

explained in terms of sequential carrier capture by the QD: If electron capture in our QDs is more likely than hole capture, the creation of the 2X state requires that a QD in state X^- capture an additional hole. Yet if the X^- emission rate increases because of a large Purcell effect, the 2X emission will be reduced because the QD is less likely to capture the second hole before the X^- recombines. On the basis of this observation, we conclude that a systematic study of the QD-cavity system, only feasible within a deterministic approach, can give new insights into the carrier capture and multi-exciton dynamics of the QDs.

The QD-cavity coupling coefficient (g) that we extract for our device I, using the data for the off- and near-resonance cases (Fig. 2B) and assuming a cavity enhancement of the collection efficiency by a factor of 20 (23), is $g \approx 80 \mu\text{eV}$. This value is only half the theoretical maximum for our cavity structure. The value of g as well as its insensitivity to positioning can be improved by using other PC-cavity designs that also exhibit higher Q values and higher fabrication defect tolerance.

By achieving a deterministic spatial and spectral overlap between a QD exciton line and a PC nanocavity mode, we have demonstrated the realization of a truly tunable solid-state cavity QED system and established a framework for the realization of a new set of cavity QED experiments previously implemented only in atomic

systems. The broad implication of this research, however, can have some immediate application in several appealing directions, such as cavity-assisted QD spin-flip Raman transition for generation of indistinguishable single photons (24), coupling of two QDs to a single common cavity mode (25), and simultaneous coupling of a cavity mode to both X and 2X lines of a single QD.

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Materials and Methods

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The Highland Mangabey *Lophocebus kipunji*: A New Species of African Monkey

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A distinct species of mangabey was independently found at two sites 370 kilometers apart in southern Tanzania (Mount Rungwe and Livingstone in the Southern Highlands and Ndundulu in the Udzungwa Mountains). This new species is described here and given the name "highland mangabey" *Lophocebus kipunji* sp. nov. We place this monkey in *Lophocebus*, because it possesses noncontrasting black eyelids and is arboreal. *L. kipunji* is distinguished from other mangabeys by the color of its pelage; long, upright crest; off-white tail and ventrum; and loud call. This find has implications for primate evolution, African biogeography, and forest conservation.

The most recently discovered species of monkey in Africa was the sun-tailed monkey, *Cercopithecus solatus*, found in Gabon in 1984 (1). Here, we report on the discovery of a new species of mangabey in Tanzania. This discovery was made almost simultaneously by independent fieldworkers on different mountain ranges in southern Tanzania. We relate the circumstances of discovery in the two sites, describe and name the new species, and discuss its conservation status.

Southern Highlands population. The Southern Highlands of southwest Tanzania (Fig. 1) rise to 2961 m above sea level (asl) and comprise mountain ranges capped by forest-grassland mosaic. The Highlands receive rainfall via convective uplift from Lake Nyasa of up to 2900 mm a year, the highest in Tanzania.

Within the Southern Highlands, the Tanzanian government is presently gazetting the

Kitulo Plateau and adjacent Livingstone Forest as the Kitulo National Park (412 km², 09°00'S to 09°16'S and 33°43'E to 34°03'E) (2). Mount Rungwe Forest Reserve (150 km², 09°03'S to 09°12' S and 33°35'E to 33°45'E) supports montane and upper montane forest, bamboo, and plateau grassland. The montane forests of Mount Rungwe and Livingstone (Rungwe-Livingstone) are joined only by a narrow corridor of degraded forest. Until now, eight species of primate were known from the Southern Highlands, including a probable new species of dwarf galago, *Galagoides* sp. (3).

During interviews in January 2003 in villages around Mount Rungwe, we heard rumors about a shy and atypical monkey known as *Kipunji* (kip-oon-jee). The local Wanyakyusa have a strong oral tradition based on both real and mythical forest animals, and validation of these rumors was protracted. We first observed an unusual primate during biodiversity surveys on Mount Rungwe in May 2003, but

