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Frenemies in Fur: neighbour–stranger discrimination and the 'dear enemy' effect in mammals, and how it relates to sociality

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Neighbour–stranger discrimination, where territorial individuals distinguish between familiar neighbours and unfamiliar strangers, is a well-documented phenomenon in the animal kingdom. It often manifests as a 'dear enemy' strategy, where territory holders respond more aggressively towards strangers than neighbours, although a 'nasty neighbour' strategy with the opposite tendencies has also been described. A connection between neighbour–stranger discrimination and animal social systems has not previously been considered, but such an association might be expected if social species were more likely to show neighbour–stranger discrimination due to a potentially higher level of individual recognition in line with the social intelligence hypothesis. Here, such an association is explored through two different approaches. (1) We critically reviewed 63 studies, involving 48 different mammal species with varying degrees of sociality, across 23 families and 5 orders, that conclusively tested neighbour–stranger discrimination. No link between social system and neighbour–stranger discrimination or behaviour was found. (2) We investigated neighbour–stranger discrimination in the distinctly solitary American mink, *Neogale vison*, observed at three different research areas in Iceland, by analysing 50 unmanipulated direct encounters between feral American mink, with 32 distinct pair combinations. These observations revealed strong evidence for dear enemy behaviour. The findings uncover that neighbour–stranger discrimination is prevalent across territorial mammalian species, irrespective of differences in social systems. This emphasizes the adaptive value of individual recognition, neighbour–stranger discrimination and behavioural modifications towards territory intruders based on identity, highlighting the complexity of social interactions and territorial dynamics even in solitary species. In addition, adherence to a dear enemy or nasty neighbour strategy is variable, influenced by multiple factors, and underscores the significance of individual recognition and aggression modulation in broader contexts, including invasive species management and self-recognition research. Future research should focus on documenting discrimination in hitherto underrepresented taxa and elucidating behaviour patterns under varying conditions.

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Understanding the spatial distribution and territorial behaviour of animals is essential for comprehending the complexities of animal cognition and social systems, and the evolutionary and environmental factors that shape them. Spatial divisions of individuals or groups of animals determine their access to critical resources such as food, shelter, mates and breeding sites, and therefore play an essential role in survival and reproduction (Nordell & Valone, 2021). The ideal free distribution model (Fretwell & Lucas, 1970; Krivan et al., 2008) describes how animals might distribute themselves among habitats based on both habitat quality and availability due to species distribution itself. This should result in approximately equal fitness of each individual no matter where they settle, with density reflecting patch richness concerning important resources. Unsurprisingly, many animals prefer to reside in a particular area for extended periods, as familiarity with the immediate surroundings provides numerous benefits (Piper, 2011). Thus, an

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individual can settle in an area and establish a home range (Burt, 1943), typically defined as the area normally used for daily activities. Such areas are not necessarily defended, and home ranges can overlap between numerous individuals of the same species. In contrast, territories refer to the exclusive use of an area, comprising the whole home range or only part of it, defended by an individual, pair or group (Adams, 2001; Burt, 1943; Hinsch & Komdeur, 2017; Maher & Lott, 1995).

Although direct aggression can be a crucial part of territory defence and contests over resources, nonaggressive tactics can be no less pivotal insofar as they can prevent the costs of fighting such as energy loss, injury and death (Duque-Wilckens et al., 2019; Hinsch & Komdeur, 2017; Ord, 2021). Hence, individuals often show a variety of behaviours of different aggression intensity levels when defending a territory (Nordell & Valone, 2021). Numerous game theory models of aggression have been developed to better understand the variability in aggression in animal contests and the factors influencing the associated decision making, such as the hawk–dove game (Maynard Smith, 1982), and models that include a difference in resource-holding power of opponents (Parker, 1974) such as the war of attrition model (Bishop & Cannings, 1978; Hammerstein & Parker, 1982; Maynard Smith, 1974; Mesterton-Gibbons et al., 1996) and the sequential assessment model (Enquist & Leimar, 1983). Differences in size, strength (e.g. due to health and energetic reserves), weaponry and experience (e.g. as a result of age or the winner/loser effects, Landau, 1951; Lindquist & Chase, 2009; Mesterton-Gibbons, 1999) can explain variation in resource-holding power and the outcome of contests (Briffa & Sneddon, 2007; Parker, 1974). In addition, the subjective net value of the resource in question has an important impact on whether, and to what extent, animals fight (Dugatkin, 2019).

