

Occupancy, coat colour pattern and social organization of mixed-species and mixed-morphotype groups of Nilgiri langur (*Semnopithecus johnii*) and tufted grey langur (*Semnopithecus priam*)

Santanu Mahato^{1,2,3}, Honnavalli N. Kumara², Mridula Singh⁴ and Mewa Singh^{1,*}

¹Biopsychology Laboratory and Institution of Excellence, University of Mysore, Mysuru 570 006, India

²Sálim Ali Centre for Ornithology and Natural History, South India Centre of Wildlife Institute of India, Coimbatore 641 108, India

³Department of Zoology, Bharathiar University, Coimbatore 641 046, India

⁴Department of Psychology, Maharaja's College, University of Mysore, Mysuru 570 005, India

A mixed-species group is formed due to an increase in close association among individuals of different species. Such groups also possibility of having diversity in size, phenotypic similarities and differences, and contrasting morphologies compared to the original species. We studied inter-individual variations in external morphology and social structure in mixed-species groups of Nilgiri langur (NL, *Semnopithecus johnii*) and tufted grey langur (HL, *Semnopithecus priam*) between 300 and 800 m in the Anamalai Tiger Reserve, Western Ghats in India. The study reports the largest number of mixed morphotypes in a population having a higher abundance of dark grey morphs at lower altitudes, light brown morphs in the mid altitudes and more dark brown morphs at higher altitudes. The group size of mixed species was mostly multi-male and multi-female and larger than the NL and HL groups. Our study provides a framework to determine their inter-specific interactions and reproductive strategies which are necessary in overlapping ranges.

Keywords: Altitudinal gradients, hybridization, langurs, mixed-species associations, sympatricity.

OCCUPATION of different niches or coexistence by closely related species of animals has been a topic of particular interest in ecology for a long time^{1,2}. Closely related species are often at the same trophic level and, hence, face more severe competition for resources than those at different trophic levels. Natural selection favours processes that reduce competition in nature. The literature abounds with examples where closely related species have been observed to spatially space out in evolutionary and ecological times. In the Indian ecosystem, for example, lions *Panthera leo* and tigers *Panthera tigris* are found in open and dense forests respectively³. Likewise, dhole *Cuon alpinus* is

generally found in relatively denser forests, whereas grey wolves *Canis lupus* and Bengal foxes *Vulpes bengalensis* inhabit open country. If related species are in the same ecosystem, they still find different habitats. In the Anamalai Hills of the Western Ghats of India, the bonnet macaque *Macaca radiata*, a frugivore, and the Hanuman langur *Semnopithecus* sp., a folivore, are sympatric in the deciduous forests at lower altitudes, while the frugivore lion-tailed macaque *Macaca silenus* and the folivore Nilgiri langur *Semnopithecus johnii* are sympatric in wet forests at higher altitudes⁴, thereby indicating that species with similar resource use, space out to different habitats. If two or more related species occur together in the same habitat, they may use different strata or substrata. Several primate species in the forests of Peru move and utilize resources in different parts of the same trees, such as vertical or horizontal and upper or lower canopy⁵. If found at the same stratum, sympatric species may specialize in different resource types or resource phenophases, but any food niche overlap, even for short periods of time, often results in inter-species agonistic interactions⁶. The distribution of resource utilization among neighbours influences the extent of overlap between space-sharing among individuals^{7–10}. Even if the resources used are largely the same, sympatricity is still possible if the food niche overlap occurs at the time of abundance in the availability of shared resources in the habitat¹¹. If the competition for food resources is minimal, species may tend to form mixed-species associations or even mixed-species groups^{12,13}. A mixed-species group is defined as ‘a group of independently moving animals from more than one species found in close proximity, which interact with one another’¹⁴. Antipredation, finding a mate, increased movement efficiency or anthropogenic factors are primarily attributed to mixed-species groups^{15–17}. A review of a large number of publications on various taxa shows enormous diversity in mixed-species groups in size¹⁴, phenotypic similarities and differences, and contrasting

*For correspondence. (e-mail: mewasinghltm@gmail.com)

morphologies. Despite many differences in the behaviour patterns of species in mixed-species groups, an organization consistency is observed where one, or sometimes a few, species become ‘catalyst’¹⁸, ‘leader’¹⁹ or ‘central’^{20,21}. By proposing a two-dimensional structure in which one axis represents the similarity of benefit types and the second axis expresses asymmetry in the relative amounts of benefits/costs accrued, Goodale *et al.*²² have provided a comprehensive framework to understand the composition and organization of mixed-species groups. Increased interaction in mixed-species groups may also result in interbreeding and hybridization, as observed among Asian colobines, where the probable hybrids show colour variation among individuals in mixed-species groups^{23–27}.

In India, several reports have confirmed the presence of mixed-species associations between two sympatric colobines, i.e. Nilgiri langurs and Hanuman langurs (tufted grey langurs) in numerous locations of the Western Ghats^{28–31}. Nilgiri langurs are more folivorous than Hanuman langurs³². The social structure, relationships and behavioural patterns of Nilgiri langurs are similar at some level to those of Hanuman langurs^{33,34}. In the mixed-species groups, brown morphs with several inter-individual colour variations are observed³¹. However, little is known about these inter-individual variations and the distribution pattern of the mixed-species groups.

In this study, we examined whether the social structure in the mixed-species/mixed morphotypes groups differed from the Nilgiri langur and Hanuman langur groups. Also, what are the inter-individual variations in colour patterns in mixed-species groups? Does the social structure among the mixed-species groups differ along the altitudinal gradient? Do vegetation cover and structure restrict the habitat suitability of Nilgiri langurs, Hanuman langurs and their mixed-species groups?

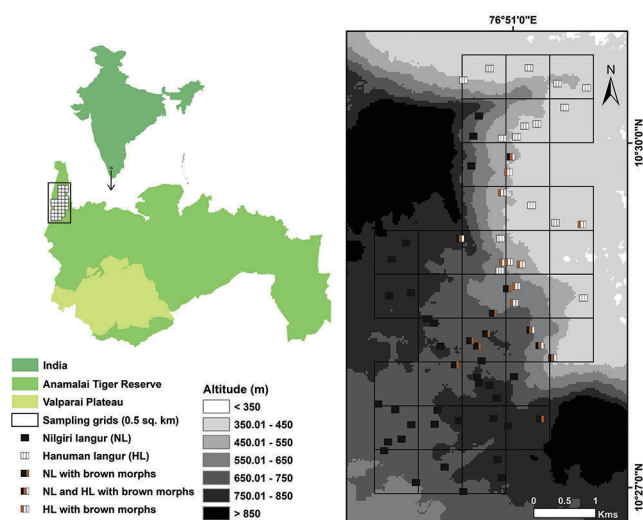


Figure 1. Location of the study area (Topslip forest at Ulandy and Pol-lachi ranges) within the Anamalai Tiger Reserve, Tamil Nadu, India, and sampling grids along the altitudinal gradient showing the distribution of different langur groups.

