



Coexistence Patterns of Sympatric Black-and-white Snub-nosed Monkeys and Rhesus Monkeys in Baimaxueshan National Nature Reserve, Yunnan, China

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ABSTRACT

Ecological niche differentiation among sympatric animal species is a primary mechanism maintaining a long-term and stable coexistence. Information on the pattern of coexistence among sympatric species is vital to provide specific conservation measures and management. This study focuses on the spatial-temporal niche differentiation strategy adopted by black-and-white snub-nosed monkeys (*Rhinopithecus bieti*) and rhesus macaques (*Macaca mulatta*) to support their coexistence along a large elevation gradient in the temperate montane forest of Xiangguqing, located in the southern section of Baimaxueshan National Nature Reserve, China. Daily activities of the monkeys were recorded with infrared camera traps installed at elevation intervals of 200 m between 2,100 m and 3,500 m from January 2018 to May 2021. The time interval between the two species appearing at the same plots and the number of individuals were calculated for each site and differences were assessed according to seasons and elevation. No direct encounters between the two species were captured by camera traps, although they did appear up in the same camera traps at altitudes between 2,900 m - 3,500 m. *M. mulatta* was also observed at elevations below 2,500 m, near the farmland and villages. The two monkey species were mostly recorded at an altitudinal spectrum within 3,100 m - 3,500 m, but with significant differences in seasonal frequencies in the same elevational gradients. The two species avoided encountering each other to limit direct competition and conflicts. Moreover, differences in foraging strategy and dietary selection contributed to the coexistence of the two primate species in mountain habitats. Our findings suggest that, to support the coexistence and survival of these two primate species living in high altitude montane regions, the habitats along the overall elevational gradients should be included in wildlife conservation policies.

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0030-9923/2024/0003-1133 \$ 9.00/0



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Article Information

Received 15 June 2022

Revised 25 September 2022

Accepted 14 October 2022

Available online 30 January 2023

(early access)

Published 29 March 2024

Authors' Contribution

YPL and WX conceived and designed the study. XN and ZPH data analysis and drafting original manuscript with the help of XLF, YHF, ZPH, KT, YPL, XN, SB, XLF, YHF, DF, KT, ZPH, YPL and WX provided valuable feedback. All authors have read the manuscript and agreed to have it published in Pakistan Journal of Zoology.

Key words

Rhinopithecus bieti, *Macaca mulatta*, Sympatric distribution, Niche differentiation, Baimaxueshan national nature reserve

INTRODUCTION

Ecological niche is an important concept in ecology, useful for describing interspecific and intraspecific relationships. When species with similar ecological needs are distributed in the same domain, stable coexistence can be achieved through the differentiation of at least one niche dimension (Hardin, 1960). The ecological niche of a given species consists of its environment and

habitat, including ecological characteristics, distribution range, resource utilization, as well as daily and seasonal diet composition (Peterson *et al.*, 2013; Yan *et al.*, 2021). Thus, the information on the niche use of different species sympatrically distributed is essential to understand whether each species can achieve its best survival expectation (Murray *et al.*, 2016; Han *et al.*, 2019). Therefore, understanding ecological niche differentiation is very important for species conservation planning (Letten *et al.*, 2017; Bimler *et al.*, 2018).