In order to minimize physical confrontations over territories and thereby reduce the cost of maintaining ownership, animals employ several behavioural tactics and recognition systems to communicate about their presence and state, and to identify and evaluate conspecifics. Vocalizations, visual displays and olfactory cues are widely used for this purpose (Bradbury & Vehrencamp, 2011; Stegmann, 2018). Furthermore, spatial memory might serve an important role in territory ownership (Araya-Salas et al., 2018). The role of intruder identity in reducing aggression in territory owners has received growing attention. Darling (1952) proposed that territories could be viewed as a kind of social network and Fisher (1954) suggested that territorial neighbours among passerine birds could be considered as dear enemies. Numerous studies have since shown the 'dear enemy effect' (or phenomenon), where territory owners respond less aggressively towards known neighbours than to strangers (Christensen & Radford, 2018; Temeles, 1994; Werba et al., 2022; Ydenberg et al., 1988). This behaviour has been described to a large extent in birds, but also in mammals, amphibians, reptiles, fish and various invertebrates such as insects and crustaceans (Christensen & Radford, 2018; Werba et al., 2022). Although several different mechanisms for this behaviour have been proposed (Getty, 1987; Temeles, 1994; Ydenberg et al., 1988), the aggression intensity of territory owners is most probably linked to the perceived level of threat imposed by the intruder. Thus, a neighbour with an already established territory signifies a lower threat than a stranger who might lack a territory and try to procure an area. Interestingly, the level of threat by neighbours can in some specific instances be greater than that of strangers (e.g. during the breeding season). In such cases, the 'nasty neighbour' phenomenon has been documented, where territory owners respond more aggressively towards neighbours than to strangers (Muller & Manser, 2007). Although the dear enemy effect is seemingly widespread, it should therefore not be viewed as a fixed outcome of neighbour–stranger discrimination, and within species neighbour–stranger behaviour has been shown to be influenced by factors such as population and territory density, seasonal changes such as breeding cycles and seasonal variation of resources, encounter location and sex (Christensen & Radford, 2018).

Individual recognition (either true or binary, Gokcekus et al., 2021; Tibbetts & Dale, 2007) is of course a prerequisite of differentiating behaviour towards neighbours and strangers. It has been suggested that individual recognition can affect group formation and structure (Rios & Kraenkel, 2017) and social relationships (Wascher et al., 2018). Hence, it is possible that neighbour–stranger discrimination might be more widespread among group- or pair-living species insofar as they may have evolved a more discerning level of individual recognition than solitary species. Such tendencies would be in line with the social intelligence hypothesis, which is receiving growing support (Speechley et al., 2024). Whether, and how, the sensitivity of neighbour–stranger discrimination relates to the differences in social systems between species has, however, not previously been explored. Investigating the acuity of neighbour–stranger discrimination in mammals could prove to be revealing in this context, as this Class exhibits great variability of social systems, from solitary to eusocial structures (Prox & Farine, 2020). However, there has been no previous critical review of neighbour–stranger discrimination among mammals with regard to their social systems.

Unsurprisingly, studies on neighbour–stranger discrimination have employed a variety of methods, reflecting the diverse individual recognition adaptations found in animals. Approaches have been either indirect, such as experiments using audio or olfactory stimuli, where recordings or scents from neighbours and strangers are strategically presented to the study subject, or direct, involving observations of face-to-face encounters in test arenas or unmanipulated natural settings (Temeles, 1994). Interpreting animal behavioural responses can be subject to various biases (Martin & Bateson, 1993), including observer bias (Freeberg et al., 2024; Tuyttens et al., 2014), confirmation bias (Marsh & Hanlon, 2007), cognitive bias (Nematipour et al., 2022) and even bias due to STRANGE study subjects (Webster & Rutz, 2020). Such biases may be relevant when inferring the emotional state of animals in neighbour–stranger discrimination studies, especially when applying indirect approaches (Stamps, 2018). However, whether methodology influences the outcomes of neighbour–stranger discrimination studies has not yet been investigated. To explore a potential link between neighbour–stranger discrimination and social systems, a possible effect of different methodological approaches needs to be ruled out.