Materials and methods

Study site

The study was conducted in the Anamalai Tiger Reserve (ATR) of the southern Western Ghats, Tamil Nadu, India (Figure 1). The altitude of ATR (an area of 958.59 sq. km) ranges from 220 m in the plains to 2513 m in the shola grasslands. The high altitudinal gradient and different rainfall patterns between the slopes have resulted in various types of vegetation. The protected area covers large regions of shola-grassland ecosystems, tropical wet evergreen forests, tropical moist and dry deciduous forests, and tropical dry thorny forests. Annual rainfall in the Reserve is 800 mm on the eastern dry rain-shadow side and 3500 mm on the western windward side.

Study species

The relatively dry deciduous and scrub forests on the eastern slopes of the Anamalai Hills system harbour tufted grey langurs *Semnopithecus priam* and bonnet macaques, while the relatively wetter regions on the ridge, valleys and the western slopes consist of Nilgiri langurs, lion-tailed macaques and the occasional bonnet macaques⁴. Nilgiri langurs and tufted grey langurs are found in the transition zone between two different habitats, i.e. tropical semi-evergreen/moist deciduous and dry deciduous forests in the reserve.

Survey design and data collection

The study began in February 2021 with the aim of assessing the population distribution patterns of langurs within ATR. We observed a few mixed-species langur groups in the transition zone of tropical moist and dry deciduous forests (between 400 m and 800 m). Based on the initial observations, we designed a grid-based study along the altitudinal gradient between December 2022 and March 2023, to further analyse the distribution pattern of different mixed-species groups.

Keeping the home range size of Nilgiri langurs^{35,36} and Hanuman langurs³⁷, a grid cell size of 0.5 sq. km or 50 ha was considered as the sampling unit. Since the tufted grey langurs are found up to 800 m and Nilgiri langurs from 200 m to the shola forests⁴, we also focused on their distribution pattern along an altitude gradient in the overlapping zone. We overlaid the 0.5 sq. km grid cell on the map of the selected site in ATR for sampling on the QGIS platform. The shape file of the grid cell was uploaded to the handheld global position system, and the same was realized on the ground. A total of 36 grid cells were sorted for sampling covering an area of 18 sq. km (Figure 1). In each grid cell, we walked 1.5–5 km of trail covering the entire grid cell (between 0600 and 1100 h at the speed of 1 km/h). On the trail, every 500 m of sampling was considered as one spatial replicate; thus, a minimum of three and a maximum of four replicates were done for each grid cell. We

Table 1. Demographic composition of Nilgiri langur, tufted grey langur and their mixed-species groups in the Anamalai Tiger Reserve, Tamil Nadu, India

Species	Group size	Adult male		Adult female		AF/AM
		(AM)	(AF)	Juvenile	Infant	
Nilgiri langur	6	1	4	1	0	4.00
	5	1	3	1	0	3.00
	7	1	4	2	0	4.00
	10	1	4	5	0	4.00
	5	1	2	1	1	2.00
	8	1	3	1	3	3.00
Mean	6.83	1.00	3.33	1.83	0.67	3.33
Mixed-species groups	14	1	7	3	3	7.00
	18	4	6	6	2	1.50
	21	3	9	4	5	3.00
	8	2	3	1	2	1.50
	10	1	3	3	2	3.00
	9	1	5	1	2	5.00
	18	4	4	3	7	1.00
	25	3	10	11	3	3.33
	20	3	4	9	4	1.33
	23	3	10	7	3	3.33
	9	1	3	3	2	3.00
	11	2	5	3	1	2.50
Mean	15.50	2.33	5.75	4.50	3.00	2.96
Tufted grey langur	13	1	6	5	1	6.00
	17	1	8	2	6	8.00
	9	1	4	2	2	4.00
	10	1	6	3	0	6.00
	11	1	5	3	2	5.00
	7	1	3	2	1	3.00
Mean	11.17	1.00	5.33	2.83	2.00	5.33

walked a total of 56.39 km. On every sighting of the langur group, we spent 15–20 min with it and recorded (i) group size, age–sex information, and (ii) body colour pattern and head tuft. Wherever the complete characterization of morphs of all individuals could not be collected during grid sampling, we revisited those groups and spent enough time to obtain details of the morphological parameters of all the individuals.

In addition, we identified different forest types within the grid cells – medium elevation wet evergreen forests (EF), semi-evergreen degraded forests (SEDF), dry deciduous forests (DDF), dry deciduous forests with bamboo (DDFB), dry deciduous forest and thorny scrubs (DDFS), gallery forest (GF), teak plantations (TP) and eucalyptus plantations (EP). By overlaying the grid layer on the classified map of the study area, we extracted the area of each forest type in the grid cell and then estimated the proportion of each forest type for the grid cell. We used the digital elevation model (DEM) layer of the study site, and overlaid the grid layer and extracted altitude for multiple locations in the grid cell; we also considered their mode as representative altitude for the grid cell.

Data analysis

Using the langur group detections in grid walk, we computed the group encounter rate for each grid cell as the number

of groups per kilometre of walk done. The mean encounter rate for each langur species and mixed-species group was computed using the encounter rate from all the grid cells.

We obtained the total group size and age/sex of all the individuals for 6 groups of Nilgiri langur, 6 groups of tufted grey langur, and 12 mixed-species/mixed morphotypes groups. We calculated the mean group size, age/sex composition, and adult female to infant ratios and compared these using Kruskal–Wallis one-way ANOVA and Z test.

The coat colour and other morphological (e.g. head crest) variations among individuals of the mixed-species groups were characterized. We estimated the proportion of these traits for each group. We presented a graphical representation of the proportion of each langur species and brown morphs in each group.

