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The relationship between social behaviour and habitat familiarity in African elephants (*Loxodonta africana*)

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Social associations with conspecifics can expedite animals' acclimation to novel environments. However, the benefits gained from sociality may change as the habitat becomes familiar. Furthermore, the particular individuals with whom animals associate upon arrival at a new place, familiar conspecifics or knowledgeable unfamiliar residents, may influence the type of information they acquire about their new home. To examine animals' social dynamics in novel habitats, we studied the social behaviour of African elephants (*Loxodonta africana*) translocated into a novel environment. We found that the translocated elephants' association with conspecifics decreased over time supporting our hypothesis that sociality provides added benefits in novel environments. In addition, we found a positive correlation between body condition and social association, suggesting that elephants gain direct benefits from sociality. Furthermore, the translocated elephants associated significantly less than expected with the local residents and more than expected with familiar, but not necessarily genetically related, translocated elephants. The social segregation between the translocated and resident elephants declined over time, suggesting that elephants can integrate into an existing social setting. Knowledge of the relationship between sociality and habitat familiarity is highly important in our constantly changing world to both conservation practice and our understanding of animals' behaviour in novel environments.

Keywords: African elephant; association; conservation; novel environment; social behaviour; translocation

1. INTRODUCTION

Animals often encounter novel environments, both naturally and owing to human activities. Dispersing individuals encounter novel habitats while searching for a place in which to settle (Stenseth & Lidicker 1992), and migrating animals locate novel habitats periodically (Mettke-Hofmann & Gwinner 2004). Furthermore, animals encounter novel places owing to human modifications to the environment, e.g. habitat loss (Sutherland & Dolman 1994), and fragmentation (Ewers & Didham 2006), or owing to wildlife management activities such as translocations and reintroductions (Griffith *et al.* 1989; Fischer & Lindenmayer 2000). In both natural and unnatural encounters with novel habitats, animals lack vital information regarding suitable forage, hiding locations, mating opportunities and predators. Social interactions with conspecifics can expedite animals' acclimation to a novel environment.

Despite the extensive work on the adaptive significance of sociality (Slobodchikoff 1988), very little is known about its importance when animals face novel environments. Several benefits may be gained from interacting with conspecifics in a novel habitat. For example, social learning and cueing are important mechanisms for rapidly gaining knowledge about a new environment (see reviews in Danchin *et al.* (2004) and Bonnie & Earley (2007)) and the presence of conspecifics is known to facilitate learning novel tasks (Moscovice & Snowdon 2006). Associating with conspecifics in a novel environment may provide protection against unknown predators (Isbell *et al.* 1990) and unfamiliar aggressive conspecifics (Cheney & Seyfarth 1983; Jack & Fedigan 2004). However, associating with conspecifics in a novel environment can also entail costs owing to resource competition (Koenig 2002) and agonistic interactions during territory acquisition (Stamps 1994).

We suggest two hypotheses regarding the relationship between sociality and animals' familiarity with a habitat. Our first hypothesis 'beneficial sociality in novel environments' (BSNE) states that animals gain added benefits from associating with conspecifics in a novel environment (e.g. through social learning), but these added benefits diminish as the habitat becomes familiar. BSNE predicts a decrease in the number of conspecifics an animal associates with over time. Our alternative hypothesis, 'costly sociality in novel environments' (CSNE) states that social associations in a novel habitat incur added costs (e.g. owing to territorial disputes), but these costs are outweighed by the benefits of sociality as the habitat becomes familiar. CSNE predicts an increase in the number of conspecifics an animal associates with over time. To our knowledge, no study has thus far investigated this relationship between sociality and habitat familiarity.

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Another important question about animal sociality in novel environments is as follows: who are the particular individuals that animals associate with? Animals can associate with either unfamiliar local residents or familiar conspecifics that arrived with them to the new location. Associating with familiar conspecifics has several advantages, including protection during encounters with aggressive unfamiliar conspecifics (Cheney & Seyfarth 1983; Jack & Fedigan 2004), inclusive fitness benefits (Ward & Hart 2003) and reducing neophobia (Coleman & Mellgren 1994). Furthermore, associating with unfamiliar conspecifics can be costly. For example, unfamiliar individuals may carry unknown diseases (Loehle 1995) or be aggressive (Goossens *et al.* 2005), and learning about unfamiliar conspecifics may come at the expense of learning about the new habitat (Burman & Mendl 1999). However, in a novel setting, there is an asymmetry in the knowledge about the new habitat: the local, unfamiliar residents have information about the new habitat that familiar conspecifics might not have (Forsman *et al.* 2007). Thus, there may be a great advantage to associating with unfamiliar residents in a novel environment.

