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SHORT COMMUNICATION

Bechstein's bats maintain individual social links despite a complete reorganisation of their colony structure

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Abstract Several social mammals, including elephants and some primates, whales and bats, live in multilevel societies that form temporary subgroups. Despite these fission–fusion dynamics, group members often maintain long-term bonds. However, it is unclear whether such individual links and the resulting stable social subunits continue to exist after a complete reorganisation of a society, e.g. following a population crash. Here, we employed a weighted network analysis on 7,109 individual roosting records collected over 4 years in a wild Bechstein's bat colony. We show that, in response to a strong population decline, the colony's two stable social subunits fused into a non-modular social network. Nevertheless, in the first year after the crash, long-term bonds were still detectable, suggesting that the bats remembered previous individual relationships. Our findings are important for understanding the flexibility of animal societies in the face of dramatic changes and for the conservation of social mammals with declining populations.

Keywords Fission–fusion · Multilevel social networks · Population crash · Social bonds

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Introduction

The multilevel social networks of several mammalian species (Wittemyer et al. 2005; Parsons et al. 2009; Kerth et al. 2011) are built on stable subunits, which consist of closely associated individuals. The underlying social relationships among individuals persist despite the regular fission and fusion of subgroups, which occurs during travelling, roosting or foraging in these species. However, to date, it is largely unclear whether social links and stable subunits in animal social networks continue to exist after a fundamental reorganisation of the groups, e.g. following a population crash. This lack of knowledge on the resilience of social networks in species with strongly declining populations hampers our understanding of the flexibility of animal social systems and impedes the conservation of species in which individuals are likely to benefit from stable social links (Silk et al. 2003; Frère et al. 2010).

In this study, we compared the social network structure in a wild Bechstein's bat (*Myotis bechsteinii*) maternity colony (GB2) before and after a 65 % decline in the number of colony members. The population crash was probably caused by harsh weather in autumn 2010 and spring 2011. Since 1996, all adult members of this colony have been individually marked with passive inductive transponder (PIT) tags and the colony's genetic, demographic and social structure has been described (Kerth et al. 2011). In this species, from April to September, about 10 to 45 adult females live together in a maternity colony where they raise their offspring communally; males are solitary (Kerth et al. 2011). Colony members switch almost daily between up to 50 communal roosts (tree cavities and bat boxes) and concurrently often split into several temporary subgroups, using different day roosts (Kerth et al. 2011). This fission–fusion behaviour is coordinated via information transfer and collective decision making about suitable roosts (Kerth et al. 2006). The coordination of their movements among different roosts allows the bats to retain energetic benefits that arise from social thermoregulation in sufficiently large roosting groups (Pretzlaff et al. 2010).

By comparing the colony's social network before (2004–2010) and after the population crash (2011–2012), we assessed whether the social structure of the GB2 colony with two stable subunits ("communities") and long-term social links endured the reduction of the colony to approximately the size of each of its previous communities. We predicted that the bi-modular social structure and individual links remain stable despite the population crash if communities are formed irrespectively of the overall colony size. Alternatively, we predicted the network structure to become non-modular after 2010 if communities only form when a colony exceeds a size of about 20 bats, as discussed by Kerth et al. (2011). Finally, if the decline of the colony resulted from a permanent fission into two new colonies along the boundaries of the previous communities, we predicted only members of one of the previous communities to be present in the colony GB2 from 2011 onwards.

Material and methods

From 2009 to 2012, we monitored the bats' roosting associations on 2 to 7 days per week each year between May and September. All 16 to 46 adult females present in the colony in these 4 years carried individual PIT tags. Using automatic PIT tag readers installed in bat boxes, we obtained 7,109 individual roosting records. Following the approach by Kerth et al. (2011), we constructed weighted undirected networks representing the bat's social links in a given year. Afterwards, we analysed whether the obtained social networks are organised into communities by maximising each network's Q modularity (Blondel et al. 2008) in MATLAB R2012a.

To evaluate the stability of roosting associations among individuals between years, we built association matrices including only the bats present in two consecutive years (Kerth et al. 2011). We subsequently ran Mantel tests (50,000 permutations, implemented in MATLAB R2012a) to compare the matrices between the years (Kerth et al. 2011). Finally, to test for differences in the strength of pairwise association between members of the same community compared to members of the other community, we used two-tailed Kolmogorov–Smirnov tests (Kerth et al. 2011).

Results

Transition of the social network structure in response to the population crash

In contrast to the years 2004 to 2010 when the colony frequently split into two to six subgroups (on 63 to 99 % of the observation days), in 2011 and 2012, the colony formed subgroups on only 12 of 133 (9 %) observation days and on 13 of 62 (21 %) observation days, respectively. The number of individuals from each community that returned after the population crash did not significantly differ between the communities (4 of 23 females of community "A"; 10 of 23 females of community "B"; two-tailed Fisher's exact test, $P=0.1075$; three individuals could not be assigned to a community as they were PIT tagged at the age of 1 year in 2011). This suggests that the observed population decline was not a result of a permanent split of the colony caused by one of the communities dispersing as a whole.

