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# Original Article Sociality across species: spatial proximity of newborn bats promotes heterospecific social bonding

Leonardo Ancillotto,<sup>a,b</sup> Claudia Allegrini,<sup>a</sup> Maria Tiziana Serangeli,<sup>b</sup> Gareth Jones,<sup>c</sup> and Danilo Russo<sup>b,c</sup>

<sup>a</sup>Dipartimento di Biologia e Biotecnologie "Charles Darwin", Università degli Studi di Roma La Sapienza, Viale dell'Università 32, 00185, Rome, Italy, <sup>b</sup>Wildlife Research Unit, Laboratorio di Ecologia Applicata, Sezione di Biologia e Protezione dei Sistemi Agrari e Forestali, Dipartimento di Agraria, Università degli Studi di Napoli Federico II, via Università 100, I-80055 Portici (Napoli), Italy, and <sup>c</sup>School of Biological Sciences, Life Sciences Building, University of Bristol, 24 Tyndall Avenue, Bristol BS8 1TQ, UK

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Mixed-species groups occur in a variety of social animals and have been widely investigated in many different orders of mammals. The advantages of mixed-species groups include improved information transfer, dilution of predation risk, and social thermoregulation. We hypothesized that interspecific associations may be facilitated by the development of heterospecific "social" preferences. We manipulated the early social environment of captive Kuhl's pipistrelles (*Pipistrellus kuhlii*) and Savi's bats (*Hypsugo savii*), raising newborns in artificial mixed-species groups to simulate conditions in natural mixed-species nurseries. We then measured association patterns among all bats and analyzed the occurrence of social interactions by behavioral observation protocols and social network analyses. Bats preferentially interacted and affiliated with former group members regardless of species, showing that social bonding may occur between different species and that it develops after close contact with newborn heterospecifics, possibly through imprinting-like mechanisms. To our best knowledge, this is the first time such a phenomenon is documented for mammals. Although thermal preferences are often advocated to explain mixed-species associations among bats, individual experience may facilitate heterospecific groups in bats and other taxa.

Key words: allogrooming, Chiroptera, colony, Hypsugo, imprinting, Pipistrellus, social network.

# INTRODUCTION

Social groups are widespread among animals and are distinguishable from random aggregations by the presence of preferred (or avoided) interactions among individuals over time (Whitehead 2008). Advantages of group living are obvious for those species that form stable monospecific groups, in which fitness can be increased by cooperating with kin (Grafen 1990) or by reciprocal altruism (Seyfarth and Cheney 1984). Some adaptive consequences of social grouping may be shared by mono- and multispecific animal aggregations, including increased foraging efficiency, dilution of predation risk, and more efficient thermoregulation. Mixed-species groups (MSGs) may, however, lack advantages derived from kin selection and thus different

© The Author 2014. Published by Oxford University Press on behalf of the International Society for Behavioral Ecology. All rights reserved. For permissions, please e-mail: journals.permissions@oup.com explanations are needed for their formation and maintenance (Farine et al. 2012).

Living in a MSG offers advantages such as increased quality of information transfer, antipredatory vigilance, and detection of foraging or roosting sites (Bogdanowicz 1983; Stensland et al. 2003; Sridhar et al. 2009; Goodale et al. 2010), yet it may also have adverse consequences including interspecific transmission of diseases or parasites (Joseph et al. 2013; VanderWaal et al. 2014). Associating with heterospecifics may also provide more benefits than those offered by intraspecific associations if the latter result in strong competition among subjects sharing an identical ecological niche (Goodale et al. 2010). Consequently, MSGs may be more frequent between species having distinct ecological niches but sharing signalling mechanisms and/or potential predators (Goodale et al. 2010).

MSGs occur in insects (Menzel et al. 2008), fishes (Ward et al. 2002), birds (Sridhar et al. 2009), and mammals (Stensland et al. 2003). Among the latter, MSGs mostly occur in primates (Heymann

Address correspondence to D. Russo. E-mail: danrusso@unina.it.