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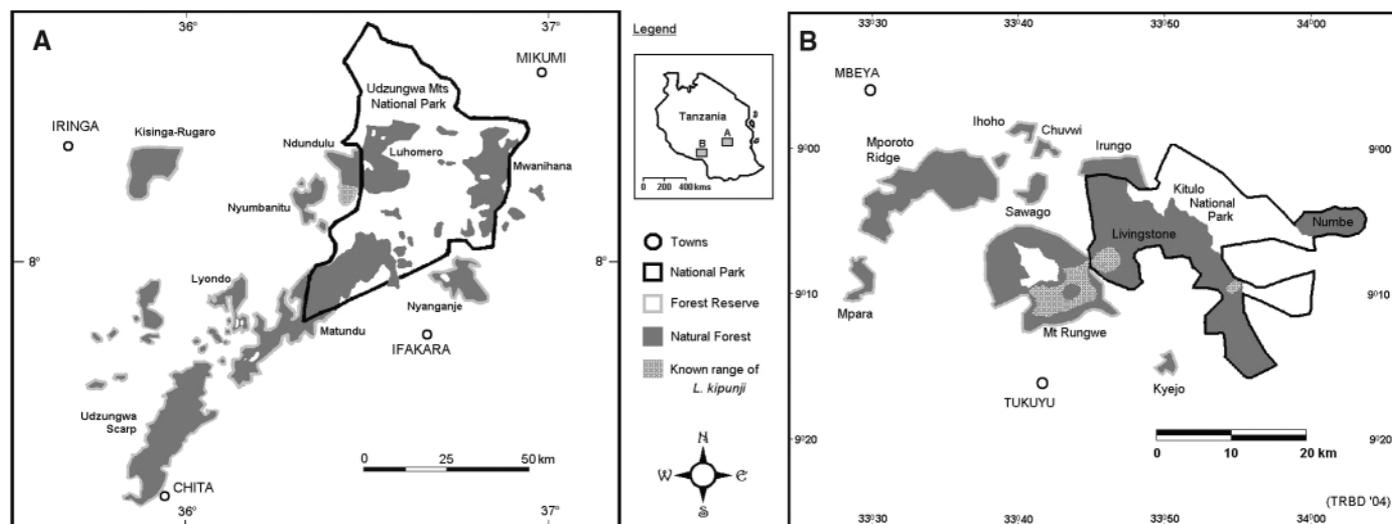


Fig. 1. Maps of Tanzania's Udzungwa Mountains (A) and Southern Highlands (B) showing the known range of the highland mangabey *Lophocebus kipunji*.

because of the terrain, thick secondary forest, and the animal's cryptic nature, sightings were infrequent and poor. It was not until December 2003, during work in the contiguous Livingstone Forest, that the monkey was clearly observed and recognized as a new species of mangabey.

Ndundulu population. The Udzungwa Mountains (Udzungwas: 10,000 km², 07°40'S to 08°40'S and 35°10'E to 36°50'E) lie 350 km to the northeast of Rungwe-Livingstone (4, 5). Supporting circa (ca.) 1017 km² of fragmented forest (6), the Udzungwas receive a maximum annual rainfall of roughly 2200 mm and were previously thought to hold 10 primate species (7), including the endemic Sanje mangabey, *Cercocebus sanjei*, discovered in 1979 (8).

Two populations of the Sanje mangabey are known from the Udzungwas (7, 9). During visits from 1991 to 2000, ornithologists working in the Ndundulu Forest Reserve (Fig. 1) reported a third population of the Sanje mangabey (10). Subsequent surveys failed to confirm the presence of this species in Ndundulu (7, 9, 11) and led to our intensified surveys in July and September 2004. During these surveys, Sanje mangabeys were not encountered or heard. However, on 7 July 2004, the new species of mangabey was discovered. It now seems certain that the ornithologists had misidentified the new species of mangabey as the Sanje mangabey.

The researchers working on each of these two new populations of mangabeys did not become aware that a second population was known until October 2004.

Lophocebus kipunji Ehardt, Butynski, Jones, and Davenport sp. nov.

Holotype. Adult male in photograph (Fig. 2). Photograph taken in the type locality at 9°07'S 33°44'E (12). The number of individuals in each of the two populations of this species is undoubtedly very small; no



Fig. 2. Holotype: adult male highland mangabey *Lophocebus kipunji* in the type locality, Rungwe-Livingstone, Tanzania. [Photograph by T.R.B. Davenport]

live individual should be collected at this time to serve as the holotype. The Rungwe-Livingstone population is designated the source population for physical specimens in support of the holotype.