The coexistence of two or more primate species in the same area is regulated by diet, home range, population structure and group size (Grueter *et al.*, 2010; Murray *et al.*, 2016). An extensive literature review of studies on 673 pairs of sympatric primate species identified eight different modes of niche separation, among which differences in diet (28 %) and vertical height (25 %) were the primary ones (Schreier *et al.*, 2009). Habitat use and dietary characteristics were the main factors supporting the coexistence of seven lemur species in the eastern rainforest of Madagascar (Ganzhorn, 1989), while differences of dietary habits and availability of food resources in different seasons regulated the coexistence between chimpanzees and gorillas in Gabon (Oelze *et al.*, 2014). By focusing on gradients of altitude, habitat, and behavior patterns, Sun (2020) found that the coexistence mechanisms of *Macaca leonina* and rhesus macaque (*M. mulatta*) in the Naban River, Xishuangbanna, China relied on their use of different altitude zones and vegetation types. Most past studies focused on the spatial-temporal distribution patterns and natural resources shared by sympatric primates occurring at relatively low elevations or with a narrow altitudinal spectrum (Sun *et al.*, 2020; Zhou *et al.*, 2009), while only a few relatively recent studies targeted niche differentiation or coexistence patterns among primates occurring at high elevations or with larger altitudinal spectra (e.g., Grueter *et al.*, 2010). The latter work by Grueter *et al.* (2010) looked at these relationships between black-and-white snub-nosed monkey (*Rhinopithecus bieti*) and rhesus macaque in China only over a reduced portion of their overall altitudinal distribution (2625 m - 3793 m). *R. bieti* is an endangered species endemic to southwest China, occurring at the highest elevation, mostly between 2,600 m-4,500 m (Huang *et al.*, 2017; Quan *et al.*, 2011). *M. mulatta* instead has a much wider elevation range than *R. bieti* and it is found in most regions of China as well as in other countries. In the nature reserves of northwest Yunnan and southeast Tibet, these two primates share some portions of their habitats (Jiang *et al.*, 1991). Within the vertical range analyzed, the study found that differential macrohabitat use and spatial avoidance facilitated the coexistence of the two monkey species (Grueter *et*

al., 2010). Moreover, when physical encounters and confrontation occurred, group size seemed to play a major role in the outcome of the contest (Grueter *et al.*, 2010). Data collection was performed by direct observation of the snub-nosed monkey group, an approach that presents some limitations. In complex terrain conditions and harsh relief, the field of vision may be shortened and the contact with the target species may be lost due to inaccessibility, therefore reducing the total contact time for *R. bieti* that can be analyzed. Moreover, although evidence of the recent presence of the species not directly tracked may be assessed indirectly (e.g., aural detection, scat, foot/hand-prints, etc.), the results provide limited and discontinued information on its location through the study period.

Building on this previous effort and in order to depict a more comprehensive understanding on the coexistence mechanisms between these two sympatric species living in temperate forests, we designed a new study using camera traps located at regular intervals along a larger elevation range, inclusive of non-sympatric sections where *M. mulatta* is known to occur. This approach has the advantage of preventing observational biases toward one species and doesn't require a continuous contact with the animals difficult to maintain in extreme relief conditions. Our research questions are as follows: (1) What form of coexistence do the two primate species adopt in sympatric areas? and (2) What is the vertical niche partitioning pattern used by the primates and how does it change in different seasons? The results will provide guidelines supporting conservation planning and management of primates as well as other key wildlife in mountainous habitats.

MATERIALS AND METHODS

Study subjects

R. bieti and *M. mulatta* belong to Cercopithecoidea primates. The former is only distributed in Yunling Mountain, between the Lancang-Mekong and Yangzi rivers, extending from Mangkang County of Tibet in the north to Yunlong County of Yunnan in the south (Xiao *et al.*, 2003). The species has been classified as wildlife of priority protection in China and listed as critically endangered by IUCN in 2020 (Long *et al.*, 2020). *R. bieti*'s habitat is composed by dark coniferous forests, coniferous and broad-leaved mixed forests, and broad-leaved deciduous forests (Xiao *et al.*, 2003). *M. mulatta* is a primate species widely distributed in China and listed as Class II of the protected wild animals in China (Jiang *et al.*, 2021), with low-risk conservation status by IUCN (Singh *et al.*, 2020). These monkeys primarily vegetarian, and their diets include fruits, seeds, flowers, leaves and buds (Mittermeier *et al.*, 2013).

Study area

The study was conducted in Xiangguqing (27°37' - 27°40'N, 99°20' - 99°22'E, Fig. 1B), the southern section of Baimaxueshan National Nature Reserve, China. The area spans about 90 km² (Li *et al.*, 2011). Its yearly average temperature is 9.4 °C and the total annual precipitation is 898 mm. The vegetation varies with elevation: Yunnan pines (*Pinus yunnanensis*) dominate between 2,100m-2300 m, then mix with broadleaved forest (*Quercus aliena*, *Cyclobalanopsis glaucoides*) up to 3000 m. Between 3,000 m and 3,500 m, the vegetation is characterized by mix dark conifers (*Tsuga chinensis*, *Abies fabri*, and *Picea asperata*) and broadleaved forests (*Q. rehderiana*, *Q. pannosa*) while above 3500 m until 4100 m the dark conifer forest takes over (Li *et al.*, 2010). A big population of *R. bieti* with 430-480 individuals inhabit this area (He *et al.*, 2021).