African elephants' (*Loxodonta africana*) social dynamics provide an excellent opportunity for studying sociality in novel environments. Elephants live in fission–fusion societies in which core family groups (second tier units) occasionally form bond groups (third tier social structures) (Moss & Poole 1983; Wittemyer *et al.* 2005). Elephants' social dynamics are governed by ecological factors (Wittemyer *et al.* 2005) and the formation of bond groups is thought to be important for gathering both social (Moss & Poole 1983) and ecological (Foley 2002) information. Furthermore, elephants are highly intelligent mammals (Hart *et al.* 2008) that are capable of distinguishing between the vocal signatures of familiar and unfamiliar conspecifics (McComb *et al.* 2000, 2003).

Recently, management of elephant populations has included translocating them from familiar to novel environments (Dublin & Niskanen 2003), providing opportunities for examining their social dynamics in novel environments. First, to distinguish between our BSNE and CSNE hypotheses, we examined the change over time in association between the translocated elephants and conspecifics (familiar and unfamiliar). Based on the African elephants' social learning abilities and their lack of territorial behaviour, we predicted to find evidence supporting the BSNE hypothesis. Second, we examined whether the translocated elephants formed bond groups with familiar or unfamiliar conspecifics, predicting that they will associate with knowledgeable unfamiliar conspecifics to learn about their new home. Finally, we explored possible explanations for the social patterns found.

2. MATERIAL AND METHODS

(a) *Translocation and sightings*

During September 2005, 150 African elephants were translocated from Shimba Hills National Reserve on the coast of Kenya (4.0° S to 4.3° S and 39.5° E to 39.3° E) to Tsavo East National Park (2.0° S to 3.7° S and 38.1° E to 39.3° E), a distance of 160 km. This translocation was part of the Kenya Wildlife Service (KWS) effort to decrease human–elephant conflict in the vicinity of Shimba Hills. Twenty elephant groups comprising adult females, juveniles and calves (average group size 6.8) and 20 independent adult males were moved over the course of 32 days. The release site differs ecologically from the source site and is separated from it by dense human population, providing a unique opportunity for examining the social behaviour of the elephants in a novel environment.

During the translocation, all the elephants were tagged with yellow zip ties on their tails to distinguish them from the local Tsavo elephant population. Unique white numbers painted on the translocated elephants' backs, natural ear marks and tusk shapes were used for individual identification of the translocated elephants (Moss 1996). Elephants' ages were estimated based on Moss (1996).

The locations, their time and the identities of the translocated and local Tsavo elephants were recorded in Tsavo East for a year post-translocation using a Geko 201 GPS unit (Garmin Ltd., USA). Road transects were conducted using a vehicle four to five times a week, alternating between four routes of similar length (50–70 km) on the existing roads within Tsavo East National Park. A total of 3371 elephant sightings were recorded, of which 386 and 2985 were the translocated and local elephants, respectively. Of the 150 elephants translocated, data on 83 were obtained, and are presented here. Because males leave the social unit in which they were born at the age of 15, and because the social behaviour of these independent males differs from that of females and their young offspring (Moss & Poole 1983), such translocated males were excluded from our analyses.

(b) *Social association*

Elephants were defined as associating with one another if they were sighted within 500 m from one another within a 2 hour time period, based on McComb *et al.* (2000, 2003). They showed that elephants can individually recognize conspecifics' vocalizations over great distances (1 km). Therefore, the definition of social association used here includes not only direct interactions but also recognizes the communicative capabilities of elephants to acquire information about the number and identities (translocated or local) of vocalizing conspecifics (McComb *et al.* 2000, 2003). Thus, the definition of social association used here allows for the acquisition of inadvertent social information about the new environment (Danchin *et al.* 2004).