Using the three or four replicates in each grid cell, we constructed a detection matrix for each species or mixed-species group for a grid cell as ‘1’ indicating detection and ‘0’ indicating no detection. Then, we estimated their occupancy (ψ) and detection probability (p) using likelihood functions³⁸. We analysed the data using maximum likelihood functions employing single-season occupancy modelling in the program PRESENCE (version 2.13.47)^{38,39}. Trail length (KM) was considered as a covariate for detection probability, and EF, SEDF, DDF, DDFB, DDFS, GF, TP, EP and altitude (ALT) were included as site covariates for species or mixed-species group occupancy in the grid cell.

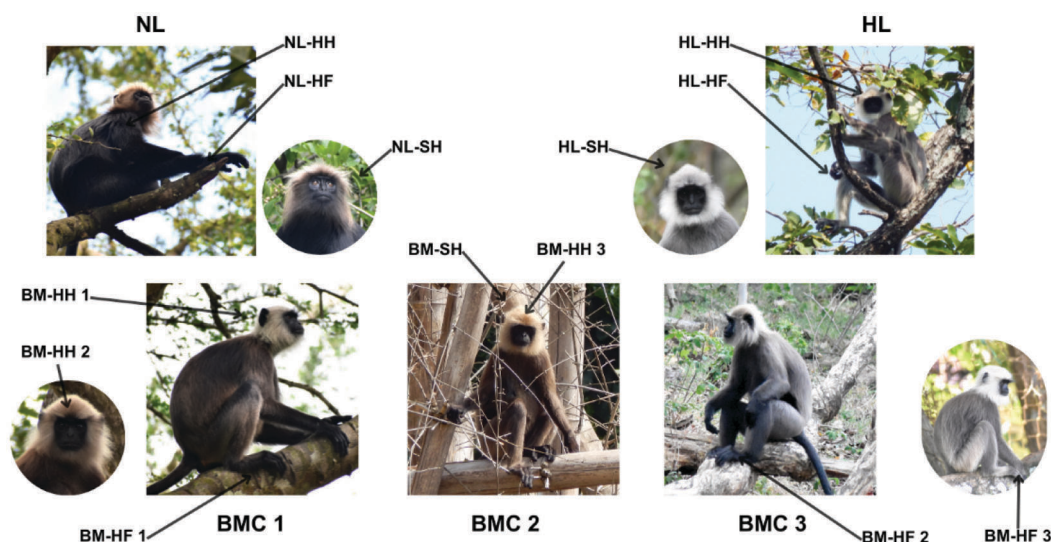


Figure 2. Inter-individual variations among brown morphs found in mixed-species groups of Nilgiri langur (NL) and tufted grey langur (HL) in the Anamalai Tiger Reserve.

Considering the habitat requirements in the overlapping zone, we hypothesized that mixed-species groups may occupy the grid cells with a larger cover of dry deciduous forests (DDF, DDFB and DDFS, as they fall in the overlapping zone of distribution of two langur species). We also expected that Nilgiri langurs may occupy high altitudes and evergreen forests, while the altitude may negatively influence the occupancy of tufted grey langurs. As the trail length (KM) in each grid cell occupies different forest types, we used this factor to model p . We generated multiple models with the associated covariates and evaluated their effects on the models. The naïve occupancy was calculated by dividing the number of grids with detections of species/mixed-species groups by the number of grids sampled ($n = 36$). Akaike's information criterion (AIC) was used to rank the models, with the lowest AIC value indicating the best-fit model to the data⁴⁰. We used the Burnham and Anderson⁴¹ framework to calculate model weights. We summed the model weights over all the models containing the particular covariate in the selected models and ranked them in descending order. To determine the effect size, we converted the beta coefficients into Z-scores by dividing the coefficient values by SE. The estimated occupancy of Nilgiri langurs, tufted grey langurs and their mixed-species groups was plotted within the sampling grid cells.

Results

Abundance and group composition

We obtained 66 detections of langur groups in 36 grid cells that provided an encounter rate (ER) of $1.18 \pm 0.66_{SD}/km$. The highest number of detections was 30 for Nilgiri langurs ($ER = 0.50 \pm 0.73_{SD}$), followed by mixed-species groups

($N = 21$, $ER = 0.41 \pm 0.70_{SD}$) and tufted grey langurs ($N = 15$, $ER = 0.28 \pm 0.50_{SD}$).

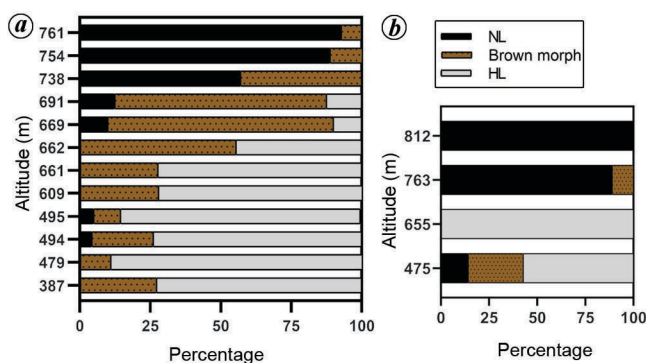
The largest mean group size was observed in the mixed-species groups ($15.5 \pm 6.05_{SD}$), followed by tufted grey langurs ($11.7 \pm 3.49_{SD}$) and Nilgiri langurs ($6.83 \pm 1.94_{SD}$; Table 1; Kruskal–Wallis $H = 6.74$, $df = 2$, $P < 0.01$). The mixed-species groups had $2.33 \pm 1.15_{SD}$ males, $5.75 \pm 2.67_{SD}$ females and $7.50 \pm 3.75_{SD}$ immatures in the group (Table 1). The Nilgiri langurs had $1.00 \pm 0.00_{SD}$ males, $3.33 \pm 0.82_{SD}$ females and $2.50 \pm 1.64_{SD}$ immatures in the group, while tufted grey langurs had $1.00 \pm 0.00_{SD}$ males, $5.33 \pm 1.75_{SD}$ females and $4.83 \pm 1.94_{SD}$ immatures in the group. About 66.66% of the mixed-species groups were multi-male multi-female societies. The per female infant output in mixed-species groups (0.52) was significantly higher than in Nilgiri langurs (0.20) and tufted grey langurs (0.38; mixed versus NL: $Z = 2.84$, $P = 0.01$; mixed versus HL: $Z = 1.56$, $P = 0.12$; NL versus HL: $Z = 1.53$; $P = 0.13$).