Camera traps installation

Eight 100 × 100 m plots were established along an altitude gradient from 2,100 m to 3,500 m, with a 200 m elevation interval (Fig. 1B). The plots located at 2,100 m and 2,300 m were equipped with two camera traps placed in opposite corners, while at all other elevations (2,500 m to 3,500 m) four cameras were placed in each plot corner (Fig. 1C). The cameras were mounted on trees about 1 m off the ground in order to avoid direct sunlight and light reflection effects. All cameras were Ltl Acorn 6210 models set to medium sensitivity for animal motion, with no shooting interval and photographing subjects at a maximum distance and depth of field reaching 8 m (Fig. 1D). In total, twenty-eight camera traps were active from January 2018 to May 2021. Every three months, the working status of the cameras was evaluated while batteries and memory cards were replaced. With a total effective monitoring time of 14,604 days, we collected 1,206 photos of *R. bieti* and 819 of *M. mulatta* (Table I).

Table I. Number of photos collected for *Rhinopithecus bieti* and *Macaca mulatta* along the elevation gradient.

Altitude (m)	Number of cameras	Working days	Photos of <i>R. bieti</i>	Photos of <i>M. mulatta</i>
2100	2	174	0	0
2300	2	1170	0	0
2500	4	1461	0	11
2700	4	1183	0	16
2900	4	1402	5	125
3100	4	3122	418	202
3300	4	1934	209	102
3500	4	4158	574	363
Total	28	14,604	1206	819

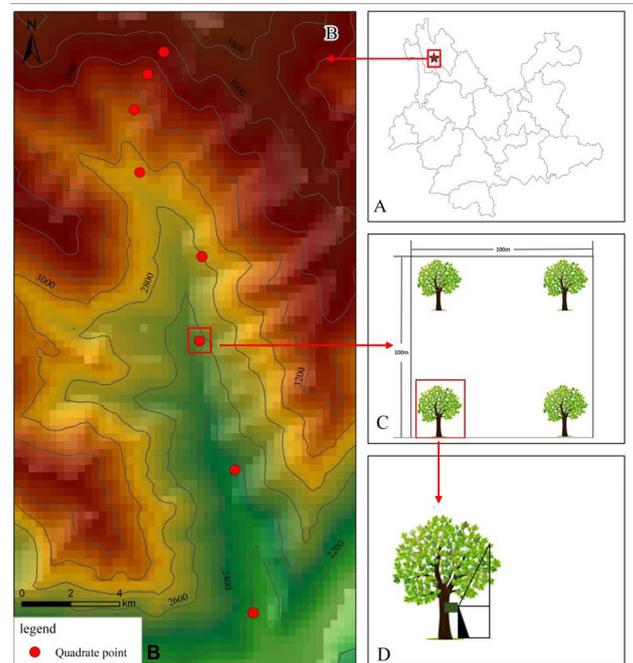


Fig. 1. Research area and camera trap layout in Baimaxueshan National Nature Reserve, Yunnan.

Data analysis

The data was processed with the software M-photov1.0, which assists with the sorting, manual species identification, and labelling of camera trap records (<http://www.eastern-himalaya.com.cn/contents/3/990.html>).

In order to measure the coexistence of the two species in a same location (camera trap), we calculated the time difference between two consecutive photos recording different species. We classified these time intervals into four levels (<1, 1-10, 11-30, and >30 days) for comparative purposes. The frequency of occurrence of the two species was calculated at each time interval and the difference in photo numbers between the two monkey species at different altitudes was assessed with the chi-square test. At the same time, the number of photos taken of *R. bieti* and *M. mulatta* in different seasons in the 3,100m-3,500m altitude range were analyzed. The four seasons of the study area were defined as follows: spring from March to May, summer from June to August, autumn from September to November, and winter from December to February (Grueter *et al.*, 2008). The number of photos taken of *R. bieti* and *M. mulatta* were counted separately according to individual appearances per photo. To evaluate the difference in group size between these two species, we categorized individuals appearing on the photos into three levels (1, 2-5, and >5) and compared such sizes differentiation at each altitude.

