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A viable tiger population in Similipal Tiger Reserve, India? Calculating if the ungulate prey base is limiting

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Low ungulate density can be a factor in limiting tiger populations, so to better manage tiger reserves one must be able assess if this is the case or if other factors might be more important. Here, we quantify ungulate density in a tiger reserve in India, compare it to other reserves, and estimate the tiger carrying capacity in order to assess this reserve can support a viable tiger population. Specifically, we studied the Similipal Tiger Reserve (STR), Odisha, India, from 2011 to 2014. The line transect method was used to estimate population density of available major ungulate prey species, i.e. sambar *Rusa unicolor*, wild pig *Sus scrofa*, barking deer *Muntiacus muntjac*, chital *Axis axis* and mouse deer *Moschiola indica*. A remarkable increase in ungulate prey density was noted in the intensive study area over the study period from 4.3 animals per km2 in the premonsoon season of 2011 to 28.9 animals per km2 in the post-monsoon season of 2014. This estimated ungulate density is very low compared to other tiger reserves of India. Density figures of ungulates when multiplied with the average weight of the respective species gave a biomass density of 1599.4kg km–2. This data was then used in two published empirical models to obtain estimates of tiger carrying capacity in STR. We used two empirical models from the published literature and concluded that the tiger carrying capacity of Similipal Tiger Reserve ranges between 1.3 and 3.8 tigers per 100 km2, much lower than our current estimates of tiger density. This suggests that the tiger population is below carrying capacity or that the estimated tiger population in critical tiger habitat falls below the threshold number. We suggest that the creation of large meadows for herbivores and the establishment of suitable fenced areas to augment breeding of the prey species chital and sambar are necessary to support a viable tiger population in the Similipal Tiger Reserve.

Keywords: density, biomass, carrying capacity, ungulate, prey, Similipal

Ungulates are distributed worldwide (except Australia and Antarctica) and are represented by 13 families, 95 genera and 257 species (Macdonald 2001, Wilson and Reeder 2005). In the Indian subcontinent the diversity of large ungulates is particularly rich with 39 species from 23 genera, 7 families and 2 orders which constitute nearly 15% of the extant ungulate species present globally (Wilson and Reeder 2005). Large ungulates are declining worldwide (Macdonald 2001, Schipper et al. 2008) and are among the most threatened mammals. They are vulnerable primarily due to their biological traits such as large body size, substantial dietary and energetic needs, small litter size and long inter-calving interval (Eisenberg 1980).

Ungulate depletion is thought to be a major factor driving the current decline of wild tiger *Panthera tigris* populations (Karanth and Stith 1999). Therefore to conserve this globallythreatened species, ungulate density needs to be monitored regularly in wildlife reserves. Since ungulates make up the major part of the tigers' diet (Schaller 1967, Seidensticker 1976, Karanth and Sunquist 1995), understanding herbivore populations and their distribution serve as an important part of studies on prey predator ecology (Karanth and Sunquist 1995, 1992). Estimating the population size or density of an animal species in an area is fundamental to understanding its status and demography and to plan for its management and conservation. The ungulate prey depends on the availability of suitable and productive habitats to maintain viable and abundant populations.

The impact of prey depletion on tiger populations has been in focus (Karanth and Stith 1999, Miquelle et al. 1999, Karanth et al. 2004). In many areas across Asia, there still exist large tracts of suitable habitat, but tigers are absent or at exceedingly low numbers, presumably due to lack of prey (Rabinowitz 1993, Check 2006). The clear relationship often seen between prey density and tiger numbers (Ramakrishnan et al. 1999, Karanth et al. 2004) supports

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the contention that prey density ultimately dictates tiger density, at least where tiger poaching is not common.

The ability to predict the carrying capacity of large predators is fundamental to their conservation, particularly in small enclosed reserves. Every predator that preys on large, readily surveyed wildlife can have its carrying capacity predicted based on the abundance of its preferred prey density or prey biomass (Fuller and Sievert 2001, Hayward et al. 2007).

The aims of our study were to quantify ungulate density in Similipal, utilize it to calculate prey biomass density in our intensive study area, and to compare our prey biomass with other potential tiger reserves in India. We also used previously published empirical formulae estimate tiger carrying capacity of the Similipal and assess whether it can support a viable tiger population.

