. Below, we discuss directions for future research on the mate attraction hypothesis, which has been less thoroughly considered in primates.

What factors can account for our results? First, the presence of male long-distance calls appears to be subject to costs of call production. Most primates produce long-distance calls that carry less than one home range diameter and long-distance calls are lost over evolutionary increases in body mass and home range size. These results suggest that long-distance call production is limited by the costs of producing such calls. In addition, long-distance calls are not found in terrestrial species living in open habitats, which is consistent with vocalizations propagating less efficiently when produced at ground level (Waser and Brown 1986).

Second, our results provide indirect evidence that long-distance call production is sensitive to the benefits. Multiple benefits appear to play a role in explaining the presence of male long-distance calls. Thus, body mass was negatively related to the D-index, and mass declined significantly over evolutionary transitions in territoriality. These results may indicate that larger-bodied species experience reduced benefits of territorial defense. In addition, long-distance calls are less common among terrestrial species living in open habitats. Terrestrial species have even larger home ranges for their body mass than arboreal species, increasing the distance between groups and thus reducing the benefits of inter-group vocal communication. Males may compete for mates more often within than between groups in these species, which typically have multi-male social groups, further reducing the benefits of inter-group communication. This may explain the lack of support for the mate defense hypothesis, because the conditions that favor mate defense, such as increased body mass and a slower life history (Mitani et al. 1996), may also increase the costs of producing long-distance calls or defending a larger home range.

Comparative tests of long-distance calling in primates

These comparative results highlight the need to combine comparative patterns with detailed study within species. Both types of studies can provide important, and independent, insights to the function of male loud calls. A comparative approach is needed to address the origins of traits and the generality of patterns across species. Moreover, comparative patterns highlight the key variables for more detailed study within species. Thus, our study indicates that body mass, home range size, habitat and defense of resources are key factors to consider in the field. By combining comparative studies of broad evolutionary patterns with detailed analysis of competing hypotheses within species (e.g., Fashing 2001; Wilson et al. 2001; Wich et al. 2002a b), it should be possible to most thoroughly illuminate the multiple factors that influence the costs and benefits of loud call production.

In addition to the possibility that long-distance calls serve multiple functions, several factors could account

for the lack of support in our comparative tests. First, our measures of competition (body mass dimorphism, relative male canine size, and socionomic sex ratio) may have been too indirect for testing the mate defense hypothesis. In addition, these measures may be more finely-tuned to patterns of male-male competition within groups, whereas our tests focused on competition among males in different social groups. At present, few alternative measures exist for conducting comparative studies of this type because inter-group competition has not been measured consistently across species. Even when the analyses are restricted to polygynous species, however, results were non-significant.

Second, our analyses may have had insufficient statistical power (Thomas and Juanes 1996). However, this explanation is contradicted by the strong statistical signal that we obtained in some analyses, even with small sample sizes or few evolutionary transitions. Our sample sizes were relatively large compared to other comparative studies in primates. Nonetheless, patterns that were in the predicted direction but not significant, such as analyses of the mate attraction hypothesis, may reflect measurement error in predictor variables and thus low statistical power.

Third, social factors may modify the production of long-distance calls. In a previous comparative study, Nunn (2000) used the presence of long-distance calls as a surrogate measure of collective action problems, in which the sharing of benefits leads to a failure to provide the benefit (see also van Schaik 1996; Nunn and Lewis 2001). Consistent with predictions, it was found that the number of males in the group and measures of testes mass were correlated negatively with the production of long-distance calls. To control for social factors such as the collective action problem, we focused on species with particular social organizations in some tests. However, we did not examine this hypothesis directly because our analyses were focused on the function of long-distance calls, and collective action problems can arise under most of the hypotheses that we investigated.

Mate attraction and the costliness of male long-distance calls

Long-distance calls may play a mate attraction role in some species (e.g., orangutan: *Pongo pygmaeus*, Utami and Mitra Setia 1995; Thomas langur: *Presbytis thomasi*, Steenbeek et al. 1999), but there is as yet no experimental evidence that long-distance calls serve a mate-attraction function (orangutan, Mitani 1985a). This hypothesis therefore deserves further scrutiny. For example, a possible prerequisite for long-distance calls to be of relevance in mate defense is that they contain cues to assess the "quality" of the caller, as has been shown for songbirds (e.g., Lambrechts 1992) and anurans (e.g., Ryan and Keddy-Hector 1992). The handicap principle predicts that signals that serve a role in mate-attraction or mate defense are likely to be costly and honest (Zahavi 1975,

1977; Grafen 1991). In addition, females may base their choice on multiple factors, including body condition, intergroup contest competition, and copying other females (Gibson and Hoglund 1992; Ryan and Keddy-Hector 1992; Sterck 1997; Steenbeek 1999).

Results discussed above regarding body mass and carrying distance provide further evidence that calling is costly, but research is needed to more directly assess the costliness of long-distance-calling. Although several studies have shown that calls are energetically costly to produce (anurans and insects, e.g., Ryan 1988; Prestwich 1994; but see Chappell et al. 1995; Horn et al. 1995, for birds), data on the costliness of primate calls remain sparse. In gibbons, calling rates decreased with altitude (temperature) and during the non-fruiting season (Cowlshaw 1996), consistent with the hypothesis that long-distance calls are costly. It has also been reported that primates give morning calls less often after rainy nights (*Hylobates klossii*, Whitten 1980; *Presbytis thomasi*, Wich unpublished data). To the extent that both altitude and rain negatively affect body condition (Cowlshaw 1996), these studies are consistent with the hypothesis that long-distance calls are costly in primates.

In summary, our results are consistent with the proposal that primate long-distance-calling is a multi-functional phenomenon (Waser 1977; Whitehead 1987). Although sometimes anecdotal, there is evidence for each of the above hypotheses from field studies, but many of the predicted patterns did not emerge when examining broad phylogenetic patterns. These comparative tests highlight the questions that can be addressed concerning the function of male long-distance calls and the need for detailed (experimental) field studies.

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