

Multiannual co-occurrences between Saimaa ringed seal individuals suggest social associations during the moulting season

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While social network analysis was originally developed for human sociology studies, it is also a valuable tool for characterizing behavioural aspects in many animal populations. For instance, social network analysis can be used for assessing the transmission of diseases or information within groups. Here, we describe co-occurrences and potential social associations of ringed seals, *Pusa hispida saimensis*, in Lake Saimaa, Finland, from 2016 to 2022, based on photoidentification data. Throughout seven successive moulting seasons (April to June), we identified 425 individuals, of which 178 had pairwise co-occurrences in altogether 185 dyads. These seals had a variable number of associates (up to 10), and co-occurrences were observed in 1–7 years. In general, observations of pairs or larger groups of seals (up to five individuals) were rare, and mainly occurred in the two most densely populated basins of the lake. Most of the group observations occurred on ice rather than on rocks. Overall, the fragmented nature of the lake system, site fidelity and moulting habitat availability are key factors that probably affect the observed co-occurrences. Most of the dyads were observed during only one year, which may indicate social tolerance while using the same moulting site. However, 21 dyads were observed during multiple moulting seasons, with some at different sites separated by up to 3 km in different years, suggesting the existence of actual long-lasting associations. Our study represents the first description of co-occurrences and potential social associations in the endangered Saimaa ringed seal. These results can be used for designing and implementing mitigation strategies in case of unforeseen and sudden changes in the environment, such as a disease outbreak.

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Originally implemented in human sociology studies (Freeman, 2004), social network analysis has subsequently been used to characterize behavioural aspects and disease transmission risk in many animal populations (e.g. Croft et al., 2005; Godfrey et al., 2010; Heinen et al., 2022; Stroeymeyt et al., 2018), making it a useful tool for wildlife monitoring and conservation (Robinson et al., 2018; Snijders et al., 2017; Villegas-Ríos et al., 2022; Whitehead, 2010). For instance, Hamede et al. (2009) used proximity-sensing radio collars to document the contact network of Tasmanian devils, *Sarcophilus harrisii*, and highlighted that the interconnection of all individuals within their study area may

favour the transmission of the devil facial tumour disease, an infectious cancer threatening the species with extinction (McCallum et al., 2009). The definition of an association varies between animal social network studies, but usually involves simultaneous usage of a specific location (Baigger et al., 2013; Snijders et al., 2014), spatial proximity (Hamede et al., 2009; Leu et al., 2016), group membership (Lusseau, 2007; Williams & Lusseau, 2006) or behavioural interactions (Balasubramaniam et al., 2016; Flack et al., 2006). Importantly, associations are rarely static over time and can be influenced by, for example, seasonality (Brent et al., 2013; Prehn et al., 2019) or diel activities (Papastamatiou et al., 2020). Solitary species may interact mainly during the mating season (Elbroch et al., 2015; Fox & Chundawat, 2016; Sandell, 1989), while individuals of highly social species, such as those living in matriarchal societies, may spend their entire lives within the same tight social unit (Bigg et al., 1990; Holekamp & Sawdy,

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2019; Wittemyer et al., 2005). Thus, the type of association index, defined as ‘a measure of propensity for individuals to be seen together’ (Hoppitt & Farine, 2018), as well as the sampling period (the time during which associations are defined to occur) should be carefully tailored to suit each particular species and research question. Several guidelines and tools exist to facilitate the choice of the right metrics, network types and general approach (Farine, 2017, 2018; Farine & Whitehead, 2015; Hoppitt & Farine, 2018; Wey et al., 2008; Whitehead, 1997, 2008a, 2008b; Whitehead & Van Parijs, 2010).

Among marine mammals, sociality has been extensively studied in cetaceans (e.g. Danaher-Garcia et al., 2022; Lusseau, 2003; Nykänen et al., 2020). For instance, fission–fusion societies, in which group size and composition varies over time, are commonly observed in bottlenose dolphins, *Tursiops* spp., and are thought to be shaped by multiple ecological and behavioural factors, including competition for mates (Connor & Krützen, 2015), feeding habits and prey availability (Parra et al., 2011), predation risk (Whitehead et al., 2012), ranging patterns (Lusseau et al., 2006) and spatial segregation (Louis et al., 2015). Kinship also plays a central role in the sociality of some cetaceans (see Rendell et al., 2019). Among pinnipeds, coloniality and/or polygynous mating systems have enabled the description of social behaviour in many species, such as Steller sea lions, *Eumetopias jubatus* (Gentry, 1970, 1974; Sandegren, 1976), harbour seals, *Phoca vitulina* (Honeywell & Maher, 2017; Sullivan, 1982; Walker & Bowen, 1993) and New Zealand sea lions, *Phocarctos hookeri* (Chilvers et al., 2005; Marlow, 1975; McNally et al., 2001). However, beyond

mother–pup bonds (e.g. Charrier, 2020; Insley et al., 2003), studies focusing on social behaviour at the individual level are less common. Examples of such studies include Bishop et al. (2015), who reported that fine-scale social stability inversely correlates with the aggression rate of male grey seals, *Halichoerus grypus*, with familiar neighbour proximity reducing the frequency of aggression and the risk of escalation by up to 50%. Casey et al. (2015), on the other hand, described associative learning during male–male contests of northern elephant seals, *Mirounga angustirostris*. There is also evidence that social associations influence the use of novel foraging grounds in California sea lions, *Zalophus californianus* (Schakner et al., 2017). None the less, very little is known about the sociality of noncolonial pinnipeds, especially at high latitudes.

The Saimaa ringed seal, *Pusa hispida saimensis*, is a freshwater subspecies of ringed seal, landlocked in Lake Saimaa, Finland (Fig. 1). Although some individuals are known to live over 40 years, their natural lifespan is estimated to be 19–23 years, with no apparent difference between sexes (Sipilä, 2003). However, the juvenile survival rate is low due to perinatal and incidental bycatch mortality (Jounela et al., 2019). The latest population size estimate from 2024, which is mainly based on the annual snow lair census, totalled approximately 500 individuals (Metsähallitus, 2024). Apart from the young of the year, which typically moult their lanugo hair by the end of April, seals moult in late spring, with a peak centred around 18–20 May (Niemi et al., 2022). From 2010 onwards, photoidentification (hereafter, referred to as photo-ID) surveys have been conducted annually during the moulting