Material and methods

Study area

The Similipal Tiger Reserve, one of the first nine tiger reserves of India, is located between latitudes 21°28′ N–22°8′ N and longitudes 86°04′ E–86°37′ E in the north-east corner of the Deccan plateau. It is part of Mayurbhanj district of Odisha and spreads over 2750km2 (Fig. 1), with a Critical Wildlife Zone of 1194.75km2. It is the largest sal *Shorea robusta* bearing forest in the state and encompasses a Wildlife Sanctuary and a proposed National Park. The tiger reserve is nestled within Similipal Biosphere Reserve; a member of the UNESCO recognized world network of biosphere reserves. The landscape of Similipal has numerous rolling

hills covered with tropical semi-evergreen forest, tropical moist deciduous forest, dry deciduous hill forest, high level Sal forest, grassland and savannah (Champion and Seth 1968). The identified fauna of Similipal include 55 species of mammals, 360 species of birds, 62 species of reptiles, and 20 species of amphibians. The landscape boasts more than 1079 plant species including 97 species of orchids.

Ungulate prey density estimation

The line transect method (Burnham et al. 1980, Buckland et al. 1993) was used to estimate ungulate prey densities in high animal concentration area (study area) as this has been effectively used to determine animal densities under similar tropical conditions (Karanth and Sunquist 1992, 1995, Varman and Sukumar 1995, Khan et al. 1996, Majumder 2011). The intensive study area was selected based on data collected during Phase IV tiger monitoring of NTCA (National Tiger Conservation Authority, Govt. of India), which suggested greater probability of finding tiger and associated co-predators in the area and consisted 45 beats of five forest ranges. The forest beats were considered as the sampling units and one transect of 2km was randomly laid in each beat. Thus 14 transects were laid in Upper Barakamuda (UBK) Range, 11 in Jenabil Range, 7 in National Park Range, 7 in Nawana North Range and rest 6 in Chahala Range. The total transect length of 90 km was monitored on three consecutive days at the beginning of the day, resulting in 270km of transect walk. The prey population data was collected during pre monsoon (February to May) and post monsoon (October to January) seasons along the transect lines between 2011 and 2014 covering a distance of 540 km in each year, so sampling was fairly intense. Transects were

Figure 1. Map showing the Similipal Tiger Reserve with critical wildlife zone, Odisha, India.

 \mathcal{D}

walked early in the morning (in the first twoh after sunrise), when animals are most active. Potential prey species of tigers were recorded during walk along transect with parameters such as species, cluster size, animal bearing (with compass) and angular sighting distance (using a laser range finder).

Visual detection of ungulates were followed by counts of group (cluster) size and measurements of sighting distances and sighting angles (Buckland et al. 2001, Thomas and Karanth 2002) to obtain perpendicular distances of sighted animals from the transect line. The animal counts and associated distance data were later used to model visual detection probabilities as a decreasing function of distance from the transect line. This modelling and the subsequent estimation of prey densities and their variances were accomplished using the estimation algorithms implemented in the computer software DISTANCE ver. 6.0 (Thomas et al. 2010). Generally, models of detectability based on the half-normal key function with one or no adjustment terms adequately fitted data from most prey species–habitat combinations, with the hazard rate or uniform–cosine key function fitting data adequately in the remaining cases (Buckland et al. 2001, Thomas et al. 2010).

Student's t-test (Zar 1984) showed that there was a significant difference $(p < 0.05)$ in the visibilities of prey species between the two seasons (pre-monsoon and post-monsoon) but not between the same seasons of the year. Hence we analysed the data of the pre-monsoon and post-monsoon line transects separately. Major ungulate prey species, such as chital, sambar, wild pig, barking deer and mouse deer were used for density estimation. Elephant and gaur were sighted along the transect line, but their densities were not estimated because of low sample sizes. No livestock was sighted during data collection.

Estimation of carrying capacity for tigers based on available prey density and their biomass

Individual prey densities obtained from DISTANCE were multiplied with average weight of individuals of prey species taken from Karanth and Sunquist (1995) to obtain biomass of prey species. Tiger carrying capacity of our intensive study area was then estimated by applying two different empirical models from the published literature.