Brown morphs of mixed-species groups with an altitudinal gradient

We observed coat colour and other morphological (e.g. head crest) variations among individuals of the mixed-species groups which were characterized accordingly with photographs (Figure 2 and Table 2 and Supplementary Table 1). The presumed hybrid brown morphs had external features resembling those of the Nilgiri langur and tufted grey langur⁴². We identified three distinct coat colours among the brown morphs, viz. dark brown, light brown and dark grey. Brown morphs with the same coat colour had different head hair, viz. white, light brown and golden brown. Most of the morphs had puffed-shaped heads that did not resemble Nilgiri langurs or tufted grey langurs.

Table 2. Inter-individual variations among brown morphs in mixed-species groups of Nilgiri langur and tufted grey langur in the Anamalai Tiger Reserve

Variation	Characteristics
Species*	
Nilgiri langur (NL)	A glossy black coat with a reddish-brown to golden brown head hair and pitch-black coloured face Sexually dimorphic Females have white patches on their peritoneal region that distinguish from the males
Tufted grey langur (HL)	A yellowish-white coat with light greyish under parts Black eyebrows and short, whitish beard Tufted crown in the head Hands and feet are light grey in colour
Coat colour of brown morphs (BM)	
BM coat 1 (BMC 1)	Morphs with dark brown coat
BM coat 2 (BMC 2)	Morphs with light brown coat
BM coat 3 (BMC 3)	Morphs with dark grey coat
Head hair (HH)	
NL-HH	Reddish-brown to golden brown
HL-HH	White
BM-HH 1	White
BM-HH 2	Light brown
BM-HH 3	Golden brown
Shape of head (SH)	
NL-SH	Round
HL-SH	Tufted
BM-SH	Puffed
Hand and foot (HF)	
NL-HF	Black
HL-HF	Light grey
BM-HF 1	Black
BM-HF 2	Dark grey
BM-HF 3	Light grey

*Walker and Molur⁴².**Figure 3.** Variation in mixed-species group composition of Nilgiri langur and tufted grey langurs along the altitudinal gradient in the Anamalai Tiger Reserve: (a) male-female and (b) all-male bands.

Hand and foot colours also differed from black to dark grey to light grey.

We identified inter-individual differences among brown morphs of mixed-species groups with an altitudinal gradient (Figures 3 and 4 and Supplementary Table 1). Brown morphs at high altitudes had darker colour, and head and body sizes were similar to the Nilgiri langurs, whereas, at

low altitudes, they were similar to tufted grey langurs in colour and size (Figure 4). Mixed-species groups from lower altitudes had a smaller proportion of brown morphs with tufted grey langurs, which increased with altitude (Figure 3 a). From 662 to 691 m amsl, brown morphs had the largest percentage in the mixed-species groups. From there on, the proportion of Nilgiri langurs in mixed-species groups gradually increased towards higher altitudes. Nilgiri langur individuals were found in some of the mixed-species groups in the lower altitudes. Additionally, we found four male bands, two of which were mixed-species groups with variation in group composition along the altitudinal gradient (Figure 3 b).

Occupancy of Nilgiri langurs, tufted grey langurs and their mixed-species groups

Nilgiri langurs had the highest detection of 30, followed by mixed-species groups (21) and tufted grey langurs (15; Table 3). The estimated detection probability (p) for Nilgiri langurs was $0.48 \pm 0.09_{SE}$, mixed-species groups was $0.26 \pm 0.10_{SE}$ and tufted grey langurs was $0.25 \pm 0.12_{SE}$. The naïve occupancy of Nilgiri langurs, mixed-species

Table 3. Number of detections, detection probability and naïve occupancy of langurs in the Anamalai Tiger Reserve

Species/group	Total detection	No. of grids with detection	Detection probability (SE)	Naïve occupancy
Nilgiri langur	30	15	0.48 (0.09)	0.42
Mixed-species group	21	13	0.26 (0.10)	0.36
Tufted grey langur	15	10	0.25 (0.12)	0.28

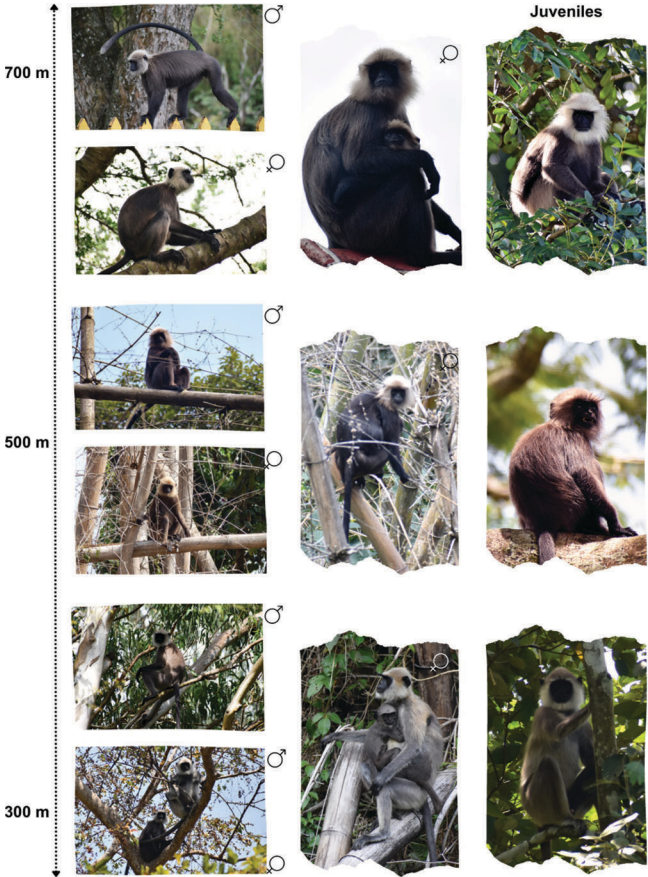


Figure 4. Inter-individual variations in colour patterns in mixed-species groups along the altitudinal gradient in the Anamalai Tiger Reserve.

group and tufted grey langurs was 0.42, 0.36 and 0.28 respectively. The distance walked (KM) in each grid influenced the detection probability of Nilgiri langurs, i.e. $w_i = 0.84$. Subsequent models for Nilgiri langurs were run with kilometer as a function of p .