The American mink, *Neogale vison*, in Iceland provides an unusual opportunity to understand further the role of social systems in neighbour–stranger discrimination. American mink are strictly solitary, small, sexually dimorphic, semiaquatic, generalist, cryptic, territorial carnivores of the Mustelidae family, native to North America (Dunstone, 1993; Wilson & Mittermeier, 2009). Due to both accidental escapes and intentional releases from mink farms throughout the world, feral American mink are now established in at least 23 countries outside their native range (Wilson & Mittermeier, 2009) and are widely considered an invasive species with negative impact on native fauna and biodiversity (Bonesi & Palazon, 2007; Genovesi et al., 2012; Kumschick et al., 2015; Nentwig et al., 2018). This is the case in Iceland, where American mink were imported in 1931 and have been established since the 1940s (Stefansson et al., 2016). The Icelandic ecosystem is greatly influenced by its isolated position in the North Atlantic, comprising relatively few species. Most notably, only two terrestrial mammal carnivores, the native Arctic fox, *Vulpes lagopus*, and the invasive American mink, inhabit the island (Hersteinsson, 2004). Intraguild competition is therefore minimal, possibly allowing the American mink to reach higher densities in Iceland than within either its

native range or other invaded areas, and thus to encounter both neighbours and strangers frequently.

Comprehensive understanding of neighbour–stranger discrimination in mammals and its underlying mechanisms can enhance insights into the evolution of individual recognition systems, nonaggressive behaviour and social connections. The aim of this study was to test the hypothesis that the sensitivity of neighbour–stranger discrimination is associated with social system, and specifically that it is more prominent in social than in solitary mammal species, insofar as the former might have evolved a more discerning level of individual recognition. This hypothesis was tested through the application of two approaches. (1) We conducted a critical review of published studies on neighbour–stranger discrimination in mammals with a focus on whether neighbour–stranger discrimination can be connected to specific social systems. In addition, we explored whether study design might have influenced the outcomes of these studies. (2) We analysed data from four behavioural studies on American mink in Iceland regarding neighbour–stranger discrimination, to answer whether this very solitary species (that has often been described as aggressive) shows neighbour–stranger discrimination, and what factors might influence the observed behaviour.

METHODS

Literature Review

Neighbour–stranger discrimination in mammals was reviewed by conducting a search in Web of Science Core Collection on 11 October 2022 with the search string: (Dear Enemy*) OR (Nasty Neighbour*) OR (neighbour–stranger discrimination*) (TOPIC). This search returned 376 papers. In addition, all papers included in the analysis of the recent review on the dear enemy effect by Werba et al. (2022) were added and duplicates removed, which left a total of 460 papers. All abstracts of the 460 papers were read, and 60 research papers on mammals identified. These 60 papers were read in their entirety, and when they cited research on mammals that seemed relevant but was not already included in our list, those papers were added to the analysis. A total of 78 studies therefore underwent full examination. Studies were analysed with regard to: (1) whether the species in question showed neighbour–stranger discrimination; (2) the type of neighbour–stranger behaviour, categorized as dear enemy, nasty neighbour, mixed strategy or no/inconclusive neighbour–stranger discrimination; (3) the social system of the species, as described in the given research paper, categorized as social (groups or pairs), solitary, or moderately social/flexible when a species was neither strictly social nor solitary (if the social system was not described in the given research paper, mammalian compendia or encyclopaedias were used to obtain this information); (4) the study implementation with regard to sex studied, settings (natural or captive), manipulation (present or absent) and type of confrontation (audio playback experiment, olfactory experiment, physical confrontation in test arena, physical confrontation in natural settings, or other). Fisher's Exact Test for Count Data with 10 000 Monte Carlo simulations was used to test for association between the different variables, using R (R Core Team, 2023). The data set did not accommodate meaningful testing for phylogenetic correlations, as some species groups comprised only a few cases. In statistical tests on social systems, each species was only counted once ($N = 48$). In statistical tests on study implementation each study was counted, but true duplicates (studies that did not differ in any aspect of all factors under consideration) were removed ($N = 59$).