In the last 2 years (2009 and 2010) before the population crash, the two communities (A and B) that had already existed between 2004 and 2008 were still present. Combining the 2004 to 2008 data of Kerth et al. (2011) and our data for 2009 and 2010 revealed that the community composition was very stable from 2004 to 2010. In 2009 and 2010, each of the adult females could be assigned to the same community (A or B) as in the year before. In line with the increase in colony size to 46 adult females in 2010, the two communities became even more distinct, with no strong links persisting between them ($Q_{\max}$ 2009=0.32, $Q_{\max}$ 2010=0.39; Fig. 1). The strength of the individual associations measured over all colony members was significantly correlated between subsequent years until 2011, including the first year (2011) after the crash (Mantel test inter-year correlations: 2004 to 2010, $0.4386<r^2<0.929$; 2010 to 2011, $r^2=0.396$; $P<0.0001$ for all years). However, there was no longer a significant correlation between the individual associations of the years 2011 and 2012 ($r^2=0.005$; $P=0.444$). After the colony declined drastically in 2011, the two communities fused into a non-modular social network (2011 to 2012 colony size, 16 and 17 individuals, $Q_{\max}=0$ in both years; Fig. 1). Combined with the data from Kerth et al. (2011), our results show that the GB2 colony was structured into two communities only when it was large (2004 to 2010 mean±S.D. colony size, 37.8±4.9 individuals; mean±S.D. community size, 20.0±3.8 individuals).

Persistence of long-term social links in the absence of distinct communities

Despite the dramatic structural transition of the colony from 2010 to 2011, the surviving 10 members of previous community B associated significantly more often with each other than with the four surviving members of previous community A, on the 12 days when the colony split into more than one roosting subgroup in 2011 (Kolmogorov–Smirnov test: $n=51$ pairwise associations, $P<0.0001$). In contrast, the four members of the previous community A did not roost more frequently with each other than with members of the previous community B (Kolmogorov–Smirnov test: $n=51$ pairwise associations, $P=0.1598$). In 2012, even the members of previous community B no longer preferred to roost with former community mates (Kolmogorov–Smirnov test: $n=51$, $P=0.1913$).