For the first model, we calculated tiger carrying capacity using Treves et al.'s (2009), who applied the same model to lions in central Africa. This model is as follows:

$$
T_1 = p^{0.725} / 16.3 \tag{1}
$$

Where T_1 stands for number of tigers per unit area, and we express densities per 100 km2 for tigers and per km2 for prey.

 $p =$ number of prey animals in the same area. Karanth et al. (2004) assumed $b = 1.0$ for tigers (i.e. all prey are potentially eaten) but their field data later placed *b* closer to 0.514. But in Treves et al. (2009) model consider *b* to reflect intrinsic factors, such as the energetic efficiency with which prey can be converted to lions (here prey tiger). Hence the model propose the scaling factor b relates to the well-known scaling factor relating body mass to metabolic rate and energy intake (0.67–0.78: McNab 1989, White and Seymour 2005, Carbone et al. 2007). The exponent $b \leq 1.0$ allows for a nonlinear relationship between prey numbers and tiger numbers. Based on field data from lions in Africa, Treves et al. (2009) assessed *b* as 0.725.

The second empirical model we used was originally developed for the Amur tiger by Miquelle et al. (1999), and resulted from their review of tiger densities and prey biomass densities in China is as follows:

$$
T_2 = (P_b + 256.3) / 476.5
$$
 (2)

Where T_2 is the number of tigers/100 km² and P_b is the prey biomass (kg km–2).

Results

Density, biomass of prey species and carrying capacity of tigers

Estimate of densities of individuals and groups along with coefficient of variation and associated confidence intervals of five potential prey species present in the study area are summarized in Table 1.

The study area was found to harbour a low ungulate density which gradually increased over time. When data were pooled within all species and seasons, the estimated ungulate prey densities was 4.3 ± 0.6 SE km⁻² in pre-monsoon and 5.3 ± 0.8 SE km⁻² in post-monsoon season during 2011. The estimate of density of clusters was 1.8 km^{-2} that varied within 95% confidence intervals from 1.1 to 2.8km–2. Half normal-cosine was best fitted model with lowest Akaike information criterion (AIC) value for overall ungulate density during pre-monsoon and post-monsoon season. When data was pooled within all prey species and seasons, the estimated ungulate prey densities was 4.9 animals km−² in pre-monsoon and 6.9animals km−2 in post-monsoon season during 2012. Half normal-cosine was the best fitting model with the lowest AIC value for overall ungulate density during pre-monsoon and post-monsoon seasons. The potential prey abundance/density in intensive study area between pre-monsoon and post-monsoon seasons were not significantly different (univariate ANOVA: F=0.5, df=12, $p > 0.20$).

During 2013, chital and mouse deer sighting along the transect line was very low; therefore observation data related to them were excluded from the analysis. When data were pooled within all species and seasons the estimated ungulate prey densities/abundance was 6.6animals km−2 in premonsoon and 10.9 animals km−2 in post-monsoon season. The potential prey density in study area between the premonsoon and post-monsoon seasons were significantly different (univariate ANOVA: $F = 0.5$, df = 12, p < 0.001). Similarly in 2014, observation of chital and mouse deer populations were low along transects. When data was pooled within all species and seasons the estimated ungulate prey densities was 22.6animals km−2 in pre-monsoon and 28.9animals km−2 in post-monsoon season. When ungulate prey densities were compared through 2011, 2012,

Table 1. Estimated population density and biomass density of principal ungulate prey in Similipal Tiger Reserve, Odisha between 2011 and 2014.