To test whether the number of conspecifics (translocated and local) with whom a translocated elephant is associated changed over time, we counted the number of conspecifics in association with each translocated elephant for each of its sightings (using the above definition for association) and analysed it using a random effects-mixed model. Time was a fixed effect in the model, elephant identity was included as a random effect to control for repeated measures of the same translocated individual and season (wet or dry) was included as a fixed effect in the model to account for the seasonal effects on social association.

To examine whether associating with conspecifics provided direct adaptive benefits, we examined the relationship between body condition (see the definition in the electronic supplementary material) and association with conspecifics using a random effects-mixed model. The number of conspecifics (translocated and local) in association with the translocated elephants and time were fixed effects in the model, and elephant identity was a random effect in the model. Since none of the interactions among the effects was significant, they were not included in the final statistical model (Engqvist 2005).

To quantify the association among the translocated elephants, we computed an association matrix using the simple ratio association index (AI; Ginsberg & Young 1992), which is often used in the studies of elephant social behaviour (McComb *et al.* 2000, 2001; Wittemyer *et al.* 2005; details in the electronic supplementary material).

To quantify the association of each translocated individual with all other translocated elephants, weighted degree (WD), a measure from social network theory (also referred to as vertex strength in Barrat *et al.* (2004)) was calculated using UCINET (Borgatti *et al.* 2002). WD is calculated for each translocated individual as the sum of its association indices with all other translocated elephants: $\mathrm{WD}_i = \sum_{j=1}^{n} \mathrm{AI}_{ij}$ where i is a certain translocated elephant; j is any other translocated elephant; and n is the number of translocated elephants. WD was calculated only for the translocated elephants older than 5 years (excluding independent adult males). Calves (younger than 5 years) seldom leave their mothers (Wittemyer *et al.* 2005), and including them would have disproportionately increased the WD of females with calves.

To examine the association between the translocated and local elephants, their association with one another (AL) was calculated as the proportion of sightings the translocated elephants were observed in association with the local elephants: $\mathrm{AL}_i = (n_{i\mathrm{L}}/n_i)$ where $n_{i\mathrm{L}}$ is the number of times the translocated elephant i was in association with any local elephant (see the association definition above) and n_i is the total number of times the elephant i was seen. AL was calculated only for the elephants older than 5 years and excluding adult males. Since calves' activities are strongly associated with their mothers' (Wittemyer *et al.* 2005), their AL would have been the same as their mothers', and including them would have biased the average AL towards that of females with calves. The relationship between WD and AL was examined using a Pearson correlation coefficient test.

(c) *Bond group formation*

To evaluate whether the translocated elephant family groups formed bond groups with other translocated (familiar) elephants or with local (unfamiliar) conspecifics, the individual sightings were grouped into core family groups (also known as second tier units; Wittemyer *et al.* 2005). The translocated elephants captured together, as a cohesive group, were considered to be a family group (see relatedness results below to support this grouping method). The local elephant family groups were assigned based on spatial proximity, since no genetic data were available for them. Local elephants within five elephant body lengths of one another when first sighted were considered to be a family unit. The number of group associations, using the association definition above, was summed for each of the following categories: TT, two translocated groups captured separately associating with one another; LL, two local groups associating with one another; TL, translocated group and local group associating with one another; and T, translocated or L, local groups alone.

To determine whether the observed association between groups differed from an expected association rate, a χ^2 was used to compare the observed values with an expected distribution, created using a permutation model (see the electronic supplementary material for permutation model details).

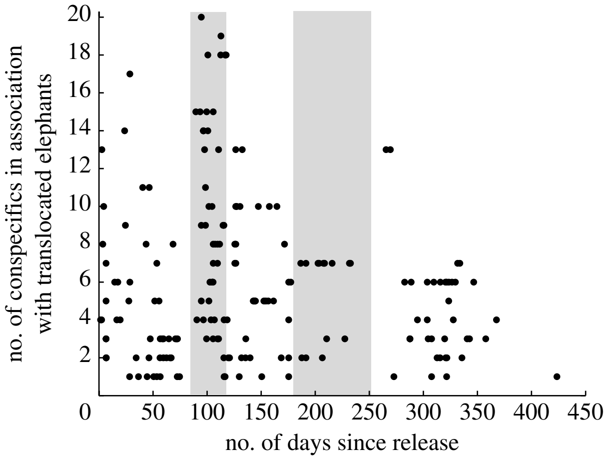

Figure 1. Relationship between social association and time. The number of conspecifics (locals and translocated) that translocated elephants associated with decreased over time ($R = -0.56$, $p = 0.008$). Shaded background denotes wet seasons and white background denotes dry seasons (wet > dry, $p < 0.0001$).