Paratype. Adult in photograph (Fig. 3). Sex not known. Photograph taken in Ndundulu Forest Reserve (07°48'45"S 36°31'05"E), Udzungwa Mountains, Tanzania.

Type locality. Rungwe-Livingstone (09°07'S to 09°11'S and 33°40'E to 33°55'E), Southern Highlands, Tanzania.

Diagnosis. Pelage of dorsum light to medium brown, center of ventrum and distal half of



Fig. 3. Paratype: adult highland mangabey *Lophocebus kipunji*, Ndundulu Forest Reserve, Tanzania. [Photograph by T. Jones]

tail off-white. Crown with very long, broad, erect crest of hair. Eyelids black, not contrasting with color of face. Adults emit a distinctive, loud, low-pitched "honk-bark" (Fig. 4). Arboreal. Found only at high altitudes (1300 m up to 2450 m asl) and low-temperature tolerant; temperatures in Rungwe-Livingstone drop to at least -3°C.

Description. A primarily brown, medium-sized, long-tailed, arboreal monkey. Muzzle elongated. Facial skin, including eyelids, black. Suborbital fossae "tear line" pronounced. Eyes brown. Pelage light to rufous brown except as follows: center of ventrum and distal half of tail, white to off-white; hands and feet, black; lower forelimbs, dark brown to black. Cheek whiskers long. Crown with very long, broad, stiff, upright crest of hair. Shoulder cape present in some individuals, although there is variation in length and color. White of ventrum sharply offset from brown in at least

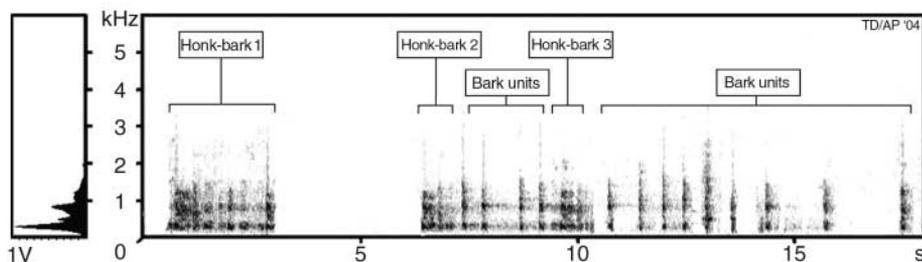


Fig. 4. Sonogram of three honk-bark calls given by adult *L. kipunji* from the type locality, with two series of barks. Honk-barks, which appear to play a role in intergroup spacing, are given singly or in series and may, as in this example, be interspersed with barks. Honk-barks are short discrete phrases, composed of a variable number of units. The first honk-bark shown here has six units. Honk-barks are frequency modulated with formants or emphasized harmonics. In the honk-bark, the first harmonic or “fundamental frequency” is that part of the call with the lowest frequency and often the greatest amplitude, and is thus the farthest traveling element. The fundamental frequency of the honk-bark is 0.28 kHz ($n = 3$), the frequency range is 0.180 to 0.304 kHz, and the mean unit interval is 0.076 s ($n = 3$). This call is thus qualitatively and quantifiably different from the type I and type II calls of other studied mangabey species (20, 21). [Call recorded by N. E. Mpunga. Sonogram prepared and interpreted by A. Perkin.]

some Ndundulu animals. Ventrums lighter than rest of body in Rungwe-Livingstone animals but not sharply offset. Small patch of off-white hair between neck and sternum in Rungwe-Livingstone animals. Individual hairs appear to be straight and devoid of bands or speckling. Tail pelage smooth, not shaggy or lax. Tail carried loosely and parallel to or below plane of the back, curving downward to feet level during locomotion. Tail not held strongly arched over back when standing, nor held vertically, except as a semi-prehensile support. No sexual dimorphism in color of adult pelage. Ischial callosities pink: fused in the male, unfused in the female. Genital swelling in oestrus females.

Measurements. None available. Head-body length of adult males in the Rungwe-Livingstone population estimated at 85 to 90 cm. Tail about equal in length to head and body. Adult male body weight estimated at 10 to 16 kg.

Etymology. The specific name acknowledges the Kinyakyusa name for this monkey in Rungwe-Livingstone.