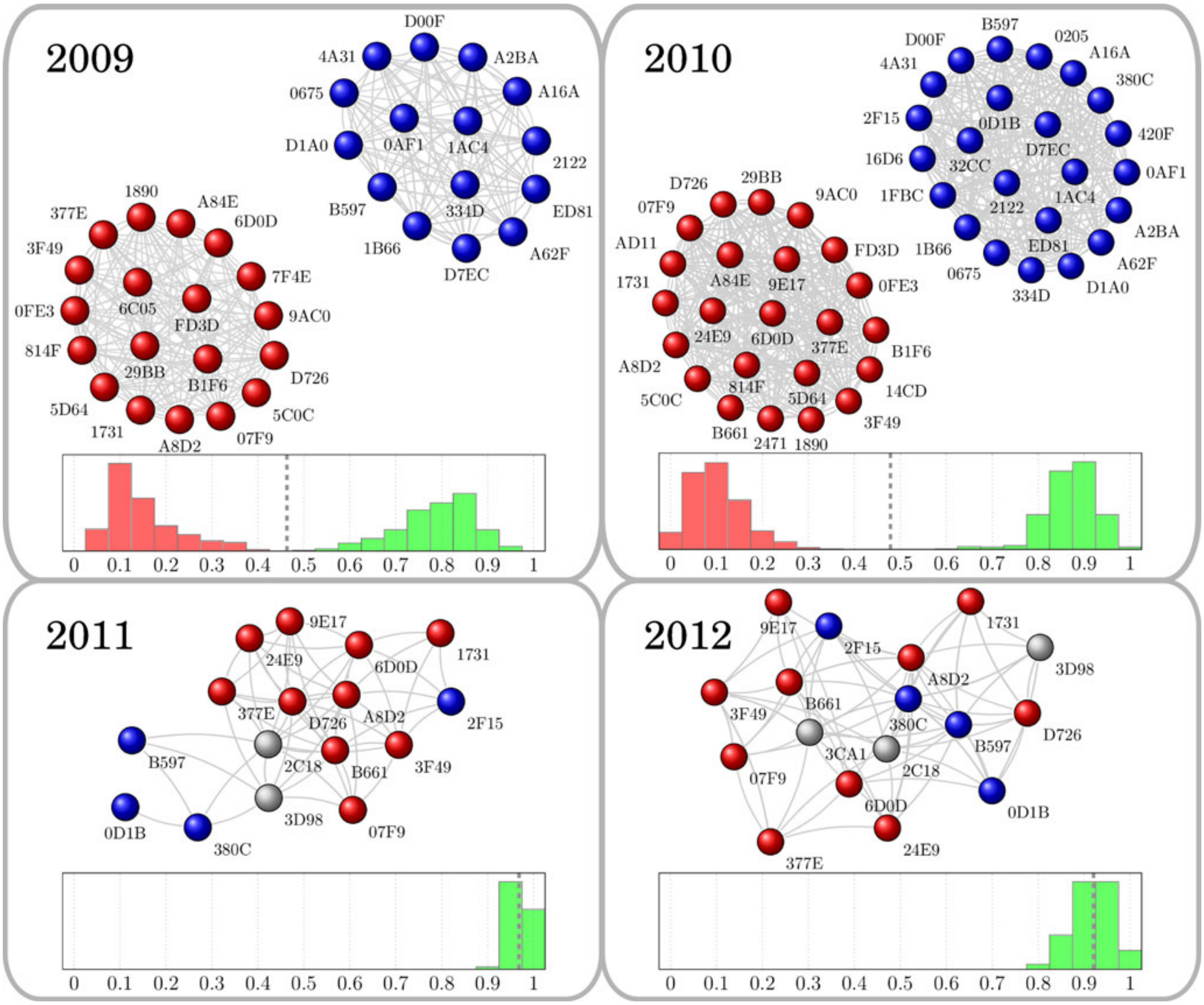

Fig. 1 Social networks of roosting associations for the colony GB2 from 2009 to 2012 (2009, n=34; 2010, n=46; 2011, n=16; 2012, n=17 individuals). The node colours correspond to the community structure in 2009 and 2010 (*blue* = community A, *red* = community B). The community structure of 2010 is used as a reference in 2011 and 2012 (*grey nodes* correspond to young individuals who entered the social network after 2010). The *inset* shows the distribution of association indices, with different colours for the intercommunity links (*red*) and intra-community links (*green*) in the years where the colony displayed a community structure. For clarity in the network layouts only the strong network ties (weight higher than the mean value of the distribution, represented by the *dashed line* in the histogram) are shown

Discussion

Our study shows a fundamental change of the Bechstein's bat colony structure in response to a population crash. The two previously present long-term stable communities merged into a non-modular colony of about the size each community had before the population crash. This finding supports the hypothesis of Kerth et al. (2011), suggesting that stable social subunits form only if a colony exceeds a size of about 20 bats. The merging of the two previous communities was probably possible, as some links always persisted between both communities. Until 2008, all colony members had been roosting with each other on at least 20 to 30 % of the days (Kerth et al. 2011). And even in 2010, when all strong links had vanished between the two communities, most colony members still occasionally roosted together with each other.

Interestingly, in the first year after the population crash, long-term links among the surviving community mates were still detectable in the previous community B. This suggests that the bats remembered community membership despite the complete structural change of the colony. Bechstein's bats could differentiate among individuals by the exchange of individual facial secretions from the interaural gland (Safi and Kerth 2003) or via individual social calls (Schöner et al. 2010). From another bat species, it is known that social relationships among colony members already form early in life (Ancillotto et al. 2012). In the second year after the structural change of our study colony, roosting association was no longer significantly stronger among previous community mates. This could mean that Bechstein's bats are able to remember social relationships only from one season to the next. As a comparison, ravens and sheep were shown to memorise affiliates for 2 to 3 years (Kendrick et al. 2001; Boeckle and Bugnyar 2012). Alternatively, after our study colony declined, previous social links may have become less important for the surviving bats than a minimum number of roosting partners required for efficient social thermoregulation (Pretzlaff et al. 2010). In accordance with this hypothesis, in 2011 significant individual associations only remained amongst the 10 members of the previous community B, whereas the four surviving members of community A no longer roosted preferentially with each other.

In conclusion, our study suggests that in Bechstein's bats the existence of stable communities within a colony depends on the size of that colony. At the same time, we found evidence that underlying long-term social links and a memory for close associates are robust to a dramatic population decline for at least 1 year. Our observations highlight the flexibility of the social structure of Bechstein's bats: it shows robustness against short-term perturbations and yet adaptability to permanent changes, both fundamental properties ensuring the resilience of biological systems (Garnier et al. 2013). Such structural features may allow for the preservation of social cohesion when a colony declines, whilst facilitating the stepwise foundation of new colonies, if a colony becomes too large (Kerth 2008). Comparative studies including other highly dynamic multilevel animal societies could point to key properties for the resilience of social networks to environmental and social catastrophes, which are essential for animal conservation.

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