Year	Prey	D_1 km ⁻² (pre-monsoon)	D_1 km ⁻² (post-monsoon)	$C_V D_1 %$ (pre-monsoon)	$C_V D_1 %$ (post-monsoon)	C_1D_1 km ⁻² (pre-monsoon)	C_1D_1 km ⁻² (post-monsoon)	Biomass density $(kg km-2)$
2011	Sambar	$\overline{2}$	3.8	12.2	9.3	$1.1 - 3.8$	$2.1 - 5.2$	
	Wild pig	2.6	3	12.1	7	$1.3 - 4.9$	$2 - 5.3$	
	Barking deer	1.1	1.2	18.4	18.3	$0.7 - 1.9$	$0.5 - 2.1$	
	Chital	1		21	21.3	$0.4 - 1.8$	$0.4 - 1.5$	
	Mouse deer	0.4	0.8	28.3	32.1	$0.2 - 1.1$	$0.5 - 1.1$	
2012	Sambar	2.8	$\overline{4}$	14.1	12	$1.9 - 4.2$	$2.8 - 6$	
	Wild pig	3.2	4.8	15.2	11.4	$2.1 - 4.9$	$3.2 - 5.2$	
	Barking deer	1.6	1.6	20.1	21.3	$0.9 - 2$	$0.7 - 2.2$	
	Chital	5	3.8	9.3	11.6	$4.1 - 6.7$	$2.5 - 5$	
	Mouse deer	0.6		26.3	20.4	$0.2 - 1$	$0.8 - 1.5$	
2013	Sambar	2.8	5.8	17.5	10.5	$1.9 - 3.5$	$3.9 - 6.2$	
	Wild pig	4.3	6.5	18	13.3	$3 - 5.3$	$4.2 - 7.4$	
	Barking deer	2.5	2.9	12.4	14.1	$1.2 - 3.3$	$1.8 - 4$	
	Chital	NA	NA					
	Mouse deer	NA	NA					
2014	Sambar	3.8	5.9	22.3	15.8	$2.2 - 4.5$	$3.7 - 7.2$	48
	Wild pig	$\overline{4}$	6.4	13.9	11.1	$3.1 - 6$	$4.8 - 7.9$	55
	Barking deer	2.1	2.4	14.5	14.2	$1.7 - 3.5$	$1.8 - 3.6$	1250.8
	Chital	0.8		34.8	23.3	$0.2 - 1.2$	$0.7 - 1.6$	2.4
	Mouse deer	0.6	0.8	25.9	27	$0.1 - 1$	$0.5 - 1.3$	243.2
	Total biomass							1599.4

D_I=density of individuals; C_vD_I=coefficient of variation of density of individuals; C_ID_I=95 % confidence intervals of density estimates of groups and individuals prey species; NA=chital and mouse deer data was very low along the transect line; Estimation of biomass density perform only in post-monsoon season of 2014, as highest ungulate prey density occur in these period.

2013 and 2014, it was noticed that density of prey animals remarkably increased over time and by 2014 there was a five-fold increase (Fig. 2). There was significant difference in prey density in different years of study (Kruskal–Wallis test, $H = 6.4$; $p < 0.0001$). While elephants were sighted five times and gaurs were sighted three times during the study period; on transect gaur was never sighted and elephants were sighted only once.

During 2012 range wise distribution of ungulates showed highest density of ungulates in UBK range followed, in order, by Jenabil, National Park ranges, Chahala, and Nawana (north) ranges. However, after 2013 onwards, the pattern changed and density of ungulates in Jenabil was highest followed by UBK, National Park Range, Chahala, and Nawana (north) range.

Figure 2. Ungulate prey density gradually increases from 2011 to 2014 in critical tiger habitat.

The density figures of ungulates during post-monsoon season of 2014, which depicts the highest density of prey animals, were considered for estimating the biomass density of prey. The density figures of ungulates when multiplied with the average weight of the respective species gave a calculated biomass density of 1599.4kg km–2 for intensive study area (Table 1).

Thus the tiger carrying capacity (T_1) and (T_2) as estimated based on prey density and biomass of ungulate prey available in intensive study area of Similipal Tiger Reserve was:

 (T_1) 1.3 tigers 100 km⁻² (as per the empirical equation developed by Treves et al. 2009).

 (T_2) 3.8 tigers 100 km⁻² (as per the empirical equation developed by Miquelle et al. 1999).

Thus the two different models applied above suggest that Similipal has at present, tiger carrying capacity in the range of 1.3 to 3.8 tigers 100 km–2.

Discussion

Population estimation of ungulates

Densities of most tropical forest ungulate species are now significantly lower and many of them are facing extinction because of human interference in their habitat, directly or indirectly (Ripple et al. 2015). As several of these species have critical ecological roles, such population changes may impact forest and agricultural ecology. The line transect method was used to estimate ungulate density in Similipal for the present study. This is considered more appropriate method for calculating prey density with the associated coefficient of variance (CV%) since it takes into account the temporal variation in species detection (Jathanna et al. 2003).