ALT and SEDF were in the top models for Nilgiri langurs, whereas DDFB was for mixed-species groups, and DDFS for tufted grey langurs (Table 4). The coefficient of ALT ($Z = 1.52$) and SEDF ($Z = 0.50$) was positive for Nilgiri langurs but negative for mixed-species groups ($Z = -0.38$) and tufted grey langurs ($Z = -0.85$; Table 5). The coefficient of DDFB ($Z = 1.24$) and DDF ($Z = 1.21$) was positive for mixed-species groups, while the coefficient DDFS ($Z = 1.63$) was positive for tufted grey langurs (Table 5). The occupancy mapping indicates the spatial seg-

regation of Nilgiri langurs, mixed-species groups and tufted grey langurs (Figure 5).

Discussion

In the study area of the Anamalai Tiger Reserve, the Nilgiri langurs were found at higher elevations in the relatively wetter forests, the tufted grey langurs in the lower elevations in the dry deciduous and scrub forests, and the mixed-species groups and groups with brown morphotypes in the dry and moist deciduous forests in the middle elevation. The mixed morphotypes or possible hybrids have been earlier reported as a single or, in a few cases, in some mixed-species populations. To the best of our knowledge, the present study reports the largest number of mixed morphotypes in a single population. The mixed-species group size was larger than the Nilgiri and tufted grey langur groups. The adult female-to-infant ratios did not differ among the groups. While the Nilgiri and tufted grey langurs were uni-male/multi-female, most mixed-species of the groups were multi-male/multi-female.

The altitudinal and forest-type distribution patterns of the Nilgiri and tufted grey langurs observed in the present study were the same as reported earlier^{4,43}. The detection probability and occupancy models employed in the present study also indicated the same distribution pattern with respect to altitude and vegetation types. In the study region, the mixed-species groups of various types, including tufted grey langurs and the brown morphs, Nilgiri langurs and brown morphs, and all three types in a single group, were found in the overlapping range. There are several explanations for the formation of mixed-species groups. The most common explanation is the benefits of foraging in mixed groups. Diana *Cercopithecus diana* and Campbell's *Cercopithecus campbelli* monkeys foraged in larger areas and more intensively when foraging in mixed-species groups than in single-species groups⁴⁴. There can be local enhancement where individuals or species in mixed groups may find food detected by individuals of other species⁴⁵. In the forests of Peru, the variance in time spent searching for new fruiting trees was less when primates foraged in mixed-species groups than as a single species⁴⁶. Mixed-species groups also allowed better defence of a feeding area among the primates⁴⁷. Goodale *et al.*¹⁴ have discussed several mechanisms by which mixed-species groups reduce predator risk. These include encounter dilution⁴⁸, shared vigilance

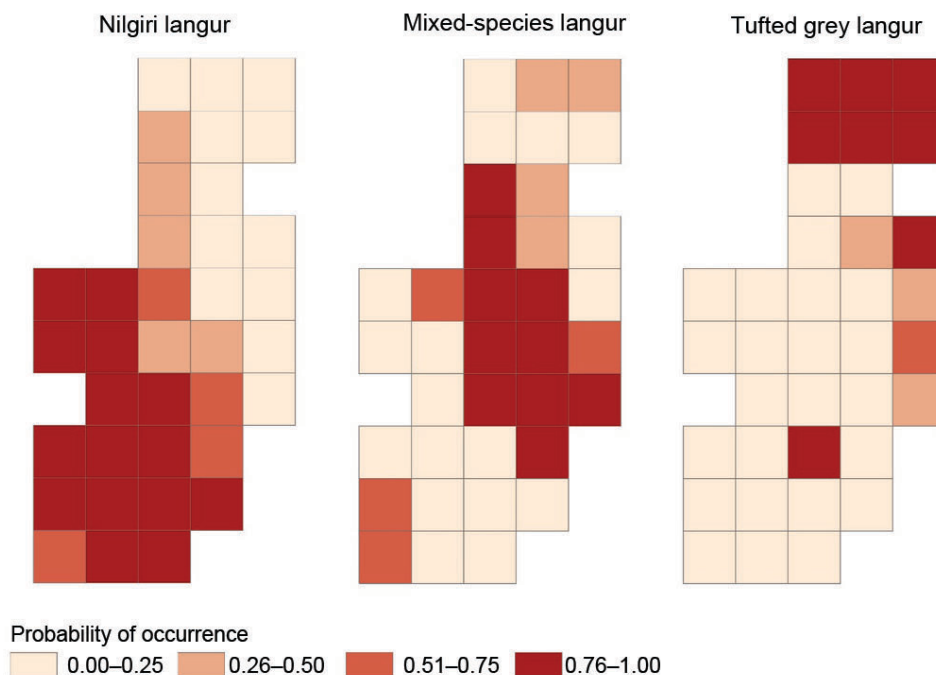
Table 4. Top models for occupancy of langurs in the Anamalai Tiger Reserve

Species/group	Model	ψ	SE	AIC _c	Δ AIC _c	w_i	K
Nilgiri langur	ψ (ALT), p (KM)	0.51	0.09	93.78	0.00	0.50	4
	ψ (ALT + SEDF), p (KM)	0.52	0.09	94.48	0.70	0.35	5
Mixed-species group	ψ (DDFB + DDF), p (.)	0.48	0.15	90.90	0	0.22	4
	ψ (DDFB), p (.)	0.49	0.15	91.17	0.27	0.19	3
	ψ (DDFB + DDF + DDFS), p (.)	0.48	0.16	92.08	1.18	0.12	5
	ψ (DDFB + DDFS), p (.)	0.50	0.19	92.20	1.30	0.11	4
	ψ (DDFB + ALT), p (.)	0.48	0.17	92.43	1.53	0.10	4
	ψ (DDF), p (.)	0.52	0.16	92.81	1.91	0.08	3
	ψ (DDFB + DDF + ALT), p (.)	0.48	0.17	92.90	2.00	0.08	5
Tufted grey langur	ψ (DDFS), p (.)	0.31	0.08	61.54	0.00	0.38	3
	ψ (DDFS + ALT + DDF), p (.)	0.30	0.09	61.68	0.14	0.35	5
	ψ (DDFS + ALT), p (.)	0.30	0.08	62.39	0.85	0.25	4

ψ , Estimated occupancy parameter; p , detection probability; SE, Associated standard error; AIC_c, AIC corrected for all small-sample bias; Δ AIC_c, Difference in AIC_c values between each model and the model with the lowest AIC_c; w_i , Model weight, K, Number of parameters estimated by the model; ALT, Altitude; KM, Effort in transect walks; SEDF, Semi-evergreen degraded forests; DDFB, Dry deciduous forests with bamboo; DDF, Dry deciduous forests and DDFS, Dry deciduous forest and thorny scrubs.