Distribution. Known to occur in ca. 70 km² of Rungwe-Livingstone in the Southern Highlands, Tanzania, from 1750 up to 2450 m asl (possibly up to 2600 m asl), and from ca. 3 km² of Ndundulu Forest Reserve, Tanzania, from 1300 up to 1750 m asl.

Habitat. From pristine submontane forest in Ndundulu to degraded montane and upper montane forest in Rungwe-Livingstone.

Mangabeys are medium-sized monkeys confined to the forests of equatorial Africa (13). Taxonomically controversial, there are currently from five to nine species (and from five to 11 subspecies) recognized in two genera (*Lophocebus* and *Cercocebus*) (14, 15). The mangabeys are diphyletic, as revealed by molecular studies and supported by anatomical and behavioral characteristics. *Cercocebus* spp. are most closely related to mandrills and drills (*Mandrillus* spp.), have pink or white eyelids that contrast with the color of the face,

and are semiterrestrial. *Lophocebus* spp. are most closely related to baboons, *Papio* spp., and the gelada, *Theropithecus gelada*; have black eyelids that do not contrast with the color of the face; and are arboreal (14, 16–18). We place this new species in the genus *Lophocebus* on the basis of the combination of its noncontrasting black eyelids and arboreality. *L. kipunji* is isolated from the nearest other species of *Lophocebus* (*L. albigena*) by about 800 km.

The other two species of *Lophocebus* (15) differ from *L. kipunji* as follows:

Gray-cheeked mangabey *L. albigena*: Body and tail blackish-brown. Cheek whiskers gray. Crown with short tuft (or tufts) of hair (14). Frequently holds tail vertical or arched over back. “Whoop-gobble” loud call. Mainly occurs below 1600 m (13), except Nyungwe, Rwanda, and Kahuzi-Biega, Democratic Republic of Congo, where it occurs up to ca. 2350 m (19).

Black mangabey *L. aterritimus*: Entire body black. Crown with tall, thin, central tuft of hair. Cheek whiskers thick and gray (14). Whoop-gobble loud call. Not known to occur above 450 m asl.

All mangabey species studied to date possess a loud call, emitted by adult males to coordinate intergroup spacing (20, 21). The characteristic whoop-gobble loud call of other *Lophocebus* species has not been detected in *L. kipunji*. Adult males in Rungwe-Livingstone do give a distinctive honk-bark (Fig. 4), which is most evident when conspecific groups meet.

In Rungwe-Livingstone, we have identified 10 groups of *L. kipunji*: five in the southern section of Mount Rungwe, four in the northern section of Livingstone, and one in the southern section of Livingstone 20 km to the east (Fig. 1). We estimate the total population of *L. kipunji* in Rungwe-Livingstone to be 250 to 500 animals.

L. kipunji are known from only 3 km² of Ndundulu Forest. Previous research in the area (7, 11, 22, 23) and lack of independent knowledge of the species among local villagers indicate that this monkey is absent from large parts of this forest. We estimate the geographic range for this population to be 3 to 50 km². Only three groups have so far been located in Ndundulu, and it seems unlikely that this population exceeds 500 animals.

Once the degree of threat status is formally assessed for the *IUCN Red List of Threatened Animals*, we expect that *L. kipunji* will be classified as a critically endangered species (24).

The presence of a third threatened species of monkey makes the Udzungwas arguably the most important single site in Africa for the conservation of primate biodiversity. The presence of *L. kipunji* in both sites also supports the hypothesis that the Southern Highlands are zoologically more aligned to the Eastern Arc Mountains than has usually been thought (25).

The threats to *L. kipunji* are considerable. The Rungwe-Livingstone forests are severely degraded. Logging, charcoal making, poaching, and unmanaged resource extraction are common. The narrow forest corridors linking Mount Rungwe to Livingstone and joining the northern and southern sections of Livingstone are almost completely encroached upon. Without immediate conservation intervention, these forests will be fragmented, resulting in three isolated subpopulations of *L. kipunji*; indeed, the easternmost animals may already be isolated. Gazettement of Kitulo National Park should help protect the smaller Livingstone Forest population. However, swift and effective action is imperative, both in the new park and especially within Mount Rungwe Forest Reserve.