RESULTS

Coexistence pattern of the two primate species

Occurrence time interval between the two species at the same altitude

The two species were recorded at the same altitude and day in 48 events, but they were never recorded together. The shortest occurrence time interval between the two species was 0.25 days in August 2018, at an elevation of 3,500 m. At the same elevation, we observed the longest interval from November 2020 to February 2021 (103 days). The average time interval was 22.17 ± 23.17 days ($N=48$), where 8.3 % ($n=4$) were below 1 day, 39.6 % ($n=19$) were between 1-10 days, 20.8 % ($n=10$) happened between 11-30 days, and 31.3 % ($n=15$) occurred more than 30 days away (Fig. 2).

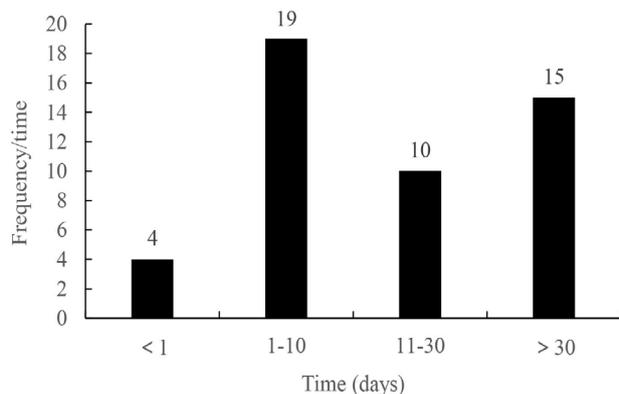


Fig. 2. Time interval frequency of the sympatric appearance of *Rhinopithecus bieti* and *Macaca mulatta* in Baimaxueshan National Nature Reserve, Yunnan, China.

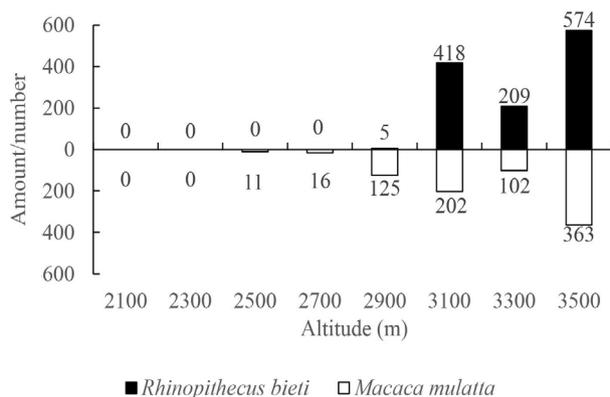


Fig. 3. The altitudinal spectrum in which *Rhinopithecus bieti* and *Macaca mulatta* were captured in Baimaxueshan Mountain National Nature Reserve, Yunnan.

Altitudinal niche differentiation between the two species

According to the photos taken at different altitudes, the two monkey species shared the same altitudinal niches between 2,900 m - 3,500 m (Fig. 3). However, *R. bieti* was observed significantly more frequently than *M. mulatta* between 3,100 m and 5,500 m ($\chi^2 = 102.70$, $df = 1$, $p < 0.001$), while the latter occurred more frequently at 2,900 m and below ($\chi^2 = 101.04$, $df = 1$, $p < 0.001$). *M. mulatta* was observed as low as 2500 to 2700m in spring, autumn, and early winter (Fig. 3).

Niche differentiation of the two primate species

Spatial-temporal niche differentiation

Within the altitude range 3,100 m to 3,500 m, the number of camera trap records of *M. mulatta* was significantly different during the overall study period ($\chi^2 = 7.103$, $df = 2$, $p = 0.029$), but not for *R. bieti* ($\chi^2 = 3.266$, $df = 2$, $p = 0.195$). Interestingly, the seasonal distribution of these occurrences was different for the two species. During spring, *R. bieti* was recorded 414 times (34.5 %, $N = 1201$) while *M. mulatta* 214 times only (32.1 %, $N = 667$), but this difference was not statistically significant ($\chi^2 = 0.547$, $df = 1$, $p = 0.460$). In summer, *R. bieti* displayed a significantly lower occurrence frequency than *M. mulatta* ($\chi^2 = 154.53$, $df = 1$, $p < 0.001$), with 161 photos taken (13.4 %, $N = 1201$) against 326 (48.9 %, $N = 667$), respectively. This pattern changed in autumn, with *R. bieti* seen 363 times (30.2 %, $N = 1201$), a significantly higher frequency ($\chi^2 = 37.39$, $df = 1$, $p < 0.001$) than *M. mulatta* which appeared in only 95 photos (14.2 %, $N = 667$). Same situation in winter: *R. bieti* was captured by the cameras 263 times (21.9 %, $N = 1201$), and *M. mulatta* only 32 (4.8 %, $N = 667$), resulting in a significant difference of occurrence frequency ($\chi^2 = 71.98$, $df = 1$, $p < 0.001$) (Fig. 4).

