

CrossMark
click for updates

Opinion piece

Cite this article: Valomy M, Hayes LD, Schradin C. 2015 Social organization in Eulipotyphla: evidence for a social shrew. *Biol. Lett.* **11**: 20150825.
<http://dx.doi.org/10.1098/rsbl.2015.0825>

Received: 1 October 2015

Accepted: 19 October 2015

Subject Areas:

evolution, ecology, behaviour

Keywords:

social system, monogamy, shrew, insectivore, social flexibility, intraspecific variation

Author for correspondence:

C. Schradin

e-mail: carsten.schradin@iphc.cnrs.fr

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2015.0825> or via <http://rsbl.royalsocietypublishing.org>.

Animal behaviour

Social organization in Eulipotyphla: evidence for a social shrew

M. Valomy^{1,2,3}, L. D. Hayes⁴ and C. Schradin^{2,3,5}¹Département de Licence Sciences de la Vie, Université Pierre et Marie Curie, UPMC, 75252 Paris Cedex 05, France²IPHc-DEPE, Université de Strasbourg, 67087 Strasbourg, France³CNRS, UMR7178, 67087 Strasbourg, France⁴Department of Biology, Geology and Environmental Sciences, University of Tennessee at Chattanooga, Chattanooga, TN, USA⁵School of Animal, Plant and Environmental Sciences, University of the Witwatersrand, Johannesburg, Wits 2050, South Africa

Shrews and their close relatives (order Eulipotyphla) are typically considered to be solitary. This impacts our understanding of mammalian social evolution: (i) the ancestor of mammals is believed to have been shrew-like, and even though Eulipotyphla are not more basal than other mammalian orders, this might have been one reason why the first mammals have been assumed to be solitary-living; (ii) Eulipotyphla are the third largest mammalian order, with hundreds of species entering comparative analyses. We review primary field studies reporting the social organization of Eulipotyphla, doing a literature research on 445 species. Primary literature was only available for 16 of the 445 species. We found 56% of the studied species to be social (38% were living in pairs), which is in sharp contrast to the 0.5 and 8% reported in other databases. We conclude that the available information indicates that shrews are more sociable than generally believed. An interesting alternative hypothesis is that the mammalian ancestor might have been pair-living. To understand the social evolution of mammals, comparative studies must be based on reliable and specific information, and more species of all orders must be studied in the field.

1. Introduction

One of the major aims of evolutionary biology is to understand the biodiversity of social systems [1,2]. The social system of a species is described by three components: social organization (composition of groups), social structure (who interacts with whom) and mating system [3]. The component of social systems most often reported in field studies is the social organization, which also influences social structure and mating system [4].

Mammals show a fascinating diversity of social organization, ranging from solitary-living (non-social) to extended families and even eusocial societies [5,6]. The diversity of mammalian social organization has received significant attention [7–9]. Recent comparative studies have addressed exciting questions about the evolutionary origins of different social organization [7,10]. These studies have made the arguments that the first placental mammal was solitary and that the more complex forms such as monogamy and cooperative breeding evolved later [7,11].

The first eutherians, which lived 160 Ma ago, were insectivores and shrew-like in appearance [12], as were the first real placentals which appeared around 100 Ma ago [13,14]. Shrews are generally believed to be solitary [15], which might explain why the first placentals have also been assumed to be solitary. Accordingly, a phylogenetic analysis including data on 367 species of shrews, 99.5% of which were believed to be solitary, found that the ancestor of placentals was most likely

Table 1. Social organization of species from the order Eulipotyphla sorted by family, as revealed by our primary literature search. For comparison, the information provided in the database by Lukas & Clutton-Brock [7] and in *Walker's Mammals of the World* [16] is provided.

	primary literature search	database Lukas & Clutton-Brock	mammals of the World
family Erinaceidae (hedgehogs and moonrats)			
number of species	24	14	20
social organization unknown	23	0	6
solitary	1	14	13
group-living	0	0	0
solitary and group-living	0	0	1
family Talpidae (moles)			
number of species	41	17	42
social organization unknown	37	0	33
solitary	2	17	4
group-living	0	0	5
solitary and group-living	2	0	0
family Solenodontidae (solenodons)			
number of species	2	1	2
social organization unknown	2	0	1
solitary	0	0	0
group-living	0	1	1
solitary and group-living	0	0	0
family Soricidae (shrews)			
number of species	378	367	322
social organization unknown	367	0	220
solitary	4	366	99
group-living	4	1	3
solitary and group-living	3	0	0

solitary [7]. However, we lack information from field studies about the social organization of most Eulipotyphla. Much of our knowledge about social organization of mammals comes from field studies on three relatively small orders of large mammals (primates, artiodactyls and carnivores) [16]. Thus, comparative studies face the problem that relatively little is known about the social organization of small mammals.