Although the submontane forest of Ndundulu is in excellent condition and no signs of recent hunting have been observed in the area from which *L. kipunji* is known, this monkey is present in low numbers. If this small population is to be protected in perpetuity, the Udzungwa Mountains National Park needs to be extended to include the Ndundulu Forest.

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Functional Genomic Analysis of RNA Interference in *C. elegans*

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RNA interference (RNAi) of target genes is triggered by double-stranded RNAs (dsRNAs) processed by conserved nucleases and accessory factors. To identify the genetic components required for RNAi, we performed a genome-wide screen using an engineered RNAi sensor strain of *Caenorhabditis elegans*. The RNAi screen identified 90 genes. These included Piwi/PAZ proteins, DEAH helicases, RNA binding/processing factors, chromatin-associated factors, DNA recombination proteins, nuclear import/export factors, and 11 known components of the RNAi machinery. We demonstrate that some of these genes are also required for germline and somatic transgene silencing. Moreover, the physical interactions among these potential RNAi factors suggest links to other RNA-dependent gene regulatory pathways.

Posttranscriptional gene silencing by RNAi is a conserved process by which dsRNA triggers the destruction of homologous target mRNAs (1). RNAi-related mechanisms also mediate heterochromatin formation, silencing of transposable elements, antiviral defense, genome rearrangements, cell proliferation, cell differentiation, cell death, and developmental timing and patterning (2–5).

Although genetic and biochemical studies have identified components of RNAi, including the dsRNA processing enzyme Dicer (DCR-1) and the effector complexes RISC (RNA induced silencing complex) and RITS [RNA-induced initiation of transcriptional gene silencing (TGS)] (1, 2), a comprehensive genomic analysis by RNAi should in principle identify the complete pathway. Using RNAi to identify RNAi factors has been demonstrated previously (6). In addition, the production of non-null phenotypes by RNAi enables the study by RNAi of essential genes, such as *dcr-1*, the only *C. elegans* Dicer. In this study, we have used a genome-wide approach to identify an extensive set of genes required for RNAi in *C. elegans*.

To monitor RNAi in vivo, we designed an "RNAi sensor" strain (GR1401) that expresses both a *gfp* (green fluorescence protein) dsRNA hairpin and a *gfp* reporter gene in *C. elegans* epithelial seam cells (Fig. 1A). In wild-type animals, *gfp* dsRNA targets the *gfp* mRNA for degradation, abrogating GFP

expression. Feeding the *C. elegans* RNAi sensor strain bacteria that express dsRNA corresponding to genes previously implicated in RNAi robustly restored GFP expression, whereas control dsRNA did not (Fig. 1B).

We screened a library of bacterial clones expressing dsRNAs designed to individually inactivate 94% of the ~19,000 predicted genes in the worm genome (7, 8) [table S1 (9)]. L1-stage larvae of the RNAi sensor strain were fed each bacterial clone, and GFP fluorescence was monitored in their progeny. For the 945 genes annotated as embryonic lethal (7), L1-stage animals were fed the bacterial clone and GFP fluorescence was monitored in the later larval or adult stage of the same generation. All experiments were scored on a GFP intensity and penetrance scale of 0 (no GFP expression) to 4 (highly penetrant, strong GFP expression), and those that scored an average of ~2 or greater were designated candidate RNAi genes (Table 1). All candidate clones were retested no fewer than five independent times in triplicate.

Screening of the genome-wide RNAi library identified 90 clones (0.5%) that reproducibly disrupt RNAi. Eleven of these correspond to loci known to be required for RNAi, including the core RNAi machinery such as *dcr-1*, *rde-1*, and *rde-4* (Table 1 and table S2). Fifty-four of the new genes are essential for viability, and one-third of the viable 25 new genes exhibit reduced brood sizes ($P < 0.01$, Student's *t* test) (table S3); 85% of the new genes have human homologs, suggesting conserved functions (Table 1 and table S4). It is possible that some of the identified factors could be non-specific; for example, inactivation of a factor (e.g., *dpy-20*) could inhibit the expression from one epidermal promoter of the RNAi sensor strain but not the other. However, because a large majority of the RNAi clones tested also affect transgene silencing in a variety of other tissues (see below), most are likely to act in the RNAi pathway.

To verify that genes uncovered in our screen are required for RNAi of endogenous

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