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and Buchanan-Smith 2000; Chapman et al. 2002), cetaceans (Frantzis and Herzing 2002), ungulates (Fitzgibbons 1990), and bats (Altringham 2011). Associations may also occur between mammals from different orders (Whitesides 1989; Desbiez et al. 2010; Koda 2012) or between mammals and birds (Ruggiero 1996; Ruggiero and Eves 1998; Coetzee and Province 2010). In all cases, interspecific associations require heterospecific spatial tolerance (Fulmer and Knörnschild 2011). An aspect of how MSGs form and maintain cohesion hitherto overlooked is whether experience, especially that acquired early in individual life, may facilitate the development of MSGs, as for intraspecific bonding (Kruijt and Meeuwissen 1991; Verzijden and ten Cate 2007; Arnold and Taborsky 2010; Ancillotto et al. 2012).

Bats constitute an excellent group for testing hypotheses about the evolution and development of sociality, as they show a great variety of social systems, ranging from solitary taxa to species living in large groups (Kerth 2008). Most temperate bat species roost in groups (colonies) for much of the year, and particularly during the reproductive season, frequently comprising 2 or more species (Dietz et al. 2009). Sociality plays an important role in the behavioral plasticity of bats (Boughman and Wilkinson 1998; Fenton et al. 2004; Gillam and Chaverri 2012; Clarin et al. 2014).

This study is based on previous work, which showed that proximity between intraspecific newborn Kuhl's pipistrelles, *Pipistrellus kuhlii* (Kuhl, 1817), leads to the development of preferential social relationships (Ancillotto et al. 2012). In colonies consisting of multiple species, this proximity may also involve heterospecific newborns roosting close to each other (Rainho and Palmeirim 2013). Thus, we hypothesize that the formation of MSGs in bats may be favored by close proximity between heterospecifics in early development through the probable action of imprinting-like mechanisms similar to those that occur between conspecifics (Ancillotto et al. 2012). To test our hypothesis, we manipulated the early social environment of 2 bat species, *P. kuhlii* and *Hypsugo savii* (Bonaparte, 1837). We raised newborns in separate MSGs, thus simulating the conditions inside mixed-species nurseries. We subsequently recorded the effects of developing in close proximity to heterospecifics on the social behavior of independent bats.

To confirm our general hypothesis, we made the following predictions:

- 1.Bats raised together as newborns tend to associate and interact through affiliative behaviors, independently of their species.
- 2. The effects of early experience on subsequent affiliative interactions are similar for both species involved.
- 3.As female bats generally form more stable associations (Kerth 2008), we expected females to be more prone to affiliative behaviors.

# **MATERIALS AND METHODS**

# Study species

*Pipistrellus kuhlii* and *H. savii* are small vespertilionids of similar body mass (5-10 g) and forearm length (31-37 mm; Dietz et al. 2009). They are sympatric over much of southern Europe (Spitzenberger 1997; Sachanowicz et al. 2006). These bats often roost in narrow spaces found in human-made structures such as under roof tiles or beneath drainpipes, sometimes sharing the same roost site (Ancillotto et al. 2013) and thus forming mixed associations involving close proximity between heterospecific subjects. Reproductive colonies typically comprise 5–40 females that may use the same roost year-round (Bogdanowicz 2004).

# Raising and housing

We selected 23 newborn bats (*P. kuhlii*, n = 12; *H. savii*, n = 11) admitted to LIPU's (Italian League for the protection of Birds) wildlife rescue center in Rome for the experiment. We aged bats according to our own experience, admittance records, and published information (Barnard 2009). In order to overcome the influence of previous experience of bats inside their natural roosts, only newborns of 1-3 days of age were included in the experiment. Following Ancillotto et al. (2012), we raised bats in 4 different groups (labeled as A, B, G, and V), each comprising 3 individuals of each species (except 1 group with 2 rather than 3 H. savii). Each group was raised in a different cardboard box (length: 25 cm; width: 30 cm; height: 18 cm) positioned in different rooms, in order to avoid acoustic, tactile, or olfactory contact among bats from different groups. The box lids were fitted with mosquito net windows  $(10 \times 10 \text{ cm})$  to allow aeration and natural dark:light cycles. Small fabric and mosquito net strips were fitted on box walls for roosting and tactile enrichment, and 2 small cardboard boxes  $(5 \times 10 \times 5 \text{ cm})$  in each rearing box provided shelter. A section of the box was warmed by a heat cable (ZooMed Europa, 15W) for terrariums, providing suitable temperature conditions (28-38 °C) in different parts of the boxes (Serangeli et al. 2012) similar to temperatures in natural reproductive roosts of congeneric species (Lourenço and Palmeirim 2004). Young bats were first fed once every 3h with powdered milk replacement (First Age by Royal Canin, Italy) for the first 3-4 weeks (Kelly et al. 2008) using a syringe equipped with a plastic cannula. Subsequently, bats were weaned with mealworms (Barnard 2009). By the end of weaning, bats were able to feed autonomously, so water and food were available ad libitum from steel bowls inside rearing boxes (Serangeli et al. 2012).