Table 5. Covariates influencing occupancy ranked by the summed β -coefficient and associated standard error for the top models

Species/group	Covariates	Summed w_i	Beta coefficients	SE	z-Score
Nilgiri langur	ALT	0.85	6.75	4.43	1.52
	SEDF	0.35	5.76	11.54	0.50
Mixed-species group	DDFB	0.82	64.47	52.05	1.24
	DDF	0.42	5.06	4.18	1.21
	DDFS	0.23	-3.55	4.05	-0.88
	ALT	0.18	-0.42	1.11	-0.38
Tufted grey langur	DDFS	0.98	36.87	22.61	1.63
	ALT	0.60	-1.58	1.86	-0.85
	DDF	0.35	1.82	1.46	1.24

**Figure 5.** Estimated occupancy of Nilgiri langur, tufted grey langur and their mixed-species groups within the sampling grids.

and collective detection⁴⁹, and sometimes deterring the predator⁵⁰. Although no detailed information on the sharing or partitioning of resources by the sympatric langur species in the Western Ghats is yet available, Nilgiri langurs have been found to be more folivorous than black-footed grey langurs *Semnopithecus hypoleucos*³². Therefore, if there is not much competition for food resources, the mixed-species groups of the present study may have anti-predation benefits by numbers and alarms since predation by large carnivores, including tigers, leopards and dholes on the langurs, has been reported to be substantial^{51,52}.

The mean group size of Nilgiri langurs ($6.83 \pm 1.94_{SD}$) in the present study was nearly the same (5.40) as in the Ullandy range⁵³, (7.00) in the Nelliampathy Reserve Forest⁵⁴ and (7.72) in the Parambikulam Tiger Reserve⁵⁵ in the Anamalai and adjoining hills. The Nilgiri langur group size in the relatively wetter forests tends to be smaller than that of grey langurs inhabiting relatively drier forests^{4,56}, which was also observed in the present study where the group size of the tufted grey langur groups and the mixed-species groups was larger than that of the Nilgiri langurs. The social organization of the mixed-species/mixed morphotypes with multi-male/multi-female structure differed from both Nilgiri langurs and Hanuman langurs, which had a uni-male/multi-female structure. Nilgiri langur groups can occur as uni-male, multi-male, all-male and all-female; however, multi-male and all-female groups are rare^{33,34,43,57}. Tufted grey langur groups also occur as uni-male, multi-male or all-male^{25,31}. However, in the present study area, Nilgiri and tufted grey langur groups were uni-male. Although the proportion of adult females against the group size was smaller in the mixed-species groups (0.37) compared to the Nilgiri langurs (0.49) and tufted grey langurs (0.47), the infant-to-adult female ratio was highest, indicating higher reproductive output in the mixed-species groups. In a review of mammalian mixed-species groups, Stensland *et al.*⁵⁸ have speculated that since young and subordinate individuals can mate without aggression from dominant individuals, it results in better mating among the efficiency group members.

The most striking observation in our study is the presence of brown morphs with colour variations from dark grey to light brown to dark brown. These brown morphs are probable hybrids between Nilgiri langurs and tufted grey langurs. Interestingly, the abundance of dark grey individuals was higher in lower elevations where groups of tufted grey langurs occurred. The abundance of light brown individuals was higher in the mid-elevation, while at higher elevations, close to the groups of Nilgiri langurs, the frequency of dark brown morphs was higher. Previous studies have also identified probable hybrid individuals in groups or mixed-species group associations in the Western Ghats^{28,31,59}. In this study, we found male bands of Hanuman langurs, Nilgiri langurs and mixed species in the same region. The information adds to the diversity of social organization in these colobines.

Recently, observations of mixed-species groups have been reported for other colobines – golden langur *Trachypithecus geei* × capped Langur *Trachypithecus pileatus* in Bhutan²³, red-shanked douc *Pygathrix nemaeus* × grey-shanked douc *P. cinerea*²⁴, purple-faced langur *Semnopithecus vetulus philbricki* × tufted grey langur *S. priam thersites*²⁵, proboscis monkey *Nasalis larvatus* × silvery lutung *Trachypithecus cristatus*²⁶, Phayre's langur *Trachypithecus phayrei* and capped langur *Trachypithecus pileatus*²⁷. Variation in coat colour patterns is common among hybrid individuals in the mixed-group associations observed. The present study adds to the understanding of how colour variation patterns change at different elevations, which may be related to the dispersion of male individuals from both langur species across the study area. Genetic data will help identify whether this variation in the coat colour of distinct brown morphs is linked with hybridization between the two species.

The process of hybridization is important biologically because it enhances the variety of genes within a species⁶⁰. It can have a number of effects on evolution, including the merging of parental lineages or the development of a new hybrid species. Overall, hybridization has been reported in at least 10% of primate species⁶¹, and hence, there is a possibility of formation of mixed-species groups^{62,63}, and hybrids are observed with intermediate external morphological features^{25,64}. Roos *et al.*⁶⁵ showed that hybridization is the main cause of discordance among gene trees in colobines. They showed that in Asia, *Semnopithecus* diverged first and that the unidirectional gene flow from *Semnopithecus* to *Trachypithecus* might have occurred until the earliest Pleistocene. Furthermore, by understanding anthropogenic changes in the natural environment, the effects of hybridization may have clear implications for conservation. Anthropogenic factors can limit the ability of two sympatric species to mate, increasing the possibility of hybridization^{66,67}. Nilgiri langurs and tufted grey langurs are sympatric species at certain elevation levels in the Western Ghats. Being primarily folivores, habitat fragmentation and degradation may significantly impact their dispersal and mating opportunities. This overlapping range of mixed-species groups necessitates extensive studies to determine their interspecific interactions and reproductive strategies. At the same time, it is also important to know whether possible hybridization will result in evolution or the local extinction of two colobines.