Group size assessment

Totally, 1,206 and 819 photos were taken separately for *R. bieti* and *M. mulatta*, respectively (Table I). For *R. bieti*, 43.7 % ($n = 527$) of the pictures included one individual; 47.0 % ($n = 567$) showed 2-5 individuals, and in 9.3 % ($n = 112$) we could count more than 5 individuals. Regarding *M. mulatta*, 78.1% ($n = 640$) of the photos displayed only one individual, 21.6% ($n = 177$) showed 2-5; and 0.3 % ($n = 2$) displayed more than 5 (Fig. 5A). When considering single altitudes, the two species presented different individual counts per photo, especially at 3,300 m, where 61.2 % ($n = 128$) of the *R. bieti* photos included 2- 5 individuals, while 71.6 % ($n = 73$) of the *M. mulatta* showed only one individual (Fig. 5C).

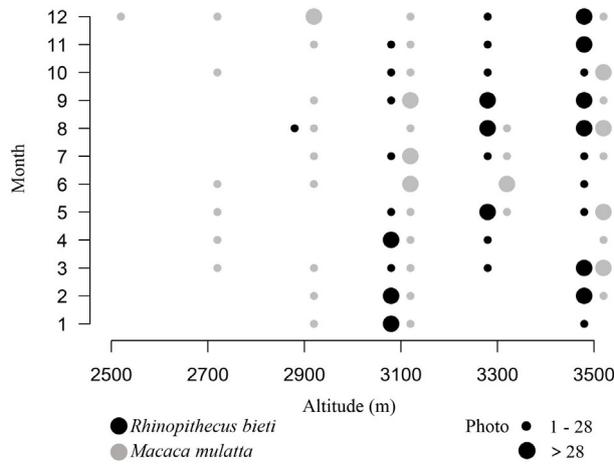


Fig. 4. Spatial-temporal niche utilization by *Rhinopithecus bieti* and *Macaca mulatta* in Baimaxueshan National Nature Reserve, Yunnan, China.

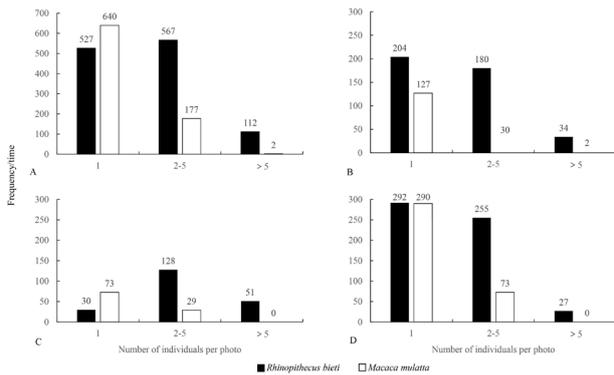


Fig. 5. Group size differentiation of two sympatric primate species recorded by camera traps installed in Baimaxueshan National Nature Reserve, Yunnan, China A, the whole altitudinal spectrum; B, C and D, 3100m, 3300 and 3500m, respectively.

DISCUSSION

Our findings indicate that the sympatric distribution of the two primate species occurs within an altitudinal spectrum between 2,900m - 3,500m. However, when analyzing the spatial-temporal distribution along the elevation gradient, we could observe a particular niche differentiation with no physical encounter ever detected by camera during the study period. Instead, the two species shared the same niches at different times of the year, moving up and down along the elevation gradient and revealing a monthly and seasonal pattern. Thus, we propose to define this sympatric type as coexistence

without physical encounter.