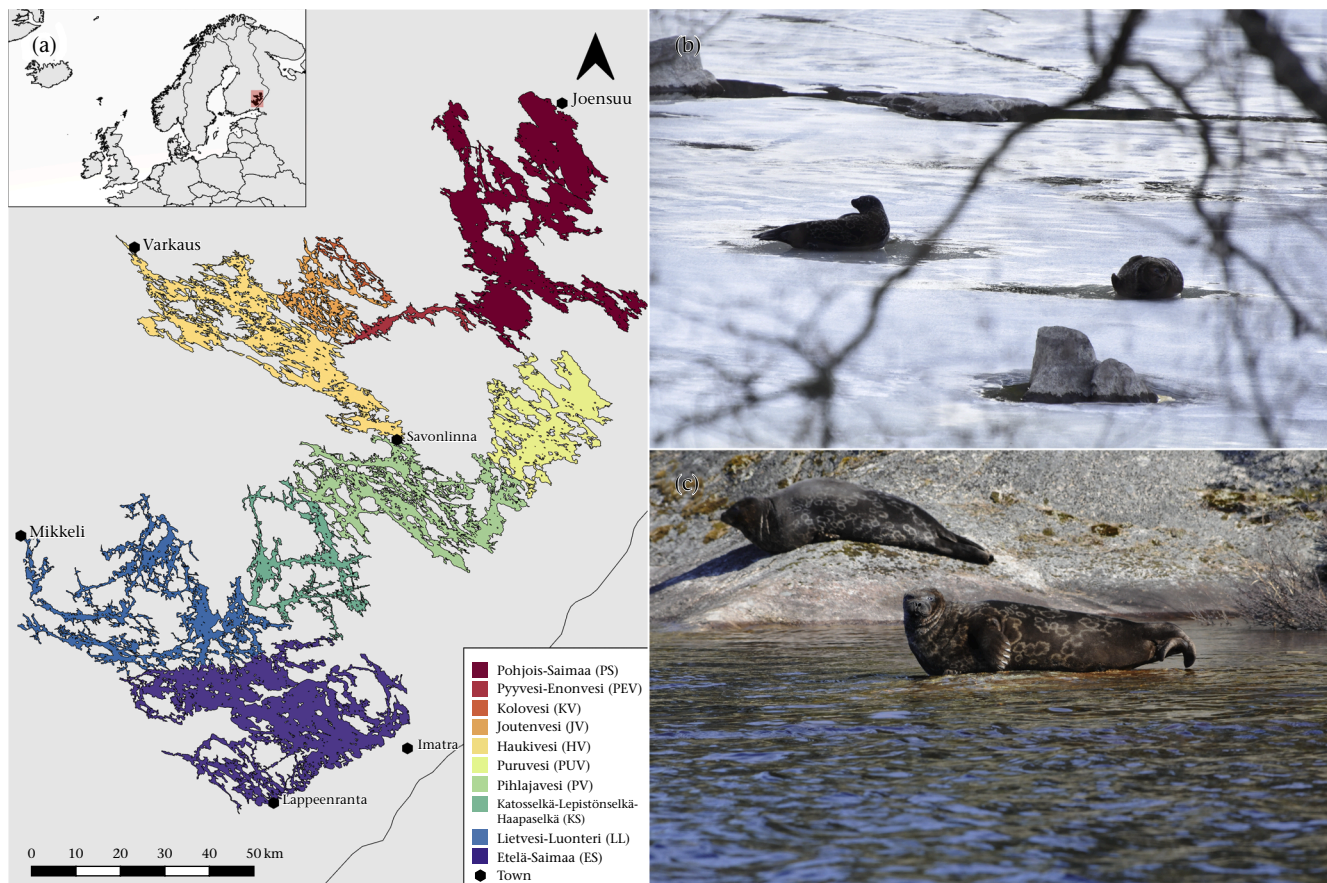


Figure 1. (a) Map of Lake Saimaa with its different main basins. Towns with over 20 000 inhabitants are indicated on the map. Base map: National Land Survey of Finland MML/24. (b) Seals that haul out on ice usually aggregate around breathing holes. Photo: Mervi Kunnasranta. (c) While these two seals hauled out on separate rocks, the distance between them was less than 50 m and they were reconsidered as a pair. Photo: Vincent Biard. Photos (b) and (c) were both taken with digital cameras.

season, when the seals spend extended periods of time hauled out (Kunnasranta et al., 2021). Each seal can be identified based on individually unique patterns in their pelage (Koivuniemi et al., 2016). As opposed to Arctic ringed seals (*P. h. hispida*), which moult on ice (Kelly, 2001), Saimaa ringed seals predominantly moult on terrestrial platforms (e.g. shoreline rocks) because of the early breakup of the seasonal lake ice. Furthermore, they show high fidelity to their moulting sites (Biard et al., 2022; Koskela et al., 2002), which are also used for resting at night in other seasons (Kunnasranta et al., 2002; Niemi, Auttila, Valtonen, et al., 2013). Since Saimaa ringed seals have mostly been observed to haul out alone (Koivuniemi et al., 2016; Sipilä & Hyvärinen, 1998) and females display some degree of avoidance of conspecifics in winter (Niemi et al., 2019), this subspecies has traditionally been considered to be solitary. However, Biard et al. (2022) reported that the same moulting site can be used by several individuals during successive moulting seasons. Moreover, groups of individuals have occasionally been observed to haul out together.

In this study, we investigated, for the first time, the sociality among Saimaa ringed seals during the moulting season. We did this by quantifying the degree of co-occurrence among the seals. Further, we investigated the role of possible drivers affecting the co-occurrences between individuals in the entire distribution of the population, with a particular focus on habitat availability, site fidelity and sex. Finally, we assessed the interannual persistence of these co-occurrences.

METHODS

Study Site and Data Collection

We conducted our study in Lake Saimaa (61°05' to 62°36'N, 27°15' to 30°00'E), which extends over 4400 km² and is the largest lake of Finland. The lake comprises 10 main basins interconnected by channels (Fig. 1a) with 13 700 islands (Kuusisto, 1999), resulting in a labyrinthine water body spanning about 180 km in the north–south direction and 140 km in the east–west direction. We collected photo-ID data during the seals' annual moulting season (1 April to 30 June) between 2016 and 2022, across the entire distribution range of the Saimaa ringed seal (see Appendix and Table A1 for further details). We photographed seals from outboard motorboats (<6 m) using digital single-lens reflex cameras with telephoto lenses (up to 300 mm). Additionally, we set up stationary game camera traps (Scout Guard 550VB and 560 K-8, and UoVision UV785 superb full HD 12MP; Scout Guard and UoVision, <https://www.uovision.com/>) at some moulting sites, primarily in the Pihlajavesi (PV) basin (average of 48 locations per year). We set the game cameras to motion trigger activation, to take two pictures over a 0.5–2 min time span (see details in Koivuniemi et al., 2016). However, from 2019, game cameras were set to time lapse, taking two pictures every 10 min. During all surveys, we recorded the GPS coordinates for each sighted seal.

We stored the image data into a Wildbook-based catalogue (<https://www.wildme.org/wildbook.html>; <https://seals.wildme.org>). The data set was supplemented by images collected by members of the public if they were associated with precise GPS coordinates. We identified individual seals by visually matching their pelage patterns to images in the catalogue (see Appendix and Table A2 for further details). We also determined their sex from ventral photographs when available.

Group Definition and Social Network Construction

For each moulting season, we reported seals' co-occurrences based on their close proximity with each other. When hauled

out on ice, seals generally concentrate around a breathing hole and, therefore, proximity is relatively easy to determine (Fig. 1b). However, once they are on rocks, judging proximity is more subjective. In Lake Saimaa, the seals haul out almost exclusively on rocks as opposed to sandy or rocky beaches. The rocks are rarely isolated and several moulting sites (rocks) can be present on the same shoreline or bay of islands, separated by a few metres to several hundred metres (Fig. 1c). We observed most of the seals' co-occurrences on the same rock or adjacent rocks set apart by only a few metres and, thus, two or more seals were considered as a group. In some cases, the seals were separated by longer distances and not initially considered to be part of the same group during a photo-ID survey. However, because phocids have relatively acute hearing, vision and sense of smell on land (for a review, see Hanke & Reichmuth, 2022) and can thus be aware of each other over longer distances, coupled with accommodating for possible GPS error, any simultaneous observation of at least two individuals within a range of 50 m was later considered as identifying a group (similarly to Biard et al., 2022). However, we also took into consideration the geographical complexity of Lake Saimaa. Thus, if the individuals were observed on different islands, shorelines or bays of islands within this 50 m range, they were not considered co-occurring (see Appendix for further information).