After weaning, we banded the study subjects with 2 colored plastic split rings each (Ecotone, Gdynia, Poland), purposely modified for bats (Mitchel-Jones and McLeish 2004), in order to identify each individual and its group membership. All bats were then released together in a  $8 \times 5 \times 3$  m flight room (Ancillotto et al. 2012), where artificial roosts (4 bat boxes, 6 net roosts) were available on each wall of the room. The flight room was not heated (temperature was  $24\pm3.2$  °C, measured with a thermometer positioned inside the flight room, with a precision of 0.1 °C), and 3 large windows provided natural dark:light cycles. Food (live mealworms) and water were available at libitum from steel and plastic bowls fitted on the walls and on the floor.

At the end of the experiment, bats were released in the same region of origin (Lazio, central Italy) by the wildlife rescue center of Rome. Although no information is available on the fate of the study subjects after release, the protocol adopted is the same as that employed in a previous study (Serangeli et al. 2012) that was successful, at least short term, for the survival of rehabilitated bats.

### Data collection

We collected data daily between 23 August and 6 September 2012. Observations after this time were not possible because bats had to be released according to rehabilitation and animal welfare protocols. We recorded individuals' positions inside the room and physical contacts among bats twice daily (at 11.00 and 19.00 h). We thus recorded a total of 30 positions and relative combinations of physical contacts for each individual. The number of recording sessions was selected to minimize disturbance, simultaneously allowing individuals to move and potentially choose a different position inside

the roost. One operator briefly opened the bat box and rapidly took 1-4 photographs of roosting bats to determine the exact position of each bat and physical contacts inside the bat boxes.

To record social interactions, we also filmed bats with 2 Sony Handycam SR501 camcorders with nightshot function. Bats were filmed during two 90-min recording sessions in the morning (from 11.00 h) and in the evening (from 20.00 h, i.e.,  $42.3 \pm 5.1$  min before sunset), respectively. At such times, bats are especially active inside roosts and more likely to show mutual interactions (Winchell and Kunz 1996). We mounted cameras on tripods beneath occupied bat boxes and directed them toward clusters of roosting individuals. In each session, groups were chosen at random for filming. To minimize disturbance, we left the video cameras unattended during recording. Video recordings were examined in the laboratory and watched several times, each time selecting a different focal subject (Martin and Bateson 1993), from which we recorded the number of occurrences of the behavioral categories selected (Altmann 1974). Overall, individual bats were observed for  $1084 \pm 185 \min$  (range: 720-1255). We classified the observed behaviors according to the ethogram of captive P. kuhlii published in Ancillotto et al. (2012), as preliminary observations on H. savii showed the same behavioral modules. For our analyses, we only used social interactions, that is, huddling, allogrooming, and aggressive interactions. For each behavioral occurrence, we distinguished a performer (the bat that initiated the action) and a receiver.

#### Individual-based and social network analyses

We used an individual-based approach to establish whether and how an individual's attributes determine patterns of association and interactions among bats. To examine the differences in extent and intensity of social connections among subjects, as well as their positions in the social structure, we also adopted a network-based approach, testing whether individuals from the same rearing group selectively established social bonds, that is, showed homophily toward former group mates (McPherson et al. 2001).

To analyze contacts between roosting bats, we organized the association data into a symmetric sociometric matrix. To examine the patterning of physical contacts among individuals in a way that is independent from marginal effects, that is, that assumes each bat has exactly the same number of potential contacts as others, we normalized the data by fitting homogeneous margins to the association matrix (Bishop et al. 2007). We developed 2 binary matrices that indicate for each pair of bats whether they belong to the same rearing group (indexed by "1") or to different ones (indexed by "0") and whether they belong to the same (1) or different species (0),

respectively. Mantel tests were used to determine whether rearing group membership and species influenced the frequency of interindividual physical contacts.