Previously, the families of the order Eulipotyphla were known as '*Insectivora*', but molecular data showed that *Insectivora* represents a paraphyletic group [17,18]. The new order Eulipotyphla contains five families: Erinaceidae (hedgehogs and moonrats), Talpidae (moles), Solenodontidae (solenodons), Soricidae (shrews) [18] and the extinct family Nesophontidae [19]. The Erinaceidae have only 24 species. The mole–shrew–solenodon clade Soricomorpha contains around 419 species, with Soricidae representing over 90% of the species [20]. The Eulipotyphla represent the third largest eutherian order (after Rodentia and Chiroptera) [17], and if one wants to understand the evolution of social organization in mammals, it is important to consider them. We review the kinds of social organization that have been described from field studies for this order, and we compare this new database based on primary literature with the information provided in *Walker's Mammals of the World* [16] and with an existing database that is largely based on secondary literature and was used for comparative studies on mammalian social evolution [7].

2. Material and methods

We used an existing database available from the electronic supplement of [7], which included a total of 399 species of Eulipotyphla. Forty-six additional species were found in an online database [21] and in [16]. We used the *Web of science* (Thomson Reuters) to search for primary literature on the social organization of the 445 species. For each species, we initially searched the Latin species name and the term 'social'. If no literature on social organization was found, only the genus and the term 'social' were used, and if still no information was found, only the Latin name. Only primary field studies were considered. Five additional articles were found from references quoted in publications or by general search on the Internet. We recorded whether a species was described as living solitarily, in pairs, in groups consisting of one male and several females, one female and several males, multiple males and females, multiple females or multiple males. We recorded whether the described social organization was reported for the breeding or for the non-breeding season.

We compared our data with the database from Lukas & Clutton-Brock which was available as electronic supplementary material [7]. Additionally, we conducted a secondary literature search in the book *Walker's Mammals of the World* [16].

3. Results and discussion

We found primary literature on the social organization of 16 (3.6%) of the 445 species (table 1). Of the 16 species that have

Table 2. The different forms of social organization identified in our primary literature research, compared with the social organization provided by Lukas & Clutton-Brock [7]. Numbers refer to the numbers of studies reporting the form of social organization. BS, breeding season; NBS, non-breeding season. References are in the electronic supplementary material.

species	Lukas & Clutton-Brock	solitary	pair	one male – several females	multi-males	multi-females	Multi-male–multi-female
Soricidae (shrews)							
<i>Crocidura leucodon</i>	solitary		1 (BS)				1 (NBS)
<i>Crocidura russula</i>	solitary	1	2 (BS)		1 (NBS)	2 (NBS)	1 (NBS)
<i>Crocidura shantungensis</i>	solitary	1					
<i>Cryptotis parva</i>	solitary						1
<i>Neomys fodiens</i>	solitary	1					
<i>Sorex araneus</i>	solitary	2					
<i>Sorex cinereus</i>	solitary						2 (BS)
<i>Sorex coronatus</i>	solitary	1 (NBS)	1 (BS)				
<i>Sorex ornatus</i>	solitary			1 (NBS)			1 (BS)
<i>Sorex unguiculatus</i>	solitary	1					
<i>Suncus varilla</i>	solitary	1	1				
Talpidae (moles)							
<i>Galemys pyrenaicus</i>	solitary	3	3				
<i>Talpa europaea</i>	solitary	1					
<i>Talpa romana</i>	solitary	2					
<i>Urotrichus talpoides</i>	solitary	1 (BS)	1 (NBS)				
Erinaceidae (hedgehogs and gymnures)							
<i>Erinaceus europaeus</i>	solitary	1					

been studied, 7 (43.8%) were described as solitary, 4 (25%) as group-living and 5 (31.3%) as group-living but also sometimes solitary-living (table 2). Most information was available for the shrews (Soricidae), where 36.4% of the species (4/11) were reported to be solitary, 36.4% to be group-living (4/11) and 27.3% were reported to be both solitary and group-living (3/11; table 1). We conclude that species of Eulipotyphla cannot be regarded as being generally solitary, as 56.3% (9/16) of the studied species exhibit some form of group-living.

Our results are in contrast to Lukas & Clutton-Brock's database [7], in which 99.5% of the 399 considered species of Eulipotyphla are reported as solitary, based on one publication that does not mention all these species [22]. In *Walker's Mammals of the World* [16], 92.1% of the 126 species with information on social organization were reported to be solitary (table 1), but for most species, information was only available on the genus level (109 species of 10 genera, all considered to be solitary). Considering only the 17 species for which the information in *Walker's Mammals of the World* [16] was on the species level, 58.8% (10/17) were reported to be social, which was very similar to our results.