We used SOCPROG2.10 (Whitehead, 2009) to build a matrix of pairwise co-occurrences (1: co-occurring; or 0: not co-occurring) using the data of identified seals only. However, on some occasions, not all members of a group were identified from photographs (partial group identifications). On these occasions, we treated the remaining identified individuals as singles if a group of two had only one identified seal (74 cases) or if a larger group had only one identified seal (five cases), or groups with a smaller number of individuals depending on how many seals were identified (18 cases) in the calculation of their pairwise co-occurrences. The sampling period for the pairwise co-occurrences was defined as one moulting season to accommodate fluctuation in survey effort between lake basins (see Appendix and Table A1) and the difference in the data acquisition rate between boat surveys and camera traps. Therefore, multiple observations of co-occurrences between the same individuals during the same moulting season were summarized as a single co-occurrence in the matrix. We used joint occurrences as the association index between two individuals (e.g. a dyad), therefore representing the number of seasons these seals were observed together. Individual degree (hereafter, referred to as degree) was calculated as the total number of connections of an individual. We used the R package igraph (Csardi & Nepusz, 2006) to visualize the co-occurrence network.

Data Analyses

We used Fisher's exact test, run in R version 4.1.1 (R Core Team, 2021), to investigate whether the co-occurrence behaviour (number of single individual/group encounters) was influenced by habitat type (ice/rock). We used a two-tailed one-proportion Z test with Yates' continuity correction to evaluate if the sex ratio among the photographed individuals for which sex could be determined deviates from the 1:1 sex ratio observed at birth by Auttila et al. (2016). We then used Fisher's exact test to investigate whether the co-occurrence behaviour (proportion of co-occurring/non-co-occurring individuals) was influenced by sex, and a Wilcoxon Mann–Whitney test to determine if individual degree was influenced by sex. Finally, a chi-square test was performed to see if the observed proportions of male–male, female–female and male–female dyads deviated significantly from proportions expected under random pairing.

We used a Monte Carlo permutation test available in SOC-PROG2.10 to determine whether the observed co-occurrence pattern was different from that expected from randomly co-occurring individuals. We performed 10 000 permutations with 1000 trials per permutation. However, this test assumes an equal probability of co-occurrences between individuals. Although possible for a limited number of individuals who undertake sporadic trips between lake basins, it would be wrong to assume that co-occurrences are equally likely among individuals within a single lake basin and between individuals from different lake basins separated by tens of kilometres. Therefore, we performed separate permutation tests, each restricted to the data collected in a single basin. Despite the large size of each basin, the assumption of random associations within each of them is more likely to be fulfilled than between them. We only focused on the Haukivesi and Pihlajavesi basins as they had the most encounters and co-occurrences.

Finally, we explored the persistence of dyads (as multiannual co-occurrences) by calculating the geodesic distance between successive co-occurrence locations using the R package *geosphere* (Hijmans, 2019). The distance between successive moulting sites has been used as a proxy of site fidelity by Biard et al. (2022) and can be used to determine whether multiannual co-occurrences are simply due to site fidelity. Although it is possible that larger groups persist between years, we only considered dyads in order to be consistent with the previous analyses performed on the data.

Ethical Note

Data collection for this study was done under permits by the Finnish environmental authorities ELY Centre (ESAELY/1290/2015, ESAELY/1319/2020, POKELY/1232/2015, KASELY/2014/2015, KASELY/2104/2020, POSELY/313/07.01/2012 and POSELY/2335/2020) and Metsähallitus (MH 5813/2013 and MH 6377/2018/05.04.01). This study involved noninvasive observation of wild animals.

RESULTS

Over seven successive moulting seasons, we recorded a total of 4512 seal encounters (35% from camera traps), of which 501 were on ice and 4011 on rocks. The majority (4034) of the encounters consisted of a single seal (Table 1). However, on 478 occasions, we observed groups composed of 2–5 seals (Fig. A1). Of these, 86

Table 1
Number of single Saimaa ringed seals and groups encountered over seven moulting seasons (2016–2022), with their identification success rate, according to habitat and lake basin

| | Single seal encounters (identification success rate, %) | | Seal group encounters (identification success rate, % all members identified; some members identified; none identified) | |
|-----|---|-----------|--|-----------------|
| | Ice | Rock | Ice | Rock |
| PS | 10 (40) | 148 (80) | – | 9 (56; 33; 11) |
| PEV | 1 (0) | 23 (74) | – | 3 (33; 67; 0) |
| KV | 7 (43) | 70 (89) | 1 (0; 0; 100) | 5 (100; 0; 0) |
| JV | 9 (78) | 77 (75) | – | 5 (60; 40; 0) |
| HV | 175 (75) | 652 (80) | 36 (67; 22; 11) | 54 (57; 31; 11) |
| PUV | 10 (40) | 115 (63) | – | 2 (0; 100; 0) |
| PV | 139 (71) | 2107 (86) | 38 (50; 39; 11) | 203 (81; 17; 2) |
| KS | 7 (71) | 132 (79) | – | 10 (50; 20; 30) |
| LL | 6 (50) | 132 (76) | – | 4 (50; 25; 25) |
| ES | 13 (38) | 201 (60) | 5 (0; 40; 60) | 17 (29; 47; 24) |

Abbreviation of the basins: PS = Pohjois-Saimaa, PEV = Pyyvesi-Enonvesi, KV = Kolovesi, JV = Joutenvesi, HV = Haukivesi, PUV = Puruvesi, PV = Pihlajavesi, KS = Katosselkä-Lepistöselkä-Haapaselkä, LL = Lietvesi-Luonteri, ES = Etelä-Saimaa.

were mother–pup pairs that were excluded from the analyses. Group encounters were more frequent on ice (17.5% of total ice encounters) than on rocks (8% of total rock encounters; Fisher's exact test, $P < 0.001$). We identified 425 individuals (140 females, 115 males, 170 undetermined sex) from 3614 encounters with photographs of sufficient quality. There was no statistically significant difference in the proportion of males and females in the data ($Z = -1.503$; $P = 0.133$). We were able to identify all group members from 264 encounters, while partial identifications were reached for 97 encounters. For 31 encounters, none of the group members were identified. For the study period, the median number of encounters per identified individual was 5 (range 1–95) and the median number of moulting seasons was 2 (range 1–7).

A total of 178 seals (80 females, 63 males and 35 of undetermined sex) were involved in 185 dyadic co-occurrences (Fig. 2). Of these dyads, 81 were composed of a male and a female, 43 of two females and 13 of two males, while the rest involved at least one individual of undetermined sex (25 undetermined–male, 19 undetermined–female, 4 undetermined–undetermined). Only two individuals, an adult female and an adult male, were involved in dyads in two different basins (Haukivesi and Joutenvesi, Pihlajavesi and Katosselkä-Lepistöselkä-Haapaselkä, respectively) in different years. The median number of associates per individual was zero (range 0–10) when considering all individuals and two (range 1–10) when considering only the individuals that were involved in co-occurrences. We did not detect a significant difference between males and females in the probability of being involved in one or more co-occurrences (Fisher's exact test, $P = 0.799$). We also did not observe a significant difference in degree between males and females ($Z = 0.356$, $P = 0.723$). However, when considering only the dyads in which both individuals could be sexed, intersexual dyads were slightly but statistically significantly overrepresented (81 observed versus 65.2 expected) and intrasexual dyads underrepresented (male–male 13 versus 20.9, female–female 43 versus 50.9) as compared to the expectation based on random pairing of individuals ($\chi^2_1 = 8.026$, $P = 0.005$).