Each video-recorded behavioral occurrence was characterized according to the sex of interacting bats (sex membership: same sex vs. different sex), species (species membership: same species vs. different species), and rearing group (group membership: same group vs. different group). We used generalized linear mixed models to test the influence of actors' (both performer and receiver) attributes (sex and species), the conditions associated with the behavioral event (sex membership, species membership, group membership), and their interactions on the observed frequencies of behaviors, using individual identity as a random factor (Ancillotto and Russo 2014). In each model, behavioral response was the dependent variable, whereas other individual attributes were the independent factors. We adopted a backward stepwise approach in selecting significant variables from a first full model, until only significant explaining variables were present in the final one (minimal adequate model). All models and tests were run in R 2.13.2 (R Core Team 2005).

We used the UCINET software package (Borgatti et al. 2002) to build 4 different networks based on the occurrence of physical contacts and on the 3 types of social interactions. For each network, we calculated the value of Q-modularity (Newman 2006), that is, a measure of network division in subgroups, calculated as the difference between fraction of nodes that fall into a given group and the expected fraction if nodes were distributed at random. We tested for homophily, as an indicator of the tendency of bats to form network ties with group members (McPherson et al. 2001), using the UCINET function for Anova density models, that is, testing a block model in which within-group ties differ from between-group ones.

For each individual, in each of the 4 networks, we separately calculated the following metrics: weighted in- and outdegree centrality, corresponding to the number of interactions initiated and received by a bat, respectively (pooled together in the case of nondirectional behavior such as physical contact); clustering coefficients, expressing the degree to which the individual's immediate neighbors in the network tend to cluster together (Croft et al. 2004); and normalized betweenness, that is, the number of shortest paths between 2 individuals that pass through the focal one, indicating the importance of a single bat in connecting different parts of the network. We tested the effects of individual attributes (sex and species) on these metrics for each individual in every network by running generalized linear models (GLMs). Network metrics were first tested for independence by running Pearson correlation tests; as no strong correlations were detected (r < 0.5), all metrics were used in the GLMs.

Table 1

Factors affecting the pattern of interactions for 3 different social behaviors in a captive mixed-species group of bats (*Pipistrellus kuhlii* and *Hypsugo savii*), calculated with generalized linear mixed models

Behavior	Factor	Estimate	SE	z	Р
Huddling	Intercept	0.58	0.04	3.78	0.05
0	Group membership	5.99	1.43	3.31	< 0.002
	Group membership $\times$ sex	-10.30	1.89	2.56	< 0.01
Allogrooming	Intercept	0.21	0.09	2.24	< 0.05
0 0	Group membership	1.08	0.25	6.13	< 0.001
	Sex	-0.21	0.09	-2.24	< 0.05
Aggressive	Intercept	0.38	0.06	2.11	< 0.05
55	Group membership	4.44	1.05	4.61	< 0.0001
	Species membership	-2.13	0.59	3.13	< 0.001

Species membership: same-species bats versus different-species bats; group membership: bats from same rearing group versus bats from different rearing groups. Final models only feature significant explaining variables selected by a backward stepwise approach.

# RESULTS

#### Behavioral analyses

Bats day-roosted in mutual physical contact significantly more often with individuals from the same rearing group (r = 0.51, P < 0.0001, based on 10 000 permutations) while no species' effect was found (r = -0.05, n.s., based on 10 000 permutations).

We recorded 295 social interactions: 107 allogrooming events, 168 huddling events, and 20 aggression events. Group membership was the most important variable explaining the patterns of social behaviors within MSGs. Affiliative behaviors were more often performed between former group members, whereas aggression events were more common between nonfamiliar bats and heterospecifics (Table 1). Group membership also showed a significant interaction with the sex of the bat initiating the interaction, as during samegroup huddling most interactions were initiated by males. Sex of the initiating bat directly influenced only the occurrence of allogrooming, with females allogrooming more frequently.