To test whether the translocated elephants captured together, as a cohesive group, were indeed family units, and to examine whether bond group formation provided inclusive fitness benefits to the translocated elephants, we analysed the genetic relatedness among the translocated elephants (see the electronic supplementary material). Genetic relatedness between the translocated elephants captured together was averaged and compared with the average relatedness between the elephants captured apart using Student's t-test. The relationship between AI and genetic relatedness was examined using a Pearson correlation coefficient test.

Finally, to examine whether familiarity with the new habitat had any effect on whom the translocated elephants associated with, we looked at the change over time in WD and AL. We compared the data from two dry seasons one year apart: the long dry seasons of 2005 and 2006. In both these seasons, the data were collected over a similar time period (three months in 2005 and four months in 2006) and a similar number of sightings were obtained (914 sightings in 2005 and 1033 sightings in 2006). The average WD and average AL were calculated for each of these time periods and compared using a Wilcoxon signed-rank test.

All analyses were implemented in MATLAB (MathWorks Inc., MA, USA) and in the statistical analysis program JMP (SAS institute, NC, USA).

3. RESULTS

The social association of the translocated elephants (excluding independent adult males) with conspecifics (both locals and translocated) decreased with time (random effects-mixed model: $R = -0.56$, $n = 385$; 'time': $F_{1,381} = 7.12$, $p = 0.008$; figure 1), supporting the BSNE hypothesis. The translocated elephants associated with more conspecifics during the wet than dry seasons ('season': $F_{1,380} = 28.63$, $p < 0.0001$; figure 1). The random effect 'elephant identity' accounted for 15.7 per cent of the data's variance, suggesting that there was individual variation among the translocated elephants in the initial number of conspecifics they associated with.

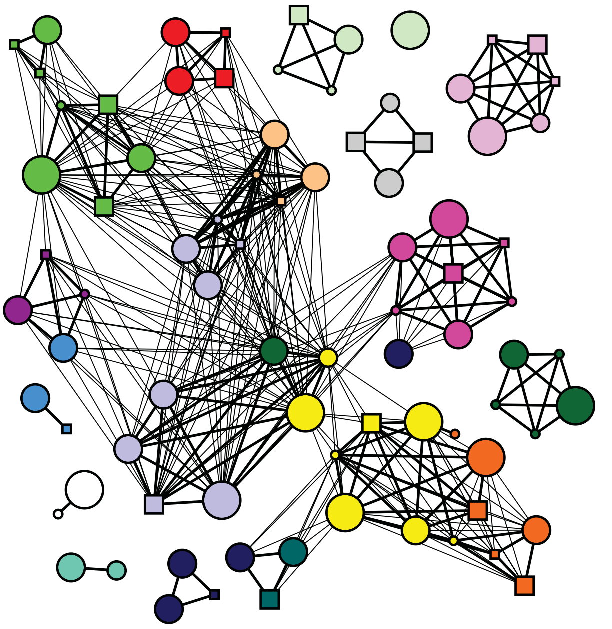

Figure 2. Social network of translocated elephants. Network nodes represent individual translocated elephants and connecting edges denote their social association (AI). Elephants captured together, as an intact social unit, are represented in the same colour. Node size denotes elephant's age in four age classes (from the smallest to the largest: 0–5; 5–15; 15–30; and 30+). Node shape indicates sex (squares, males; circles, females). Edge thickness denotes association strength: the darker and wider the edge, the greater the AI value. This network graphical representation was created using the program Cytoscape (http://cytoscape.org).

Body condition of the translocated elephants (excluding calves and adult males) positively correlated with the number of individuals with whom they associated and with time (random effects-mixed model: $R=0.64$, $n=151$; 'association with conspecifics': $F_{1,147}=7.48$, $p=0.007$; 'time': $F_{1,147}=11.21$, $p=0.001$), suggesting that elephants gain direct benefits from sociality. The random effect 'elephant identity' accounted for 23.9 per cent of the data's variance, suggesting that there was individual variation among the translocated elephants in their initial body condition.