Most co-occurrences took place in the main breeding areas (Haukivesi and Pihlajavesi basins), with 52 and 115 dyads, respectively, and the overall co-occurrence pattern was nonrandom based on permutation tests (as reported below). For the Haukivesi basin, the mean joint occurrence was 0.011, which did not differ significantly from the permuted random data (mean = 0.011, $P > 0.05$). However, the standard deviation (SD = 0.130) and coefficient of variation (CV = 12.178) in the real data were significantly higher than in the random data (SD = 0.104, $P < 0.001$; CV = 9.779, $P < 0.001$), suggesting that the co-occurrence pattern observed within the Haukivesi community is different from what you would expect by chance and that some individuals preferentially associate with other individuals over several sampling periods (Whitehead, 2009). At the same time, the proportion of nonzero elements was lower in the real data than in random data (real: 0.009, random: 0.011, $P < 0.001$), indicating that some individuals avoid each other, although this could be an artefact of site fidelity and the fragmented nature of the lake system. Similarly, for the Pihlajavesi basin, the mean joint occurrence (0.008) did not differ significantly from the permuted random data (mean = 0.008, $P > 0.05$). However, both the SD (0.109) and the CV (13.795) in the real data were significantly higher than in the random data (SD = 0.090, $P < 0.001$; CV = 11.370, $P < 0.001$), indicating a nonrandom co-occurrence pattern between seals also in this basin. The proportion of nonzero elements was likewise lower in the real data than in random data (real: 0.007, random: 0.008, $P < 0.001$) in this basin.

Twenty-one dyads (13 male–female, 4 male–male, 3 female–female and 1 female–undetermined) were observed

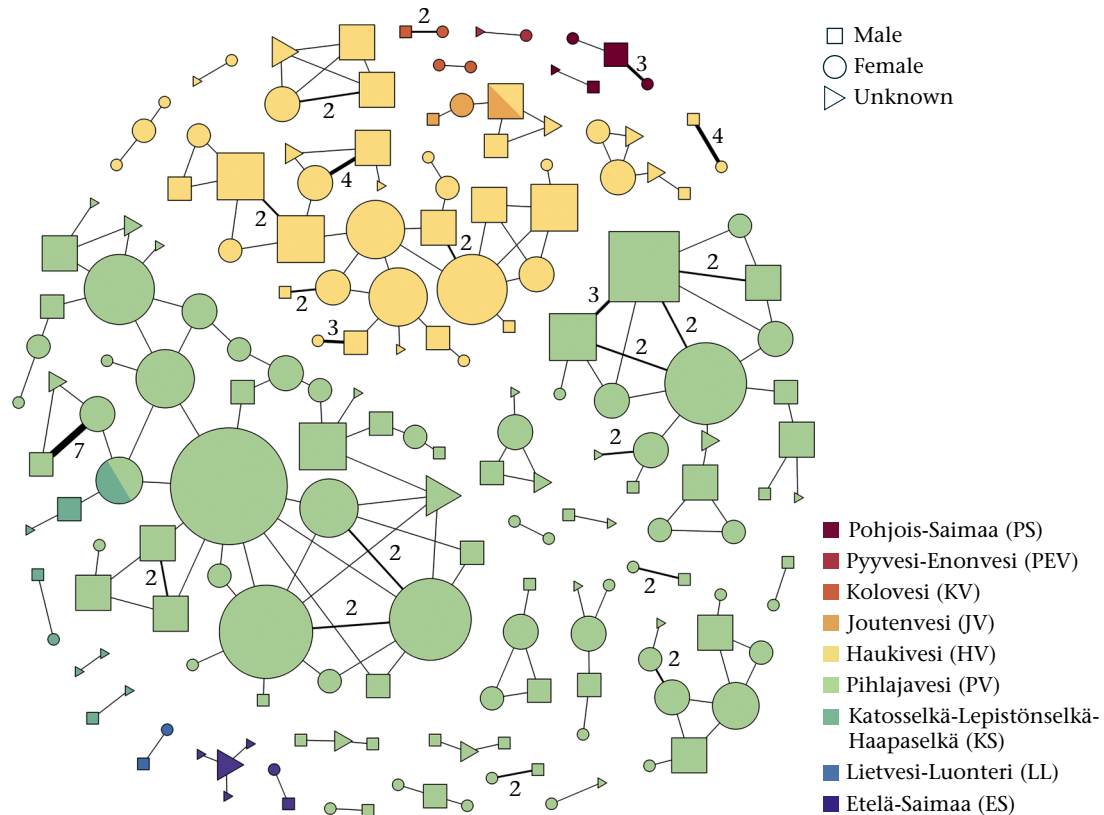


Figure 2. Co-occurrences of Saimaa ringed seals during seven successive moulting seasons (2016–2022). Node size is proportional to individual degree (i.e. total number of connections per individual), and edge width proportional to the number of years during which a co-occurrence was observed. For multiannual co-occurrences, the number of years during which a co-occurrence was observed is indicated next to the edge. Individuals that travelled across lake basins during the study period have a double affiliation, resulting in a bicoloured node. For clarity, only individuals for which co-occurrences were observed are included in the network.

during at least two different moulting seasons (range 2–7 years). Five of the multiyear dyads were observed in the same location in successive years. For the remaining 16 dyads, both individuals were found together in a new moulting site located between 60 m and 3148 m away from the previous location. When considering all the multiannual dyads, the median distance between successive locations was 130 m (range 0–3148 m; Fig. A2), indicating that habitat availability and site fidelity may play a part in defining co-occurrences. However, four dyads (3 male–female and 1 female–female) travelled further than 1000 m from their original haul-out site suggesting that not all co-occurrences can be explained by site fidelity alone (Fig. 3).

DISCUSSION

Studies on individual associations in pinnipeds have typically focused on species that breed in large terrestrial colonies (e.g. Giardino et al., 2022; Pomeroy et al., 2005; Schakner et al., 2017; Wolf et al., 2007). As a consequence, little is known concerning the extent of sociality in noncolonial species (but see Baker et al., 2016). This is also true for the Saimaa ringed seal, for which only a few studies characterizing mother–pup vocalization (Rautio et al., 2009) and female avoidance during the breeding season (Niemi et al., 2019) have heretofore been available. Here, we utilized an extensive photo-ID database on the Saimaa ringed seal population, created from photographs taken during the annual moulting season through boat surveys, camera traps and citizen science. This database provides a unique opportunity for studying grouping patterns and potential social associations in a solitary

pinniped outside of the breeding season. To our knowledge, our study is the first to describe long-term individual level co-occurrences between ringed seals. Our results show that, although rare, co-occurrences between moulting Saimaa ringed seals are probably structured by habitat availability and site fidelity. However, some co-occurrences can extend over multiple years with relatively long displacements, suggesting active associations whose drivers are yet to be identified.

Saimaa Ringed Seal Groups are Rare

Ringed seals are generally considered solitary (e.g. McLaren, 1958), although their behaviour changes during the moult and small groups may congregate around breathing holes in the Arctic (Kelly, 2022; Lindsay et al., 2023; Smith & Hammill, 1981). Based on our observations, the same can be said about the Saimaa ringed seal as 91% of the seal encounters reported in our study consisted of single individuals. However, pairs of seals, and occasionally larger groups (up to five individuals), were also observed, although group sizes were considerably smaller compared to other low-latitude populations. Ladoga ringed seals, *P. h. ladogensis*, are known to haul out in large herds of up to several hundreds of individuals (Sipilä & Hyvärinen, 1998; Trukhanova et al., 2024) and groups of up to 80 Baltic ringed seals, *P. h. botnica*, have been observed on ice and rocky islands during the ice-free season (Halkka & Tolvanen, 2017; Härkönen et al., 1998).