We found a high variety of social organization in Eulipotyphla (table 2). Interestingly, living in pairs was common (37.5% or six of the 16 species), and the solitary individuals that have been observed in these species might have been individuals that had not yet found a pair partner after natal dispersal [23]. Multi-male–multi-female groups were also common, both during the breeding season [24,25] and as overwintering groups, which probably benefited from reduced

costs of thermoregulation due to communal huddling [26,27]. In sum, the social organization of Eulipotyphla is variable both between and within species.

For seven out of the 16 species, more than one form of social organization was reported, and the variation seemed to be related to seasonal differences (table 2). By contrast, Lukas & Clutton-Brock did not consider intraspecific variation in social organization, and *Walker's Mammals of the World* mentioned this for only one species. This could partly explain the huge discrepancy in the frequency of solitary species between the databases. Intraspecific variation in social organization is an important phenomenon and must be considered when comparing social organizations between species [4].

Our study suggests that the generally held assumption that shrews and other Eulipotyphla are solitary is incorrect. Only 16 out of 445 species have been studied, of which over one-half are to some degree gregarious. While the first placentals were shrew-like in appearance, Eulipotyphla are not basal within placentals and the social organization of modern shrews is not indicative of the social organization of basal placentals. Thus, to understand social evolution of placental mammals, we need information about the social organization from species of all orders—not just the largest ones and ones that are easiest to study under field conditions.

4. Conclusion

While it is still possible that most Eulipotyphla are solitary, and that being solitary is the ancestral state of mammals,

our study suggests the possibility for alternative hypotheses, such as that the mammalian ancestor was pair-living. One of the major problems of the previous analysis [7] is that solitary-living was entered as assumed social structure for many mammalian species for which no primary literature was available, such that the emerging result that solitary-living is the ancestral state could be a self-fulfilling hypothesis. Future comparative analysis should rely on primary literature, to ensure that the most accurate data are entered. For example, the pattern emerging in *Walker's Mammals of the World* based on assumptions on the genus level (92% of species are solitary) is in contrast to the specific information in the same book on the species level (41% solitary). In recent years, it has been acknowledged that we have to increase efforts to taxonomically describe the biodiversity

on the Earth [28]. Similarly, we need more research done by field biologists describing the biodiversity of social systems to be able to perform meaningful comparative studies about the evolution of sociality.

Authors' contributions. M.V. did the literature survey under the supervision of C.S. M.V., L.D.H. and C.S. wrote the manuscript. All authors gave final approval for publication.

Competing interests. The authors declare that they have no competing interests.

Funding. Funding was provided by the University of Strasbourg Institute for Advanced Study and the University of Tennessee at Chattanooga.

Acknowledgements. We are grateful to Werner Haberl and Liz de Villiers for scanning old publications for us. We thank Dieter Lukas who provided additional information about his database.