# Social networks

Network metrics differed greatly among bats forming the artificial MSGs (Table 2). The network of physical contacts was poorly structured (Q-modularity: -0.01, Figure 1): bats established contacts on average with about 50% of the individuals in the group (mean  $\pm$  standard deviation; degree centrality:  $11.2\pm5.0$ ); females generally established more contacts than males ( $F_{1,7} = 11.6$ , P < 0.05). Clustering coefficients ( $0.63\pm0.11$ ) indicate a tendency to form closed

subgroups, but this index was influenced neither by an individual's species nor sex.

The huddling network was only moderately structured (Q-modularity: 0.40, Figure 1), but individuals occupied similar relative positions inside the network as no metric differed between sexes or species (Table 2). The aggression network was similarly structured (Q-modularity: 0.44, Figure 1), and neither sex nor species influenced it.

The allogrooming network was, however, highly structured (Q-modularity = 0.64): bats groomed (Figure 2) in relatively closed subgroups (clustering coefficient:  $0.34 \pm 0.24$ ). Although, relative to males, females failed to show a statistically significant tendency to form cliques, the result was borderline ( $F_{1,7} = 4.6$ , P = 0.05). In this network, *P. kuhlii* had higher betweenness values ( $F_{1,7} = 6.2$ , P < 0.05), indicating that bats of this species were more important in connecting different parts of the group. *Pipistrellus kuhlii* also more often initiated an allogrooming event ( $F_{1,7} = 7.5$ , P < 0.05). No difference was evident in the numbers of allogrooming events received by bats of different species or sex, but both in- and outdegree values indicate that bats interacted with a reduced number of other individuals, that is, about 25% of those available in the group (indegree centrality:  $4.6 \pm 3.4$ ; outdegree centrality:  $4.6 \pm 2.4$ ).

The tests for homophily toward former group members were significant for all behaviors quantified (Table 3), meaning that bats selected familiar individuals for behavioral interactions; this pattern was more evident for affiliative/cooperative behaviors (huddling and allogrooming: Figure 2) than for simple physical contacts, which did not reach significance for all experimental groups.

 Table 2

 Individual attributes (sex and species) and network descriptive metrics of a captive mixed-species group of bats

			Physical contact		Huddling			Allogrooming			Aggression						
ID S	Sex	Sp	CC	ВТ	DG	CC	BT	IDG	ODG	CC	BT	IDG	ODG	CC	BT	IDG	ODG
B01	F	Hs	0.72	1.5	19	0.26	19.5	16	11	0.67	0.3	6	5	0.00	3.5	2	5
B02	Μ	Hs	0.67	0.1	7	0.25	11.3	17	17		0.0	7	5	0.00	0.0	0	2
B03	F	Hs	0.60	0.3	7	1.00	0.0	18	11	0.00	4.1	7	8	0.00	0.4	2	1
B04	F	Pk	0.70	2.0	14	0.48	4.0	13	7	0.50	10.7	5	6	0.00	0.9	1	2
B05	F	Pk	0.52	5.5	10	0.67	0.2	2	7	0.33	11.9	1	7	0.00	0.4	1	1
B06	F	Pk	0.56	8.6	17	0.25	25.1	11	11	0.33	7.4	6	4		0.0	0	0
A01	F	Hs	0.68	2.9	17	0.34	15.6	11	18	0.42	10.8	5	5		0.0	3	0
A02	Μ	Hs	0.69	1.4	8	0.83	0.1	8	6	0.75	0.0	2	5		0.0	1	0
A03	F	Pk	0.79	1.0	19	0.70	1.0	7	3	0.42	20.6	4	7	0.00	1.1	3	0
A04	Μ	Pk	0.68	3.0	15	0.48	5.3	13	7	0.45	0.9	13	5	0.00	2.3	3	3
A05	Μ	Pk	0.76	1.3	15	0.50	0.9	10	8	0.23	24.9	13	10	0.00	2.2	1	3
V01	F	Hs	0.67	1.0	7		0.0	0	2	0.83	0.0	2	4	_	0.0	0	0
V02	Μ	Hs	0.42	3.7	4	0.10	7.8	6	3		0.0	0	0	_	0.4	1	2
V03	F	Hs	0.57	1.1	5	0.00	0.0	0	4	0.50	0.0	0	3	_	0.0	0	0
V04	F	Pk	0.62	1.5	8	0.33	0.0	9	0	0.50	0.9	5	7	_	0.0	0	0
V05	Μ	Pk	0.62	3.9	11	0.15	3.5	1	6	0.30	9.7	5	3	_	0.0	0	0
V06	F	Pk	0.44	5.3	10	0.33	0.0	1	7	0.50	0.2	6	3	_	0.0	1	0
G01	Μ	Hs	0.39	3.3	5	0.20	3.9	4	3	0.00	4.1	4	1	_	0.0	0.0	0.0
G02	F	Hs	0.78	1.2	18	0.45	11.6	13	5	0.17	18.7	8	4	_	0.0	0.0	0.0
G03	Μ	Hs	0.70	1.1	6	0.58	0.9	4	1	0.50	0.0	3	0	_	0.0	1.5	0.0
G04	F	Pk	0.60	3.7	13	0.20	5.6	1	8	0.25	9.6	2	7	_	0.0	3.0	0.0
G05	Μ	Pk	0.50	0.3	2	0.50	0.0	2	2		0.0	1	2	_	0.0	1.5	0.0
G06	F	Pk	0.70	2.3	16	0.38	8.7	5	15	0.25	2.4	2	6	_	0.0	1.5	0.0
Mean			0.63	11.3	11.2	0.39	5.4	7.3	7.3	0.39	5.9	4.6	4.6	0.0	0.5	1.4	1.4
(SD)			(0.11)	(9.2)	(5.0)	(0.3)	(6.8)	(5.4)	(5.0)	(0.2)	(7.3)	(3.4)	(2.4)	(0.0)	(0.9)	(1.4)	(2.0)