The translocated elephants and the local Tsavo residents were socially segregated. The translocated elephants associated with one another throughout the study period (figure 2). Translocated family groups captured separately associated significantly more with one another than expected according to the permutation model and less than expected with local resident groups (χ^2 test: $\chi^2_4=680.45$, $p<0.001$; figure 3). Moreover, a significant negative correlation was found between the translocated elephants' association with the local elephants (AL) and their WD as a measure of their association with other translocated elephants (Pearson correlation coefficient test: $R=-0.35$, $n=56$, $p=0.007$). In other words, the more a translocated elephant associated with other translocated elephants, the less it associated with the local elephants and vice versa.

The translocated elephants did not gain inclusive fitness benefits from forming bond groups with familiar conspecifics. Genetic relatedness between elephants captured together was on average, $X\pm\text{s.e.}=0.13\pm0.02$, similar to the relatedness found within the family groups of undisturbed African elephant populations (Archie *et al.* 2006). This finding supports our grouping method for the translocated elephants in the permutation model. By contrast, average genetic relatedness among the translocated elephants belonging to separate groups was $X\pm\text{s.e.}=-0.02\pm0.003$. In relatedness analysis using microsatellite data, negative relatedness values indicate with high confidence that two individuals are unrelated (Konovalov & Heg 2008). The difference between the relatedness of elephants captured together and those captured apart was statistically significant (Student's *t*-test: $T_{90}=-3.15$, $p=0.002$). In addition, the social association (AI) between the translocated elephants captured together correlated positively and significantly with their genetic relatedness (Pearson correlation coefficient test: $R=0.51$, $n=60$ pairs, $p<0.001$), as one might expect based on the previous work (Archie *et al.* 2006). However, the social association (AI) between the translocated elephants belonging to separate family groups did not significantly correlate with their genetic relatedness (Pearson correlation coefficient test: $R=0.29$, $n=32$ pairs, $p=0.1$).

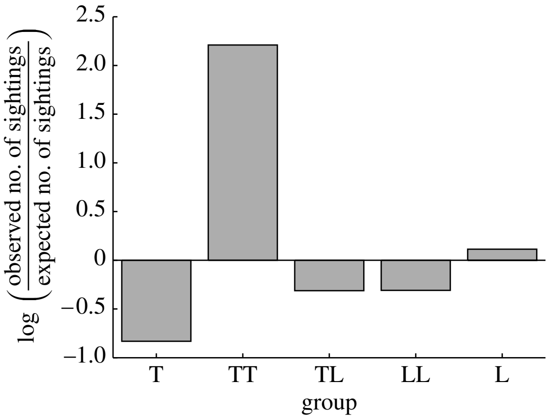

Figure 3. Bond group formation. Log of the ratio between the observed and expected (as computed by the permutation model) number of times translocated elephant groups were seen alone (T); translocated groups captured separately associated with one another (TT); translocated groups and local groups associated with one another (TL); distinct local groups associated with one another (LL) and local groups were seen alone (L). Differences between the observed and expected values are significant ($p<0.001$, χ^2 test).

The social segregation between the translocated elephants and the local population did not persist over time. The average WD of the translocated elephants decreased significantly between the long dry season of 2005 and that of 2006 (Wilcoxon signed-rank test: $T=101$, $n=80$, $p<0.0001$; figure 4*a*). Furthermore, the association of the translocated elephants with the locals (AL) was more frequent during the long dry season of 2006 than that of 2005 (Wilcoxon signed-rank test: $T=1.5$, $n=14$, $p=0.04$; figure 4*b*). Thus, the translocated elephants transitioned from a closed immigrant enclave to integrating into an existing social structure.