American Mink in Iceland

Behavioural data on mink were obtained in three separate study areas in Iceland: one freshwater habitat at Sog river system (south Iceland, 64°02′N, 20°58′W) in 1996–2000 and two different coastal habitats, Lonakot on the Reykjanes peninsula (southwest Iceland, 64°02′N, 22°05′W) in 1997–1999 and Kolgrafafjordur on the Snaefellsnes peninsula (west Iceland, 64°57′N, 23°05′W) in 2003–2004 and 2006–2007 (Fig. S1 in Supplementary material 1). The Sog river system area is characterized by somewhat dense vegetation cover, dominated by downy birch, *Betula pubescens*, non-native conifers, tea-leaved willow, *Salix phylicifolia*, and various herbaceous plants. Such vegetation can provide cover and shelter for mink but makes direct observations of behaviour challenging. It has a rich birdlife, consisting of both waterfowl and waders, and thriving fish populations, all important food sources for the American mink in Iceland (Magnusdottir et al., 2012). The Lonakot area is a rocky coast habitat with numerous large tidal pools, where marine prey gets trapped during low tide and is easily accessible for the mink. Apart from an unusually lush tidal zone, it is very sparsely vegetated, as it consists mainly of lava fields with some moss and lichen, in addition to patches of heavily grazed, thus very short, grasses. The lava fields provide plentiful opportunities for dens and burrows. The Sog river and Lonakot areas are both considered prime habitats for American mink in Iceland. In contrast, the Kolgrafafjordur area mainly consists of gravel beaches, relatively poor in prey for the mink, and grazed grasslands, and is generally not considered an optimal mink habitat in terms of prey and den availability. Descriptive photos of all research areas are found in Figs. S2-S8.

Mink were captured in wire mesh cage live traps (Tomahawk Live Trap Company, https://www.livetrap.com) baited with capelin, *Mallotus villosus*. Mink were tagged with intraperitoneal radiotransmitters (Telonics, Telemetry-Electronics Consultants, https://www.telonics.com), which have no detectable impact on the streamlined body shape of the mink and are recommended for long-term telemetry studies on the species (Zschille et al., 2008). Mink were immobilized with the inhalant isofluran (Forene, Abbott Laboratories, https://www.abbott.com), then anaesthetized by intramuscular injection of a mixture of ketamine hydrochloride and xylazine (Fuglei et al., 2002). The surgical procedure followed Arnemo et al. (1997). Mink were sexed and aged during surgery, and categorized as juveniles until they reached sexual maturity (<9 months) or adults (≥9 months), according to veterinary inspection of the baculum, teats, teeth and fur. Mink were released at the location of capture, typically the day after capture and surgical intervention. Locations were obtained using handheld receivers (TR-4 and TR-5, Telonics) and either two or three element Yagi antennas (e.g. RA-14K, Telonics), with a combination of triangulation and homing-in techniques (White & Garrott, 1990). Average location accuracy was estimated to be <5 m at Lonakot and <10 m at Sog river system and Kolgrafafjordur. During data collection, mink were located and observed in the field multiple times within a given day, and at different times throughout the 24 h solar cycle. Stringent measures were implemented to minimize observer interference with radiotagged mink, thereby aiming to ensure the documentation of undisturbed natural behaviour.

Behavioural data on neighbour–stranger discrimination in mink were obtained in conjunction with collecting data on habitat utilization, home range sizes and activity as part of other studies. As solitary animals, mink are typically not engaged in social activities and most observations included single animals. However, when two or more individuals that were not part of a family during female rearing (May–July) were directly observed together,

the interaction was documented in detail. Interactions were categorized in three types: (1) aggressive (agonistic), when mink showed clear signs of aggression such as fighting and/or screaming at each other and/or chasing one another at a very fast pace; (2) neutral (nonagonistic), when mink were seen within a distance of 2–15 m from each other and were very probably aware of the other mink (due to close proximity, or behaviour such as looking or sniffing in the direction of the other mink) without any signs of aggression or other change in their behaviour; (3) friendly (nonagonistic), when mink showed apparently friendly behaviour, such as sharing a den simultaneously within 1 m from each other for at least 15 min or travelling slowly together 0–3 m apart for a distance of at least 50 m.

In addition, the identities of the mink engaged in each encounter were documented. Tagged mink were of known sex and age and were resident in the research area. Untagged mink were sexed visually in the field when possible, by clear size difference of sexes, and were assumed to be floaters or newcomers, thus nonresident strangers. A targeted trapping protocol aimed to minimize the likelihood of untagged mink establishing residency undetected. Social encounters were grouped according to interaction category (aggressive, neutral and friendly) and participant identity (resident+resident, resident+stranger, stranger+stranger) and the association tested with Fisher's Exact Test for Count Data in R (R Core Team, 2023).