When comparing to other low-latitude ringed seal subspecies, it should also be noted that the Saimaa ringed seal population is currently substantially smaller than it would have been without

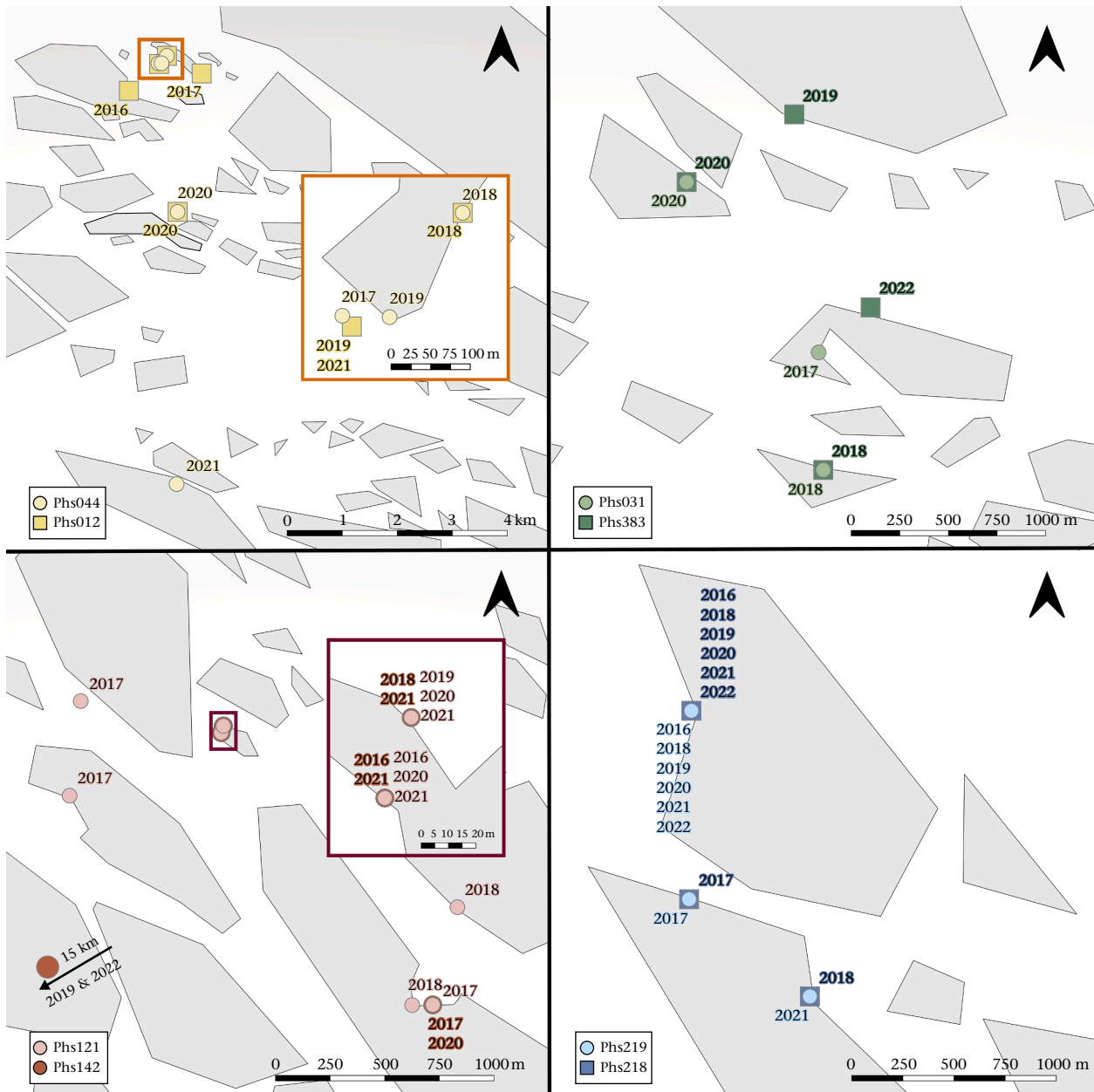


Figure 3. Locations of four Saimaa ringed seal dyads with long-term associations across multiple moulting seasons during the 7-year study period (2016–2022). Circles represent moulting sites of females, and squares, those of males. Grey areas are land. The maps represent subsets within the Haukivesi (HV) and Pihlajavesi (PV) basins. Due to protection by law (Council Directive 92/43/EEC; European Union, 1992) of the resting sites of the Saimaa ringed seal, islands have been simplified to polygons to prevent the localization of the haulouts. Base map: National Land Survey of Finland MML/24.

the anthropogenic bottleneck that the population went through in the 1950s–1980s (Kunnasranta et al., 2021). Human exploitation until the middle of the 20th century drastically reduced the population size, which has been estimated to have been a few thousands historically (Hyvärinen & Sipilä, 1992; Kokko et al., 1998, 1999; Nyman et al., 2014; Sipilä, 2003). Niemi et al. (2019) even suggested that, based on their breeding habitat requirement, up to 4000 seals could inhabit Lake Saimaa. The small average group size and the infrequent occurrence of groups may thus be a consequence of low seal densities. According to historical accounts by local fishermen, it was not rare to see herds of seals hauled out along Lake Saimaa islets before the early 20th century (Seppovaara, 1958). Due to protection and successful conservation measures, the population is currently increasing (Koivuniemi

et al., 2019), and over time this recovery could lead to the re-establishment of previously existing grouping patterns. None the less, it is interesting to note that 42% of the identified individuals were co-occurring in pairs or larger groups at some point of the data collection period, suggesting that some degree of sociality exists within the Saimaa ringed seal population. However, the fact that most of the seal encounters consisted of single individuals points towards a dynamic system where individuals are solitary in some years and in groups in other years.

Habitat Availability and Site Fidelity Shape Seal Co-occurrences

As noted by Giardino et al. (2022), associations between individuals can result from habitat preference or availability and,

thus, qualify as passive. Indeed, those authors reported that the association dynamics between some male South American sea lions, *Otaria flavescens*, resulted from shared affinity to particular terrestrial platforms. During their moult, Saimaa ringed seals experience a significant transformation in their surrounding habitat. In late spring, the ice cover of Lake Saimaa breaks gradually, and the lake is generally ice free within the first 2 weeks of May. Interestingly, groups of seals were more frequent on ice than on rocks. It can be argued that individuals preferring this habitat congregate towards the remnants of ice prior to the final breakup and that these co-occurrences probably derive from habitat availability. However, logistical challenges due to the ice conditions prevented us from fully evaluating the haul-out patterns of seals on ice. Therefore, our observations (10% of encounters) are probably an underestimation of the use of this habitat and of its relevance in shaping the sociality of the seals. Nevertheless, considering the numerous terrestrial moulting sites provided by the highly fragmented lake system, habitat availability is unlikely to be a determinant of the seals' co-occurrences on rocks.

Our results show that co-occurrences are restricted to single basins, the only exception being the two individuals that changed basins and were associating with different individuals in their new locations. Moreover, site fidelity extends across years as all multiannual dyads stayed in the same basin. These results are consistent with previous findings of long-term site fidelity (Biard et al., 2022; Koivuniemi et al., 2016; Koskela et al., 2002) and limited dispersal (Löytynoja et al., 2023; Niemi et al., 2012; Valtonen et al., 2012, 2014; but see Niemi, Auttila, Viljanen et al., 2013) in the Saimaa ringed seal. However, this site fidelity is not just limited to the basin, but is actually centred around specific rocks used for moulting. Although rocks are abundant along the shorelines of Lake Saimaa, Biard et al. (2022) reported that, in a 4-year period, the median number of terrestrial haul-out sites used by an individual seal was four, many of which were reused over the years. This fine-scale site fidelity is probably seen in the results of the permutation tests. Rather than indicating true avoidance among individuals, these results may reflect how high site fidelity further limits co-occurrences even within the same basin. However, Biard et al. (2022) also found that a moulting site can be used by several seals, although not always simultaneously. Therefore, the seals' co-occurrences we observed could result from the random use of the same location. Additionally, the observed low prevalence of multiannual co-occurrences could simply be attributed to the use of different locations in successive moulting periods (Biard et al., 2022), which is further emphasized by the fact that, during some years, many of the seals were observed alone. Although the observed co-occurrences may not translate to active associations, they nevertheless reflect some tolerance towards the presence of conspecifics at a moulting site.