4. DISCUSSION

In this study, we examined two aspects of sociality in novel environments: its temporal dynamics and its composition. The social association between the translocated elephants and conspecifics (both the locals and translocated)

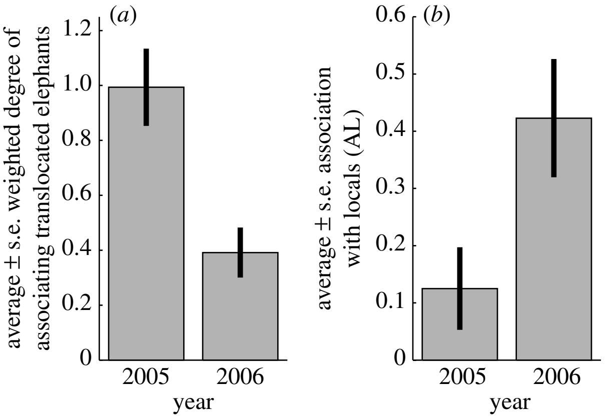

Figure 4. Change in association with translocated and local elephants over time. (*a*) Average weighted degree (WD), as a measure of association among translocated elephants, was significantly higher during the long dry season of 2005 than that of 2006 ($p<0.0001$, Wilcoxon signed-rank test). (*b*) Average association between translocated and local elephants (AL) was significantly lower during the long dry season of 2005 than that of 2006 ($p=0.04$, Wilcoxon signed-rank test). Error bars indicate standard errors.

decreased over time. This result supports our BSNE hypothesis, which states that animals gain added benefits from associating with conspecifics when arriving at a novel environment, but these added benefits diminish as the habitat becomes familiar. We found more social associations in the wet than the dry seasons, coinciding with the social behaviour of undisturbed elephant populations in which resource competition may drive this trend (Leuthold 1976; Wittemyer *et al.* 2005). Our finding that body condition positively correlated with the number of individuals a translocated elephant associated with implies that elephants indeed gain direct benefits from sociality. However, this does not exclude elephants in poor body condition having few social associations for other reasons (e.g. being sick or wounded). The relationship we found between sociality and habitat familiarity for elephants was expected based on their reliance on social knowledge for gaining information about their habitat (Foley 2002). However, it is possible that in other species (e.g. territorial animals), a different relationship between sociality and habitat familiarity will be found.

Contrary to our predictions that the translocated elephants would associate with the local residents to gain information about their new home, the translocated elephants formed bond groups with other, genetically unrelated, translocated groups and not with the local residents. It is safe to assume that association among the translocated elephants post-release reflected social bonds among familiar individuals when considering elephants' extraordinary social memory (McComb *et al.* 2001; Hart *et al.* 2008), long-distance communication abilities (McComb *et al.* 2003), the small site from which the elephants were translocated (250 km^2) and their ranging patterns there (Kahumbu 2002). Animals that rely on social learning and are not territorial may benefit from associating with local unfamiliar knowledgeable conspecifics. Newly released translocated primates often integrate into the local resident groups (Goossens *et al.* 2005) and conspecific cueing is successfully used for manipulating colonial birds into settling novel habitats (Jeffries & Brunton 2001). However, accounts of translocated birds avoiding established residents exist (Clarke & Schedvin 1997), shoaling fish preferentially interact with familiar conspecifics in novel environments (Ward & Hart 2003) and humans are known to form immigrant enclaves upon arrival at a new country (Wierzbicki 2004).

What may explain the social segregation that we found between the translocated and local elephants? Forming bond groups with familiar conspecifics did not provide inclusive fitness benefits to the translocated elephants. The genetic relatedness among elephants captured in separate family units was low, and no correlation was detected between this low genetic relatedness and their social association. However, the fact that the social segregation did not persist throughout our study suggests that habitat familiarity or familiarity with the local population may have influenced bond group formation. The costs of associating with unfamiliar conspecifics (both to the translocated and local elephants) could have initially outweighed any potential benefits. Indeed, on the two observations of direct interactions between the translocated and local groups (which occurred within a month from the translocated elephants' release), the locals exhibited aggressive behaviour towards the translocated elephants.

Forming social enclaves by animals in a novel environment is a phenomenon seldom documented. Animals' ability to sustain social bonds when moved into a novel habitat and later assimilate socially into an existing population, as seen here, can provide important insights for wildlife management actions, enhance our understanding of animals' response to human-induced environmental changes and augment behavioural studies of animals' natural life stages such as dispersal and migration. As the world continues to change, understanding animals' behavioural dynamics in relation to habitat changes will be increasingly important for developing conservation tools and enhancing our basic understanding of animals' acclimation to novel environments.

The research presented was approved by UCD Institutional Animal Care and Use Committee (IACUC) protocol no. 10087.

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