Differences in foraging habits and dietary selection may contribute to promoting the coexistence of the two monkey species in this montane region. The dietary preferences of *R. bieti* and *M. mulatta* are similar to some extent; twenty-two plant species are consumed by *M. mulatta*, and at least 16 of them are also used by *R. bieti* in the same areas (Grueter *et al.*, 2009). On the other hand, another study has shown that *R. bieti* and *M. mulatta* have different foraging strategies to overcome seasonal food scarcity: *M. mulatta* heads to lower altitudes in search of food supplies while *R. bieti* moves to higher elevations seeking lichens (Grueter *et al.*, 2010).

Spatial-temporal ecological niche differentiation is the key factor in the coexistence of co-distributed species (Vanak and Gompper, 2009; Murray *et al.*, 2016). An appropriate application of alternative spatial-temporal niches, environments, altitudes, and habitats between species can effectively reduce the possibility of physical conflicts and competition for natural resources (Zou *et al.*, 2021). In the present study, *R. bieti* lived at a higher altitude than *M. mulatta* (Fig. 4). Because, from middle autumn to early winter, the food resources started to be scarce, *M. mulatta* descended to low elevation to ransack crop fields, and remained during spring and early summer to feed on new buds and young leaves (Fig. 5). We also found that *R. bieti* stayed at higher elevations in autumn and early winter, probably to forage on abundant lichen and benefit higher solar radiation, as suggested by (Quan *et al.*, 2011), while during the coldest period of winter they descended at relatively lower elevations in search of buds and young leaves (Li *et al.*, 2010). As a result, the two species were observed in different sections of the sympatric altitudinal areas, especially within 3,100m-3,500m, and with different seasonal preferences (Fig. 5). Therefore, vertical spatial niche differentiation and spatial-temporal altitude differentiation are the primary strategies used by the two species to insure a cordial coexistence in the same area.

Avoiding encounters has been recognized to reduce direct competition and conflicts for natural resources and territory among sympatric species (Yao *et al.*, 2021). Animals can reach such a pattern through alternative ways, such as visual, auditory, olfactory, and other signals (Fan and Fang, 2016). The absence of encounter events between *R. bieti* and *M. mulatta* found in the present study indicates that the two species are able to maintain a peaceful relationship. The shortest distance between *R. bieti* and *M. mulatta* ever reported was about 150 m, in which *M. mulatta* engaged in alert screams and climbed to higher spots to monitor *R. bieti*. Instead, the *R. bieti* group, probably due to their larger number, remained relatively calm (Grueter *et al.*, 2010). Our population count findings

reported a larger number for *R. bieti* (Fig. 5), confirming this hypothesis. Avoiding the encounters of two primate species is the key to their coexistence in the same area. Based on this findings, it is suggested that to support the coexistence and survival of these two primate species living in high altitude montane regions, the habitats along the overall elevational gradients should be included in wildlife conservation policies.

CONCLUSION

R. bieti and *M. mulatta* avoid encountering each other and use alternative spatial-temporal frames to maintain a peaceful coexistence relationship. *M. mulatta* approaches areas at lower elevations, while *R. bieti* is more likely to move up to higher elevations. Thus, an integrative environmental protection design inclusive of the overall elevational gradient of the Baimaxueshan National Nature Reserve would certainly benefit these two primate species and other wildlife living in the same reserve, resulting in more effective conservation outcomes.

ACKNOWLEDGEMENTS

We thank Baimaxueshan National Nature Reserve for its fieldwork help provided by the rangers. Our thanks also are given to our students Wen Hui and Li Junjie for their help with graphics and data analysis. We are grateful to Pan Ruliang for his comments on the article.

Funding

This study was sponsored by the National Natural Science Foundation of China (Grant no: 31860168, 31860164), the Local Universities Union Project of Yunnan Province Natural Science Foundation (202001BA070001-227), the Ten-thousand Talent Plan of Yunnan Province (YNWR-CYJS-2018-052; YNWR-QNBJ-2019-262), and Biodiversity Survey, Monitoring and Assessment Project of Ministry of Ecology and Environment, China (2019HB2096001006).

Ethical compliance

There are no research conducted on animals or humans.

Statement of conflict of interest

The authors have declared no conflict of interest.

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