Intersexual Co-occurrences are More Frequent

We did not find evidence of sex influencing the likelihood of being involved in co-occurrences or on the number of connections individuals had, suggesting that the observed co-occurrences are individual specific and/or are more influenced by the local environment than by sex. However, these results may partly reflect low statistical power, since we were unable to determine the sex of 170 individuals (40%). None the less, intersexual co-occurrences were statistically significantly more frequent than expected (59% of the dyads in which the sex of both individuals could be determined). This was even more pronounced when only considering multiannual dyads (65%). During the winter, male and female ringed seals are known to use the same breathing holes and may also share subnivean lairs (Kelly et al., 2010; Kunnasranta et al., 2001;

Smith & Stirling, 1975). It has also been hypothesized that Saimaa ringed seal males provide lairs to females as a strategy for attracting potential mates (Niemi et al., 2019). Our study provides further evidence of intersexual interactions among ringed seals outside the mating and breeding seasons, although the reasons are yet to be determined. However, considering that our focal study period starts soon after the peak of the mating season that occurs in mid-April in Lake Saimaa (see Young et al., 2025) and that ringed seals are slightly polygynous (K. J. Robinson & Pomeroy, 2022), it could be speculated that some of these co-occurrences are between pairs that have mated prior to the moulting season.

Male ringed seals defend underwater territories against other males in the vicinity of lairs occupied by females (Crawford et al., 2012; Kelly et al., 2010; Kelly & Wartzok, 1996; Krafft et al., 2007; Smith & Hammill, 1981), and females are known to avoid each other during the breeding season (Niemi et al., 2019; Smith & Hammill, 1981). Our observations that both female–female and male–male co-occurrences (31% and 9%, respectively, of the dyads in which the sex of both individuals could be determined) are less frequent than expected based on random pairing suggest that intrasexual avoidance may also occur during the moulting season. We note that, while we were unable to determine the sex of at least one member from 26% of the dyads, this should not affect the estimated relative proportions of intrasexual versus intersexual dyads as long as sexing failure is random with respect to the composition of the dyads.

Multiannual Dyad Movements Suggest Social Associations

Pinniped colonies are generally structured by several factors, such as sex, age class or reproductive success, probably affecting the grouping patterns between individuals and, thus, the identification of social associations (Poland et al., 2008; Pomeroy et al., 2000; Wolf et al., 2007; Wolf & Trillmich, 2008). Moreover, as colonial pinnipeds are often philopatric (e.g. Chilvers & Wilkinson, 2008; Hastings et al., 2017; Liu et al., 2022), the first challenge remains to determine whether or not observed co-occurrences are passive, simply resulting from site fidelity. One way to counteract this issue is to look at the movement of the identified dyads. For instance, Pomeroy et al. (2005) described the interannual movements of pupping females within a breeding colony of grey seals in North Rona, Scotland, and revealed, using predictive models, that members of multiannual dyads that have moved together over 40 m (median observed pupping site fidelity in the study) probably represent active associations. Although Saimaa ringed seals are not colonial, their site fidelity behaviour results in similar obstacles regarding the evaluation of the persistence of their co-occurrences, and a similar reasoning could be applied to suggest the existence of social associations in Lake Saimaa.

The distance between successive moulting sites has previously been used as a proxy for site fidelity in the Saimaa ringed seal (Biard et al., 2022), with a median distance of 982 m between successive moulting sites used in different years. The majority of the dyads identified in our study were observed in a single year, thus lacking information for being conclusive. However, 21 dyads persisted over several moulting seasons and may reflect the existence of tighter social connections between some individuals. Five of these multiannual dyads were observed in the same location, and therefore, could not be distinguished from solely being the result of randomly using the same location because of site fidelity. For 12 dyads, both individuals were found together in new moulting places, but the distance between the sites was less than 982 m. Although these displacements are curious, we could not exclude the possibility that, because of their site fidelity behaviour, both members of a dyad have overlapping moulting ranges and

randomly use the same sites. However, the four remaining dyads moved beyond a kilometre and, even though both individuals could have travelled independently and ended up in the same location by chance, it is more likely that factors other than site fidelity apply to these pairs. Interestingly, three out of these four dyads were male–female pairs, which could hypothetically reflect codispersal of breeding pairs. We acknowledge that only reporting the movements of the dyads and simply comparing them to the median of a site fidelity proxy does not alone indicate the existence of long-term social associations among the seal population. None the less, combined with the low number of co-occurrence encounters and the low number of multiannual dyads, these movements constitute intriguing observations that will be investigated more thoroughly in future studies.

Conclusions and Future Perspectives

To our knowledge, our study is the first to describe interindividual co-occurrences within ringed seals and supplements the sparse evidence of social associations in noncolonial pinnipeds. At the population level, these co-occurrences are primarily structured by the labyrinthine nature of Lake Saimaa. Although the availability of the seasonal receding lake ice seems to explain the existence of some dyads, site fidelity is likely to be one of the main determinants of co-occurrences or their absence at finer scales. However, the low frequency of multiannual co-occurrences suggests social tolerance while using the same moulting site rather than long-lasting social connections. None the less, our observations of some dyads over multiple years that travel long distances imply that more complex factors may be driving the associative behaviour.

The moulting period of Saimaa ringed seals lasts only a few weeks, with a peak in late May (Niemi et al., 2022), which may generate a biased view of their true social network (Blonder et al., 2012). Future studies should therefore aim for a broader temporal range to cover other aspects of their life history and sociality. Combined with genetics, additional research should also focus on the effect of kinship and mating behaviour on the structuring of the associations. Conservation measures aimed towards protecting the endangered population have resulted in its slow but steady demographic growth. Our study provides a baseline for monitoring social changes in a population recovering from a severe anthropogenic bottleneck. Finally, climate change might affect overall health and the occurrence of diseases within populations of marine mammals (Burek et al., 2008; Sanderson & Alexander, 2020). In the case of disease outbreaks in Saimaa, the results presented here can be used as a first step towards a disease epidemic mitigation plan based on our improved understanding of ringed seal sociality.

Author Contributions

Vincent Biard: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Piia Mutka:** Data curation, Writing – review & editing, Investigation. **Mairi Young:** Writing – review & editing, Investigation, Data curation. **Marja Niemi:** Writing – review & editing, Methodology, Investigation, Conceptualization. **Tommi Nyman:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Milaja Nykänen:** Writing – review & editing, Supervision, Methodology, Investigation, Conceptualization. **Mervi Kunnasranta:** Writing – review & editing, Supervision, Methodology, Investigation, Fundraising, Conceptualization.

Data Availability

Co-occurrence data, individual metadata and R script to reproduce the analyses of this study are available at <https://zenodo.org/doi/10.5281/zenodo.12515932>. The GPS coordinates of seal observations are not publicly available due to protection by law (Council Directive 92/43/EEC; European Union, 1992) of the resting site of the Saimaa ringed seal, but are available from the corresponding authors on reasonable request.