4

During the present study data was gathered using a laser rangefinder for distance and compass for bearing of the animal groups from the line transect. Detections near the line, as shown by the low χ^2 values of the first distance interval, were as expected for each model for all species. There was no evidence of heaping or a sharp drop-off indicating evasive movement in response to the observer for most species (Majumder 2011).

The chital density in Similipal Tiger Reserve is low and restricted to some areas such as Chahala, Debasthali and Nawana as availability of grassland or open area is very low in Similipal. The wild pig population was found to be higher than other ungulates and this may be due to its adaptive nature, and being less affected by poaching than ungulates like sambar, chital and barking deer. Mouse deer is also found in the reserve with good population but taking its photograph or observing it was not possible due to its agile nature.

Comparison of ungulate prey densities/abundance between 2011 through 2014 shows gradual but remarkable increase in prey density on temporal scale. It would be pertinent to mention that on 29 March 2009, there were vicious violent attacks in Similipal Tiger Reserve. The staffs and tourists were assaulted; rest houses and offices were burnt. All the staff posted in the core area and adjacent buffer area deserted their posts. No staff ventured inside the core area of the Reserve till August 2009. Thereafter the staff gradually started venturing in the core area and with gradual but sustained efforts spanning over a year most of the anti-poaching camps started working again. Wildlife field staff also joined their posts. Up to July, 2009 the poachers and hunters had a field day and they indiscriminately killed thousands of small and large animals, adversely affecting ungulate population in the reserve. The presence of a number of carcasses of ungulates with arrows stuck in their bodies, and extensive poaching of ungulates, evidenced by the frequency of snares found in the forest spoke of the mayhem. As the staff regained lost ground, poaching declined and more animals were observed. Further management interventions including anti-poaching measures over the years have shown a bounce back in the ungulate population.

While analysing ungulate density variation between the Ranges during the period, it was observed that from 2013 onwards the ungulate density of Jenabil Range has overtaken that of UBK (Upper barakamuda) Range (both of these ranges are occupied by major prey species in Similipal Tiger Reserve). Here it is significant to note that Jenabil village was completely relocated outside of Similipal Tiger Reserve, to a place near Udala named Ambadiha in 2010. This provided a new open space of around 120ha, which was more than the total open grasslands available in the critical wildlife zone area. The abandoned agriculture fields turned slowly into meadows having tender, nutritious grasses. The availability of new grassland coupled with drastically-reduced human interference has contributed to a resurgence of the ungulates in Jenabil range. This shows why undisturbed spaces are important and why properly planned and executed relocation can improve tiger habitat.

Ungulates can play a very important role in maintaining the population of predators (Karanth and Sunquist 1992). Our analysis revealed that the overall density of ungulate prey and that of individual species was very low in Similipal compared to other tiger landscapes in India. This may be due to the unavailability of suitable habitat with large grassy meadows, and the presence of high anthropogenic pressure exerted by villages present in the core, buffer and within 10km of the park boundary (1265 villages).

Estimation of carrying capacity for tigers based on available prey density and prey biomass

Considering the importance of prey for tiger conservation (Karanth and Stith 1999), it may be critical to understand tiger carrying capacity to ensure that there is an adequate prey base. The all India tiger estimation in 2010, by the Wildlife Institute of India through camera trapping and field surveys across tiger occupied habitats, estimated a carrying capacity of 2.11tigers 100km–2 for Similipal (Jhala et al. 2011). In the present study, two empirical models for predicting the tiger carrying capacity of Similipal were used. Using the first (Treves et al. 2009) model, the tiger carrying capacity (T_1) was estimated to be 1.3 tigers 100 km⁻². Using the second (Miquelle et al. 1999) model, the carrying capacity of Similipal for tigers was estimated to be 3.8 tigers 100 km⁻². This model was developed for the Amur tiger in a different habitat in China where ungulate density is very low in the tiger's range and the area is vast, and we used this model because Similipal also has a relatively low ungulate density and the area of tiger reserve is also very large. Thus, based on these two models we estimate that the carrying capacity for tigers in Similipal Tiger Reserve is between 1.3 and 3.8 tigers 100km–2. To produce their empirical model, Treves et al.'s (2009) estimated lion abundance using total counts of lions from Uganda. They predict potential number of lion could exist if prey recovers and lion-specific mortality is curbed. They developed three empirical equations based on prey availability and their biomass. The tiger carrying capacity of Similipal was estimated through (Eq. 2) developed by Treves et al. 2009. A weakness of the theoretical model (Eq. 2) is the uncertain use of the exponent b. Many factors may lower b; some intrinsic biological constrains (e.g. metabolic costs of search time, injury, social behaviour and conversion of carcasses into reproduction), and others extrinsic constraints affecting predators across sites (e.g. predator-specific mortality).