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1. MacArthur, R. H., On the relative abundance of bird species. *Proc. Natl. Acad. Sci. USA*, 1957, **43**, 293–295.
2. Schoener, T. W., Resource partitioning in ecological communities. *Science*, 1974, **185**, 27–39.
3. Schnitzler, A. and Hermann, L., Chronological distribution of the tiger *Panthera tigris* and the Asiatic lion *Panthera leo persica* in their common range in Asia. *Mamm. Rev.*, 2019, **49**, 340–353.

4. Singh, M. *et al.*, Distribution and research potential of non-human primates in the Aliyar–Valparai sector of Indira Gandhi Wildlife Sanctuary, Tamil Nadu, India. *Trop. Biodivers.*, 1997, **4**, 197–208.
5. Terborgh, J., *Five New World Primates: A Study in Comparative Ecology*, Princeton University Press, Princeton, NJ, USA, 1984, pp. xiv, 260.
6. Sushma, H. S. and Singh, M., Resource partitioning and interspecific interactions among sympatric rainforest arboreal mammals of the Western Ghats, India. *Behav. Ecol.*, 2006, **17**, 479–490.
7. Kaufmann, J. H., Ecology and social behavior of the coati, *Nasua narica*, on Barro Colorado Island, Panama. *Univ. Calif. Publ. Zool.*, 1962, **60**, 95–222.
8. Person, D. K. and Hirth, D. H., Home range and habitat use of coyotes in a farm region of Vermont. *J. Wildl. Manage.*, 1991, **55**, 433–441.
9. Pearce, F., Carbone, C., Cowlshaw, G. and Isaac, N. J., Space-use scaling and home range overlap in primates. *Proc. Royal Soc. B*, 2013, **280**, 20122122.
10. Wartmann, F. M., Juárez, C. P. and Fernandez-Duque, E., Size, site fidelity, and overlap of home ranges and core areas in the socially monogamous owl monkey (*Aotus azarae*) of northern Argentina. *Int. J. Primatol.*, 2014, **35**, 919–939.
11. Singh, M., Roy, K. and Singh, M., Resource partitioning in sympatric langurs and macaques in tropical rainforests of the Central Western Ghats, South India. *Am. J. Primatol.*, 2011, **73**, 335–346.
12. Waser, P. M., Primate polyspecific associations: do they occur by chance? *Anim. Behav.*, 1982, **30**, 1–8.
13. Waser, P. M., ‘Chance’ and mixed-species associations. *Behav. Ecol. Sociobiol.*, 1984, **15**, 197–202.
14. Goodale, E., Beauchamp, G. and Ruxton, G. D., *Mixed-Species Groups of Animals: Behavior, Community Structure, and Conservation*, Academic Press, UK, 2017, pp. xii + 203.
15. Couzin, I. D. *et al.*, Collective memory and spatial sorting in animal groups. *J. Theor. Biol.*, 2002, **218**, 1–11.
16. Zoratto, F., Santucci, D. and Alleva, E., Theories commonly adopted to explain the antipredatory benefits of the group life: the case of starling (*Sturnus vulgaris*). *Rend. Lincei Sci.*, 2009, **20**, 163–176.
17. Jiang, D., Sieving, K. E., Meaux, E. and Goodale, E., Seasonal changes in mixed-species bird flocks and antipredator information. *Ecol. Evol.*, 2020, **10**, 5368–5382.
18. Hoffman, W., Heinemann, D. and Wiens, J. A., The ecology of seabird feeding flocks in Alaska. *Auk*, 1981, **98**, 437–456.
19. Goodale, E. and Beauchamp, G., The relationship between leadership and gregariousness in mixed-species bird flocks. *J. Avian Biol.*, 2010, **41**, 99–103.
20. Munn, C. A. and Terborgh, J. W., Multi-species territoriality in Neotropical foraging flocks. *Condor*, 1979, **81**, 338–347.
21. Sridhar, H., Jordan, F. and Shanker, K., Species importance in a heterospecific foraging association network. *Oikos*, 2013, **122**, 1325–1334.
22. Goodale, E. *et al.*, Mixed company: a framework for understanding the composition and organization of mixed-species animal groups. *Biol. Rev.*, 2020, **95**, 889–910.
23. Choudhury, A., Primates of Bhutan and observations of hybrid langurs. *Primate Conserv.*, 2008, **23**, 65–73.
24. Rawson, B. and Roos, C., A new primate species record for Cambodia: *Pygathrix nemaeus*. *Cambodian J. Nat. Hist.*, 2008, **1**, 7–11.
25. Lu, A. *et al.*, Mixed-species associations and attempted mating suggest hybridization between purple-faced and tufted gray langurs of Sri Lanka. *Primates*, 2021, **62**, 11–17.
26. Lhota, S. *et al.*, Is Malaysia’s ‘mystery monkey’ a hybrid between *Nasalis larvatus* and *Trachypithecus cristatus*? An assessment of photographs. *Int. J. Primatol.*, 2022, **43**, 513–532.
27. Al-Razi, H. *et al.*, Mixed-species association and a record of a hybrid offspring between *Trachypithecus pileatus* and *Trachypithecus phayrei* in Bangladesh. *Primates*, 2023, **64**, 9–15.
28. Oates, J. F., Coat color aberrations in *Presbytis johnii*: a founder effect? *Primates*, 1982, **23**, 307–311.
29. Hohmann, G. M. and Herzog, M. O., Vocal communication in lion-tailed macaques (*Macaca silenus*). *Folia Primatol.*, 1985, **45**, 148–178.
30. Hohmann, G., Comparative study of vocal communication in two Asian leaf monkeys, *Presbytis johnii* and *Presbytis entellus*. *Folia Primatol.*, 1989, **52**, 27–57.
31. Nag, C., A new report on mixed species association between Nilgiri langurs *Semnopithecus johnii* and tufted grey langurs *S. priam* (Primates: Cercopithecidae) in the Nilgiri Biosphere Reserve, Western Ghats, India. *J. Threat. Taxa*, 2020, **12**, 15975–15984.
32. Kavana, T. S., Erinjery, J. J. and Singh, M., Folivory as a constraint on social behaviour of langurs in South India. *Folia Primatol.*, 2015, **86**, 420–431.
33. Tanaka, J., Social structure of Nilgiri langurs. *Primates*, 1965, **6**, 107–122.
34. Poirier, F. E., Nilgiri langur (*Presbytis johnii*) territorial behavior. *Primates*, 1968, **9**, 351–364.
35. Horwich, R. H., Home range and food habits of the Nilgiri langur, *Presbytis johnii*. *J. Bombay Nat. Hist. Soc.*, 1972, **69**, 1–13.
36. Kavana, T. S., Erinjery, J. J. and Singh, M., Male takeover and infanticide in Nilgiri langurs *Semnopithecus johnii* in the Western Ghats, India. *Folia Primatol.*, 2014, **85**, 164–177.
37. Sugiyama, Y., Group composition, population density and some sociological observations of Hanuman langurs: *Presbytis entellus*. *Primates*, 1964, **5**, 7–37.
38. MacKenzie, D. I. *et al.*, Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 2002, **83**, 2248–2255.
39. MacKenzie, D. I. *et al.*, *Occupancy Estimation and Modeling*, Academic Press, UK, 2005, p. 344.
40. Akaike, H., Maximum likelihood identification of Gaussian autoregressive moving average models. *Biometrika*, 1973, **60**, 255–265.
41. Burnham, K. P. and Anderson, D. R., *Model Selection and Multi Model Inference*, Springer, New York, NY, 2002, pp. XXVI, 488.
42. Walker, S. and Molur, S., *Guide to South Asian Primates for Teachers and Students of All Ages*, Zoo Outreach Organization, Primate Specialist Group South Asia and Wildlife Information Liaison Development, Coimbatore, 2007, p. 64.
43. Kumara, H. N. and Singh, M., Distribution and abundance of primates in rain forests of the Western Ghats, Karnataka, India and the conservation of *Macaca silenus*. *Int. J. Primatol.*, 2004, **25**, 1001–1018.
44. Wolters, S. and Zuberbühler, K., Mixed-species associations of Diana and Campbell’s monkeys: the costs and benefits of a forest phenomenon. *Behaviour*, 2003, **140**, 371–385.
45. Galef, B. G. and Giraldeau, L. A., Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Anim. Behav.*, 2001, **61**, 3–15.
46. Podolsky, R. D., Effects of mixed-species association on resource use by *Saimiri sciureus* and *Cebus apella*. *Am. J. Primatol.*, 1990, **21**, 147–158.
47. Gautier-Hion, A., Quris, R. and Gautier, J. P., Monospecific vs polyspecific life: a comparative study of foraging and antipredatory tactics in a community of *Cercopithecus* monkeys. *Behav. Ecol. Sociobiol.*, 1983, **12**, 325–335.
48. Turner, G. F. and Pitcher, T. J., Attack abatement: a model for group protection by combined avoidance and dilution. *Am. Nat.*, 1986, **128**, 228–240.
49. Beauchamp, G., *Social Predation: How Group Living Benefits Predators and Prey*, Academic Press, Amsterdam and Boston (Massachusetts), 2014, pp. xi + 317.
50. Quinn, J. L. and Ueta, M., Protective nesting associations in birds. *Ibis*, 2008, **150**, 146–167.
51. Karanth, K. U. and Sunquist, M. E., Prey selection by tiger, leopard and dhole in tropical forests. *J. Anim. Ecol.*, 1995, **64**, 439–450.
52. Andheria, A. P., Karanth, K. U. and Kumar, N. S., Diet and prey profiles of three sympatric large carnivores in Bandipur Tiger Reserve, India. *J. Zool.*, 2007, **273**, 169–175.