Declaration of Interest

The authors declare no conflicts of interest.

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Appendix

Saimaa Ringed Seal Photo-ID Surveys

The annual photo-ID surveys of the Saimaa ringed seal generally start as soon as the seasonal ice breaks up, usually late April to early May, and end within the first 2 weeks of June. This temporal window expands over the peak of the moulting season (Niemi et al., 2022). In our study, we used photographs collected from 1 April to 30 June to accommodate for individual variation in moulting phenology, annual and regional fluctuations in the seasonal ice breakup and variation in game camera trap deployment periods.

The annual surveys are conducted by a team composed of seal researchers and trained volunteers, totalling around 20 people. Each surveying person ('boat' in Table A1) is assigned an area of the lake (main basin or portion of a main basin) and is asked to conduct as many surveys as possible within the temporal window previously described. However, the assigned areas may be so large that it is logistically impossible to cover them entirely during a single surveying day. None the less, the compilation of all the surveying days results in the entire coverage of each assigned area, with a minimum effort of at least 1 surveying day. We do not directly target known haul-out sites (e.g. located during the previous years' surveys), but rather conduct random routes around the islands to limit bias in the sampling effort. Typically, a seal encounter lasts for a few minutes at maximum to minimize the

disturbance to the seals. Once a seal is spotted, the surveying team slightly redirects its route to approach the seal, keeping a distance of at least 150 m when possible, and takes photographs while remaining aboard the boat and passing by the haulout.

As the surveying team is largely composed of trained volunteers, there are differences in the total number of surveying days between the lake basins. Moreover, the surveys are generally not coordinated between the different areas. However, as the assigned lake areas are nonoverlapping, the observation of the same seal or group of seals by different surveying persons is highly unlikely, thus preventing an overestimation of the seal occurrence prior to individuals' identification. None the less, this difference in surveying effort between the basins may lead to regional differences in the number of observations per individual or number of identified moulting sites per individual that need to be taken into consideration during the interpretation of the data. For this particular study, we acknowledge that the regional difference in sampling effort may affect the observation rate of seal co-occurrences. However, to limit this bias, we used a single joint co-occurrence within a surveying year as our association index. Details regarding the number of surveying boats and days are presented in Table A1.

Saimaa Ringed Seal Photo-ID Database

The Saimaa ringed seal presents a bilateral asymmetry in its pelage ring pattern. When the database was created at the beginning of the photo-ID surveys in 2010, it was arbitrarily decided that the right side ring pattern will be used for the entry of new individuals. Left side, belly and/or back photographs are also included if associated with a right side photograph at least on one occasion. In addition, we keep an 'unofficial' database consisting of left side, belly and back photographs that are not associated with right side photographs and compare it annually to the main database in case a match can be made with a newly acquired right side photograph, as sometimes it is possible to photograph both sides of the seal. This is to ensure that we obtain as detailed encounter history as possible of each individual.

Currently, seal identifications are performed by visually matching ring patterns to ones from the database. A similarity in at least three different pelage locations is used as a threshold for a match. Any no-match of a right side photograph results in a new individual entry in the database after confirmation from a second identifier, regardless of its age class (i.e. young of the year, juvenile, subadult or adult). Prior to the completion of the identifications from the 2023 photo-ID survey (not included in this study), the database currently includes over 500 individuals, with 1 to more than 300 photographs per individual, although some of these individuals have since died. When available, individuals' information is complemented with their sex, age class, kinship (e.g. mother–pup pairs) and co-occurrence with other seals.

Typically, we are unable to identify the seal in approximately 20–30 % of the encounters per year. Based on our observations, several factors are preventing successful identification, such as too great a distance to the seal when photographed, insufficient light exposure or sharpness of the photograph, awkward angle of the seal to the camera, the moulting stage (i.e. in early or advanced moulting stage the seals can present a diminished quality in their ring patterns compared to the seals that have completed their moult) and if the seal is wet when it is photographed. Moreover, we also noticed that habitat type influenced the identification success rate of seals, with 72 % of successful identifications for seals observed on ice and 83 % for seals observed on rocks (Fisher's exact test, $P < 0.001$). We think that this difference is mainly due to

the greater distance to the seal when photographed on ice because of the extent of the ice, and the moulting stage of the seals.

Details regarding the photo-ID database are presented in [Table A2](#).

Range of 50 m for Group Definition

We acknowledge that the chosen 50 m limit used to define seals as 'grouped' is arbitrary. None the less, we assume that the seals within this range are aware of each other. It is also possible that this distance underestimates the seals' awareness capacity but we currently do not possess data that would justify the use of a longer distance. Although the range of 50 m is not optimal for

some especially large island bays and a greater distance could have been considered, we decided to systematically keep this distance to avoid the further introduction of subjectivity in our data. We are also aware that, by using this 50 m range, we introduce some bias in our data, as we assign and treat dyads consisting of seals with the capacity of physical contact the same way as seals separated by 50 m. However, the purpose of the study was not to report type of interactions, but solely co-occurrences and their eventual repetitions over the years. Based on the seal density and our observations during the moult, several seals hauled out at the same time in the same shoreline or bay of islands is unusual, even though they may be distant by a few tens of metres.

Table A1

Number of surveying days and total number of survey boats in each basin of Lake Saimaa during the seven study seasons (years).

| | 2016 | | 2017 | | 2018 | | 2019 | | 2020 | | 2021 | | 2022 | |
|-----|------|-------|------|-------|------|-------|------|-------|------|-------|------|-------|------|-------|
| | Days | Boats | Days | Boats | Days | Boats | Days | Boats | Days | Boats | Days | Boats | Days | Boats |
| PS | 10 | 1 | 11 | 1 | 11 | 1 | 6 | 2 | 5 | 3 | 13 | 2 | 8 | 3 |
| PEV | 1 | 1 | 2 | 1 | 2 | 2 | 4 | 2 | 1 | 1 | 2 | 1 | 7 | 1 |
| KV | 5 | 1 | 1 | 1 | 4 | 3 | 3 | 1 | 1 | 1 | 3 | 1 | 5 | 1 |
| JV | 5 | 2 | 9 | 1 | 13 | 2 | 7 | 1 | 7 | 1 | 4 | 1 | 6 | 3 |
| HV | 16 | 3 | 28 | 5 | 27 | 7 | 25 | 5 | 26 | 6 | 21 | 6 | 25 | 8 |
| PUV | 11 | 2 | 13 | 2 | 14 | 2 | 11 | 2 | 10 | 2 | 12 | 1 | 10 | 2 |
| PV | 35 | 7 | 27 | 4 | 32 | 4 | 40 | 4 | 40 | 4 | 31 | 4 | 30 | 9 |
| KS | 10 | 2 | 6 | 3 | 6 | 3 | 12 | 3 | 10 | 3 | 19 | 3 | 13 | 2 |
| LL | 10 | 4 | 13 | 5 | 13 | 2 | 9 | 2 | 24 | 4 | 28 | 5 | 24 | 5 |
| ES | 11 | 4 | 21 | 3 | 16 | 3 | 8 | 4 | 25 | 4 | 20 | 3 | 12 | 4 |

Note that each boat did not necessarily participate in each day of the survey. Abbreviations of the basins: PS = Pohjois-Saimaa, PEV = Pyyvesi-Enonvesi, KV = Kolovesi, JV = Joutenvesi, HV = Haukivesi, PUV = Puruvesi, PV = Pihlajavesi, KS = Katosselkä-Lepistöselkä-Haapaselkä, LL = Lietvesi-Luonteri, ES = Etelä-Saimaa.