Metrics are presented separately for each network derived from different social behaviors. Sex: m = male and f = female; Sp = species—Hs = *Hypsugo savii* and Pk = *Pipistrellus kuhlii*. The letter in individuals' ID indicates group membership. CC = clustering coefficient; BT = betweenness; DG = degree; IDG = indegree; ODG = outdegree. SD = standard deviation.



#### Figure 1

Mixed-species social networks. Social networks of a mixed-species group of captive bats, based on 4 different social behaviors: (a) physical contacts inside roost, (b) huddling, (c) allogrooming, and (d) aggressive behavior. Node shape indicates an individual's group of origin. Black nodes = males and white nodes = females. Large nodes = *Hypsugo savii* and small nodes = *Pipistrellus kuhlii*. Tie strength between nodes is proportional to line thickness. A spring-embedding algorithm derives distances between nodes.



#### Figure 2

Interspecific physical contact (a) and affiliative social behavior (allogrooming, b) between young captive *Pipistrellus kuhlii* (subject to the left in a and b) and *Hypsugo savii* (subject to the right in a and b). In both images, the interacting bats came from the same rearing group (see color of plastic ring on bat forearms in a). Bats in (b) show no plastic ring as the picture was taken during rearing, soon before ringing them.

## DISCUSSION

In accordance with our predictions, we demonstrated that 1) bats raised in the same group as newborns show a higher frequency of affiliative behavior regardless of species membership and 2) bats of different species have similar roles in a MSG (yet *P. kuhlii* was particularly important in facilitating social interactions). Our third hypothesis, that is that females are more prone to affiliative behavior, was also confirmed as they establish mutual contacts and allogroom more frequently than males yet, among former members of the same raising group, huddling is initiated more often by males.

When given the choice to associate with familiar individuals (both conspecifics and heterospecifics) or with nonfamiliar conspecifics, bats actively selected the former. To our best knowledge, this is the first description of such a phenomenon for mammals. Imprintinglike mechanisms may facilitate interspecific social aggregation and cooperation.

MSGs of bats, commonly reported in field studies, are generally explained in terms of social thermoregulation or as a consequence of limited roost availability (McFarlane 1989; Arita and Vargas 1995; Rodriguez-Duran 1998). The species we tested usually roost in buildings, so their roosts are unlikely to be limiting (Dietz et al. 2009): their MSGs formed in natural conditions (Ancillotto et al. 2013) must, therefore, be explained otherwise. So far, direct amicable social interactions between species involved in MSGs have not been recorded in natural conditions (Swift and Racey 1983; Wohlgenant 1994); nevertheless, clustering of individuals from different species is not rare in reproductive roosts (Serra-Cobo et al. 2002; Boratyński et al. 2012; Rainho and Palmeirim 2013).