Empirically, Karanth et al. (2004) found b to be close to 0.51, whereas Treves et al. (2009) found b closer to 0.76 by adjusting the exponent to equal the number of lions in Queen Elizabeth National Park in 1999. Such a value falls close to the daily, energy-intake, scaling factor of $0.79 \pm$ SE 0.09 expected of large mammalian predators (Carbone et al. 2007). The different scaling factors of tigers and lions could reflect differences between solitary and group hunting.

As the tigers are mostly within a narrow region of about 318km2 within the tiger reserve of 2750km2 and the overall prey density is low across the whole area; the second empirical model suggests the upper end of the tiger carrying capacity that can be supported.

Similipal has the lowest prey biomass density among all major tiger areas of the country like Pench, Nagarhole, Bandipur, Chitwan and Bardia, (Eisenberg and Seidensticker

Table 2. Biomass of ungulate species from different tropical areas in South Asia.

1976, Dinerstein 1980, Johnsingh 1983, Karanth and Sunquist 1992, Biswas and Sankar 2002). The highest prey biomass density of 7638 kg km−2 was reported from Nagarhole in Karnataka (Karanth and Sunquist 1992). As these sites represent few of the last remaining suitable habitats for tigers, the tigers in the subcontinent have the highest chance of survival in areas that have high biomass densities comparable to these sites (Table 2).

As for reserves in general, the estimated carrying capacity of Similipal Tiger Reserve would be very helpful in preparing the management action plans necessary to enhance available food resources and to determine the potential of an area to support minimal viable tiger populations. This technique can be used to improve the accuracy of population viability analysis (PVAs) by including a prediction of the carrying capacity and approaches like ours should become a valuable tool for conservation managers.

The carrying capacity of tigers in Similipal was quantified in this study based only on the prey base abundance and their available biomass in high prey concentration area of 318 square kilometres within the critical Wildlife area of the Park. Since 2011, there was gradual increase of prey base till 2014. The estimated ungulate density of 28.9 animals and biomass of 1599.4 kg km–2 in 318km2 for 2014 was the basis for further calculation of carrying capacity.

Previous study in Similipal estimated ungulate density of 19.98 per square kilometre and biomass of 1264 kg km–2 in 421 km2 for the period between 2012 and 2013 (Palei et al. 2016). This corroborates the fact that since 2011, there has been a gradual increase in prey base until 2014. But, as the prey base is very low in other parts of the Reserve, the present tiger carrying capacity cannot be extrapolated to the area beyond the study area or to total area of the Park. However, the improvement in prey base in the study area due to positive management interventions that we noted shows that the prey base could be substantially raised in the whole of the Tiger Reserve with appropriate management intervention.

For a demographically viable tiger population, a minimum of 20 to 25 breeding units are believed to be essential to preserve a tiger landscape (Yumnam et al. 2014). The conclusion drawn from recent study in Similipal indicate that future of tigers is at great risk as the estimated tiger population in critical tiger habitat is near or below the threshold number required to support a viable tiger population. The prey base must gradually increase in other parts of the park to support a viable tiger population in future.

Conclusions

Ungulate prey depletion can be serious threat to the survival of tigers (Karanth et al. 2004). Our analysis reveals that the prey base of Similipal Tiger Reserve is lower than other tiger reserves in India and can barely support a viable tiger population. We suggest that it is therefore of utmost importance to take steps like the creation of meadows, and establishment of fenced areas for the breeding of chital and sambar inside the critical wildlife area/buffer area of Similipal to augment their populations. As the poaching of ungulates on which the tiger population depends for food may be as serious as the poaching of tigers themselves, strict antipoaching measures along with habitat improvement are needed to ensure the long term survival of tigers in the Similipal Tiger Reserve.

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