Table A2

Composition of the Saimaa ringed seal photo-ID database prior to the completion of the identifications from the 2023 surveys.

| | ID seals | Sex (M; F; U) | Sightings | Median number of sightings per individual (min; max) | Number of photographs | Median number of photographs per individual (min; max) | Availability of left sides (%) |
|-----|----------|---------------|-----------|--|-----------------------|--|--------------------------------|
| PS | 22 | 6; 6; 10 | 135 | 5 (1; 16) | 433 | 14 (3; 68) | 95.5 |
| PEV | 9 | 0; 2; 7 | 25 | 2 (1; 8) | 65 | 4 (1; 26) | 66.7 |
| KV | 14 | 3; 6; 5 | 102 | 5 (1; 20) | 337 | 18 (1; 60) | 64.3 |
| JV | 36 | 7; 10; 19 | 188 | 3 (1; 36) | 459 | 9 (2; 61) | 75.0 |
| HV | 155 | 47; 54; 54 | 1708 | 6 (1; 93) | 3553 | 14 (1; 150) | 83.9 |
| PUV | 21 | 5; 6; 10 | 209 | 9 (1; 25) | 743 | 32 (1; 109) | 95.2 |
| PV | 208 | 64; 76; 68 | 3292 | 9 (1; 107) | 9352 | 29 (1; 321) | 87.5 |
| KS | 44 | 10; 13; 21 | 335 | 6 (1; 33) | 955 | 14 (1; 99) | 68.2 |
| LL | 40 | 8; 9; 23 | 205 | 3 (1; 20) | 638 | 12 (1; 66) | 72.5 |
| ES | 34 | 4; 7; 23 | 210 | 3 (1; 30) | 410 | 6 (1; 62) | 58.8 |

Note that some seals moved between basins over the years and are then counted in both basins. Abbreviations: PS = Pohjois-Saimaa, PEV = Pyyvesi-Enonvesi, KV = Kolovesi, JV = Joutenvesi, HV = Haukivesi, PUV = Puruvesi, PV = Pihlajavesi, KS = Katosselkä-Lepistöselkä-Haapaselkä, LL = Lietvesi-Luonteri, ES = Etelä-Saimaa, M = male, F = female, U = undetermined sex, min = minimum, max = maximum.

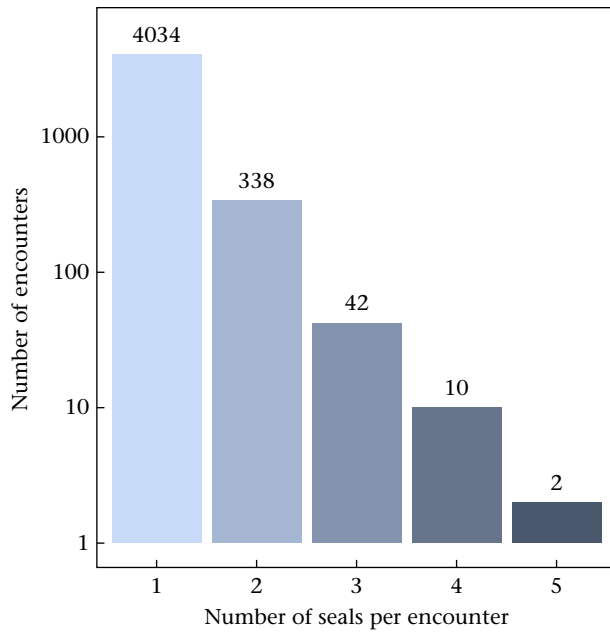


Figure A1. Frequency distribution of Saimaa ringed seal group size during the moulting season. The number above each bin corresponds to the number of encounters for this bin. Note that mother–pup pairs are not included. Number of encounters (Y axis) is given in logarithmic scale.

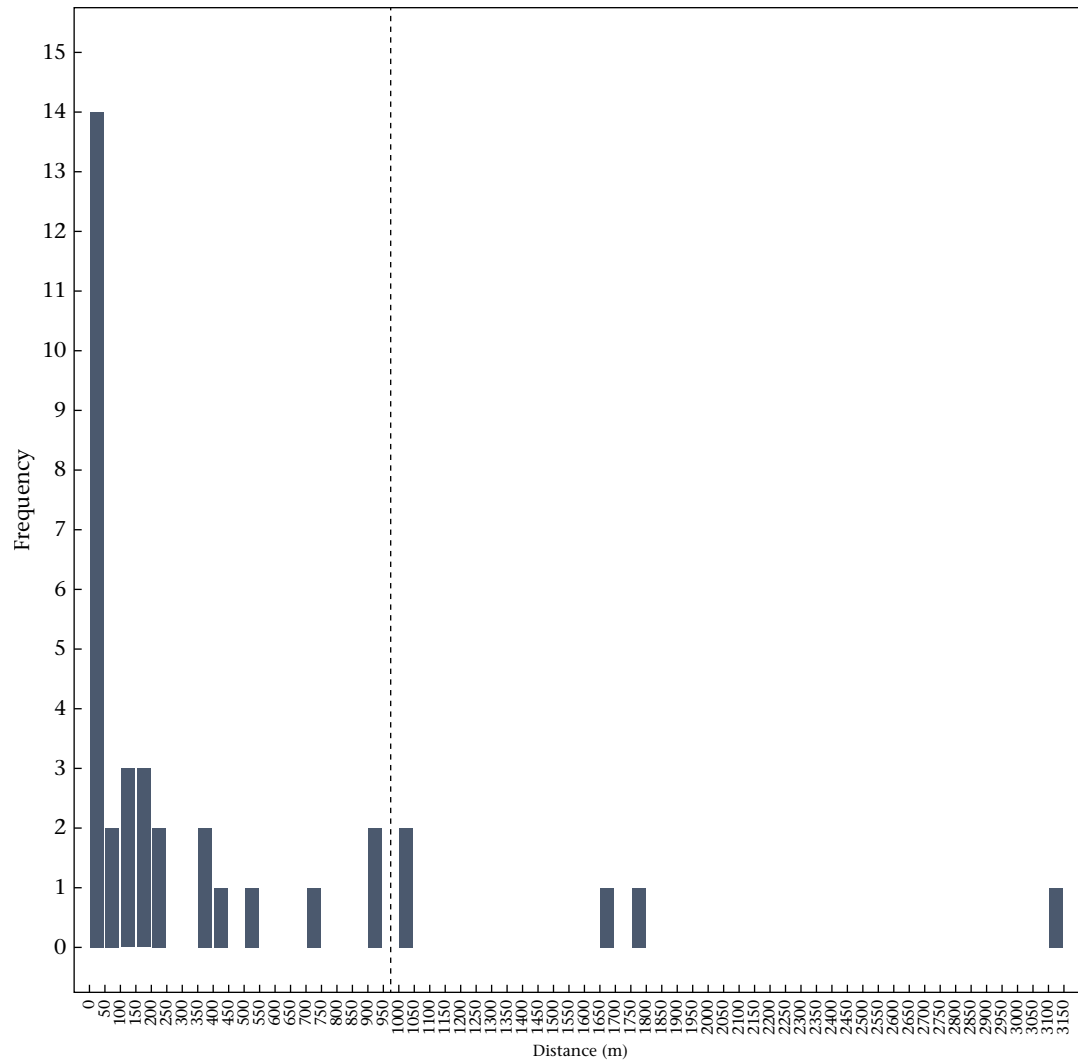


Figure A2. Frequency distribution of the distance between co-occurring locations for the 21 dyads presenting multiannual co-occurrences. The dashed line indicates the median distance between successive moulting sites (982 m) used in different years by Saimaa ringed seals (Biard et al., 2022).