We found that affiliative associations are not only restricted to relatively passive behaviors such as physical contact but can also involve cooperative behaviors (e.g., reciprocal grooming) and rely on preferential interindividual bonding.

	Physical contact		Huddling		Allogrooming			
	$R^2 0.07$	<i>P</i> -value < 0.05	$R^2 0.21$	<i>P</i> -value < 0.001	$R^2 0.29$	<i>P</i> -value < 0.001 <i>P</i> -value		
	Coefficient	<i>P</i> -value	Coefficient	<i>P</i> -value	Coefficient			
Intercept	5.56	< 0.001	0.09	n.s.	0.02	n.s.		
Group B	-2.89	< 0.05	1.67	< 0.001	1.04	< 0.001		
Group A	-5.56	< 0.001	1.60	0.001	1.48	< 0.001		
Group V	-2.22	n.s.	0.47	n.s.	0.58	< 0.01		
Group G	-1.56	n.s.	0.70	0.03	0.58	< 0.01		

Table 3		
Homophily in a mixed-species group	of Pipistrellus kuhlii an	ł Hypsugo savii

Anova density models for variable homophily of networks derived from physical contacts, huddling, and allogrooming interactions of a captive mixed-species group of bats, based on 5000 permutations. Group letters (B, A, V, G) indicate different rearing groups. n.s., not significant.

Surprisingly, for all affiliative behaviors, we found strong effects of an individual's previous social experience (bats selectively established social interactions with familiar individuals) but no species effect. Only when grooming mutually, bats from 1 species (*P. kuhlii*) were more often the initiators of a behavioral event: perhaps, this reflects the tendency of *P. kuhlii* to live in large colonies (personal observation) and thus be more social.

The degree of clustering changed according to the behavior recorded: it was loose for general physical contact and huddling and much tighter for allogrooming. Because allogrooming implies spatial tolerance as well as coordinated movements between interacting individuals (Grueter et al. 2013), bats strictly selected members from the same original raising group to perform it. Allogrooming is often a social-related rather than a hygiene-related interaction (Dunbar 1991; Wiens and Zitzmann 2003; Carter and Wilkinson 2013; Chadwick et al. 2013; Grueter et al. 2013); thus, the occurrence of this behavior between different species supports our hypothesis that social bonding may occur in MSGs of bats.

Interestingly, affiliative behaviors were more often performed between members of the same rearing group, whereas aggressive events were more common between nonfamiliar bats despite the close spatial association among familiar individuals. This finding supports previous results indicating that bats' aggressiveness is selectively directed toward nongroup members (Ancillotto and Russo 2014).

Potential advantages of reciprocal social imprinting between 2 (or more) different bat species may be represented by improved thermoregulation and higher antipredatory vigilance, as well as effective information transfer, when searching for new suitable roosts or foraging sites. Interspecific eavesdropping on echolocation, social (Dorado-Correa et al. 2013) and distress calls (Russ et al. 2004) may also occur to obtain information about the location of potential roosts, foraging areas, or predators (Dorado-Correa et al. 2013). Interspecific communication may increase and improve information transfer; although in some cases passive information transfer may have undesired consequences for the emitter, private intraspecific communication bandwidths potentially evolved to minimize unintended heterospecific communication (Russo et al. 2007). The ability to recognize heterospecific calls may be learnt early during the development of bats born in MSGs.

Social imprinting may also facilitate hybridization between bat species (between *Pipistrellus* ssp.: Sztencel-Jablonka and Bogdanowicz 2012; *Myotis* ssp.: Berthier et al. 2006). However, to our best knowledge, no hybridization has yet been reported for the species we used in our experiment.

We see our work as a step toward unraveling mechanisms that underlie interspecific sociality in bats. This is fundamental for understanding behavioral and ecological interactions at the community scale. For example, patterns of social behaviors and associations among bats can have consequences for the spread of diseases such as lyssavirus infections or white nose syndrome (Serra-Cobo et al. 2002; Langwig et al. 2012).

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