References

- Emlen ST. 1995 An evolutionary theory of the family. *Proc. Natl Acad. Sci. USA* **92**, 8092–8099. (doi:10.1073/pnas.92.18.8092)
- Pennisi E. 2005 How did cooperative behavior evolve? *Science* **309**, 93. (doi:10.1126/science.309.5731.93)
- Kappeler PM, Schaik CPV. 2002 Evolution of primate social systems. *Int. J. Primatol.* **23**, 707–740. (doi:10.1023/A:1015520830318)
- Schradin C. 2013 Intraspecific variation in social organization by genetic variation, developmental plasticity, social flexibility or entirely extrinsic factors. *Phil. Trans. R. Soc. B* **368**, 20120346. (doi:10.1098/rstb.2012.0346)
- Burda H, Honeyscutt RL, Begall S, Locker-Grütjen O, Scharff A. 2000 Are naked and common mole-rats eusocial and if so, why? *Behav. Ecol. Sociobiol.* **47**, 293–303. (doi:10.1007/s002650050669)
- Clutton-Brock TH. 1989 Mammalian mating systems. *Proc. R. Soc. Lond. B* **236**, 339–372. (doi:10.1098/rspb.1989.0027)
- Lukas D, Clutton-Brock TH. 2013 The evolution of social monogamy in mammals. *Science* **341**, 526–530. (doi:10.1126/science.1238677)
- Thierry B, Iwaniuk AN, Pellis SM. 2000 The influence of phylogeny on the social behaviour of macaques (Primates: Cercopithecidae, genus *Macaca*). *Ethology* **106**, 713–728. (doi:10.1046/j.1439-0310.2000.00583.x)
- Kleiman DG, Malcolm JR. 1981 The evolution of male parental investment in mammals. In *Parental care in mammals* (eds DJ Gubernick, PH Klopfer), pp. 347–387. New York, NY: Plenum Press.
- Clutton-Brock TH, Lukas D. 2012 The evolution of social philopatry and dispersal in female mammals. *Mol. Ecol.* **21**, 472–492. (doi:10.1111/j.1365-294X.2011.05232.x)
- Gebo DL. 2004 A shrew-sized origin for primates. In *Yearbook of physical anthropology*, vol. 47 (ed. S Stinson), pp. 40–62. New York, NY: Wiley-Liss.
- Luo Z-X, Yuan C-X, Meng Q-J, Ji Q. 2011 A Jurassic eutherian mammal and divergence of marsupials and placentals. *Nature* **476**, 442–445. (doi:10.1038/nature10291)
- O'Leary MA *et al.* 2013 The placental mammal ancestor and the post-k-pg radiation of placentals. *Science* **339**, 662–667. (doi:10.1126/science.1229237)
- Simeonovska-Nikolova D. 2004 Seasonal changes in social behaviour and spatial structure of *Crocidura leucodon* in north-western Bulgaria. *Acta Theriol.* **49**, 167–179. (doi:10.1007/BF03192518)
- Churchfield S. 1990 Social organisation. In *The natural history of shrews*, pp. 55–72. Bromley, UK: Comstock Publishing Associates.
- Nowak RM, Wilson E. 1999 *Walker's Mammals of the World*, 6th edn. Baltimore, MD: Johns Hopkins University Press.
- Ye JP *et al.* 2006 Cross-species chromosome painting unveils cytogenetic signatures for the Eulipotyphla and evidence for the polyphyly of Insectivora. *Chromosome Res.* **14**, 151–159. (doi:10.1007/s10577-006-1032-y)
- Douady CJ, Chatelier PI, Madsen O, de Jong WW, Catzeflis F, Springer MS, Stanhope MJ. 2002 Molecular phylogenetic evidence confirming the Eulipotyphla concept and in support of hedgehogs as the sister group to shrews. *Mol. Phylogenet. Evol.* **25**, 200–209. (doi:10.1016/S1055-7903(02)00232-4)
- Orihuela J. 2014 Endocranial morphology of the extinct Antillean shrew *Nesophontes* (Lipotyphla: Nesophontidae) from natural and digital endocasts of Cuban taxa. *Palaeontol. Electron.* **17**, 22A. (<http://paleo-electronica.org/content/2014/760-endocast-of-cuban-nesophontes>)
- Hutterer R. 2005 Order Erinaceomorpha. In *Mammal species of the World* (eds D Wilson, DM Reeder), pp. 212–219, 3rd edn. Baltimore, MD: Johns Hopkins University Press.
- Wilson DE, Reeder DM. 2005 *Mammal species of the World. A taxonomic and geographic reference*, 3rd edn. Washington, DC: Smithsonian Institution Press.
- Murariu D, Benedek AM. 2005 New reports on the presence of *Sorex alpinus* Schinz, 1837 (Insectivora: Soricidae) in the southern Carpathians (Romania). *Travaux du Muséum National d'Histoire Naturelle 'Grigore Antipa'* **48**, 395–405.
- Lynch CD. 1991 Population dynamics in the lesser dwarf shrew, *Suncus varilla* (Mammalia: Soricidae). *Navorsinge van die Nasionale Museum Bloemfontein* **7**, 465–473.
- Maier TJ, Doyle KL. 2006 Aggregations of masked shrews (*Sorex cinereus*): density-related mating behavior? *Mammalia* **70**, 86–89. (doi:10.1515/MAMM.2006.015)
- Hays WST, Lidicker WZ. 2000 Winter aggregations, Dehnel effect, and habitat relations in the Suisun shrew *Sorex ornatus sinuosus*. *Acta Theriol.* **45**, 433–442. (doi:10.4098/AT.arch.00-44)
- Cantoni D, Vogel P. 1989 Social organization and mating system of free-ranging, greater white-toothed shrews, *Crocidura russula*. *Anim. Behav.* **38**, 205–214. (doi:10.1016/S0003-3472(89)80083-1)
- Merritt JF, Zegers DA. 2014 Social thermoregulation in least shrews, *Cryptotis parva*. *Mammalia* **78**, 11–22. (doi:10.1515/mammalia-2012-0112)
- Fontaine B. 2010 European bounty for taxonomists. *Nature* **468**, 377. (doi:10.1038/468377a)