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53. Hohmann, G. and Sunderraj, F. S. W., Survey of Nilgiri langurs and lion-tailed macaques in Tamil Nadu, south India. *Primate Conserv.*, 1990, **11**, 49–53.
54. Ramachandran, K. K. and Suganthasakthivel, R., *Ecology and Behaviour of the Arboreal Mammals of the Nelliampathy Forests*, KFRI Research, Report no. 382, Kerala Forest Research Institute, Thirussur, 2010.
55. Roy, D., Group-size and age–sex composition of Nilgiri langur *Trachypithecus johnii* (Primates: Cercopithecidae) in India. *TAPROBANICA*, 2012, **4**, 83–87.
56. Singh, M. *et al.*, Demography and reproductive output in langurs of the Western Ghats, India. *Primates*, 2016, **57**, 501–508.
57. Sunderraj, S. F. W., Ecology and conservation of Nilgiri langur (*Trachypithecus johnii*). *ENVIS Bull. Wildlife and Prot. Areas*, 2001, **1**, 49–59.
58. Stensland, E., Angerbjörn, A. and Berggren, P., Mixed species groups in mammals. *Mamm. Rev.*, 2003, **33**, 205–223.
59. Hohmann, G., Analysis of loud calls provides new evidence for hybridization between two Asian leaf monkeys (*Presbytis johnii*, *Presbytis entellus*). *Folia Primatol.*, 1988, **51**, 209–213.
60. Dowling, T. E. and Secor, C. L., The role of hybridization and introgression in the diversification of animals. *Annu. Rev. Ecol. Evol. Syst.*, 1997, **28**, 593–619.
61. Willis, P. M., Why do animals hybridize? *Acta Ethol.*, 2013, **16**, 127–134.
62. Li, Z., Jiang, Z. and Beauchamp, G., Nonrandom mixing between groups of Przewalski's gazelle and Tibetan gazelle. *J. Mammal.*, 2010, **91**, 674–680.
63. Hodgins, N. K., Dolman, S. J. and Weir, C. R., Potential hybridism between free-ranging Risso's dolphins (*Grampus griseus*) and bottlenose dolphins (*Tursiops truncatus*) off north-east Lewis (Hebri- des, UK). *Mar. Biodivers. Rec.*, 2014, **7**, e97.
64. Aguiar, L. M., Pie, M. R. and Passos, F. C., Wild mixed groups of howler species (*Alouatta caraya* and *Alouatta clamitans*) and new evidence for their hybridization. *Primates*, 2008, **49**, 149–152.
65. Roos, C. *et al.*, Nuclear versus mitochondrial DNA: evidence for hybridization in colobine monkeys. *BMC Evol. Biol.*, 2011, **11**, 77.
66. Detwiler, K. M., Burrell, A. S. and Jolly, C. J., Conservation implications of hybridization in African cercopithecine monkeys. *Int. J. Primatol.*, 2005, **26**, 661–684.
67. Miller, J. M. and Hamilton, J. A., Interspecies hybridization in the conservation toolbox: response to Kovach *et al.* *Conserv. Biol.*, 2016, **30**, 431–433.

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