Ethical Note

The field studies on mink were approved by the Chief Veterinary Officer at the Icelandic Food and Veterinary Authority (1996–2000) and the Icelandic Food and Veterinary Authority (2003–2004, 2006–2007), licence no. UMH02050139/13-4-1/MBS and no. 0906–1102. During field studies, care was taken to prioritize the welfare of the subjects. All live traps were strategically placed in sheltered locations, further concealed with stones and vegetation for added protection. Fresh grass or hay were provided inside traps for additional shelter, along with sufficient bait to sustain a captive mink for at least 24 h. Baited live traps were checked at a minimum of once daily and often more frequently, to ensure the well-being of captured individuals. All surgical procedures involving the implantation of radiotransmitters were conducted by licensed veterinarians in professional settings. Mink were transported to the vet on the day of capture and typically released back into the wild on the next day. This approach aimed to minimize disturbance to both the tagged animals and to the territorial system of the study area. Mink showed rapid recovery after surgery, with 1–2 days generally sufficient for mink to resume natural behaviours. Total trap mortality for all studies was 0.9%, surgery mortality was 6.5% and post release mortality was 3.4% (mortalities within 1 week after surgery). Most mortalities occurred at the Lonakot research area in autumn 1998, when mink were, for unknown reasons, in worse body condition than at other times (see Table S1 in Supplementary material 1 for detailed information on mortalities related to all studies). It should be noted that mortalities other than study-related in mink in Iceland can be quite high during the autumn and winter, at around 10% per month (Stefánsson et al., 2008), due to natural mortality and mink hunting. Post release, efforts were made to avoid influencing or disturbing the animals during data collection, emphasizing a commitment to documenting their natural behaviour. At the conclusion of each study, humane endpoints were carefully considered, and despite the invasive status of mink in Iceland the research team decided to let nature take its course regarding the tagged mink. Therefore, tagged mink still alive at the end of the projects were left to their natural fates.

RESULTS

Literature Review

Of the 78 studies on mammals that underwent full analysis, 63 studies, involving 48 different mammal species of 23 families and five orders, conclusively tested neighbour–stranger discrimination. The majority of species belonged to the order Rodentia (52%), followed by Carnivora (21%), Primates (19%), Lagomorpha (6%) and Hyracoidea (2%). The 63 studies were published during the period 1967–2022 (Fig. S9). In total, 85% of species showed clear neighbour–stranger discrimination (Table 1). In most cases this involved the dear enemy phenomenon (56%). There was no significant difference between social systems regarding either neighbour–stranger discrimination ($P = 0.724$) or neighbour–stranger behaviour ($P = 0.574$). For the three orders with sufficient sample size for statistical testing (Rodentia, Carnivora and Primates) there was no significant difference between orders concerning neighbour–stranger discrimination ($P = 0.232$) and neighbour–stranger behaviour ($P = 0.813$). A full list of the 63 studies and species involved is provided in Supplementary material 2.

Natural study settings (59%) were more common than captive (41%) in the 63 studies. The majority of studies (91%) employed some form of manipulation to test for neighbour–stranger discrimination, the most common being physical confrontations in a test arena (34%), followed by an equal number of studies conducting audio playback experiments (28%) and olfactory experiments (28%). Only four studies (6%) examined neighbour–stranger discrimination in natural settings without any form of manipulation, as a part of the animal's natural behaviour. Most studies (69%) included both males and females in their observations. However, 27% only tested males and 3% only tested females. Sex-related differences in vocalization (seven studies), aggression (three studies), territoriality (two studies) and olfactory behaviour (one study) explained why the given study focused on only one sex, but in seven instances no clarification was given. Thus, choice of methodology explained the one-sex approach in most cases (see Table S3 for further information regarding these studies).

Table 1
Results of the critical review of 63 studies on neighbour–stranger discrimination and behaviour among mammals

	Number of species	Neighbour–stranger discrimination						Neighbour–stranger behaviour							
		Yes		No		Inconclusive		Dear enemy		Nasty neighbour		Mixed strategy		Inconclusive or no NSD	
Social	25	21	(84)	2	(8)	2	(8)	14	(56)	4	(16)	2	(8)	6	(24)
Moderately social/flexible	10	8	(80)	2	(20)	0	(0)	6	(60)	1	(10)	2	(20)	2	(20)
Solitary	13	12	(92)	1	(8)	0	(0)	7	(54)	0	(0)	4	(31)	2	(15)
Total	48	41	(85)	5	(10)	2	(4)	27	(56)	5	(10)	8	(17)	10	(21)

Mixed strategy refers to cases where a population, sex or age group of the same species in the same study showed dear enemy behaviour while another showed nasty neighbour behaviour or no neighbour–stranger discrimination, or the behaviour changed between seasons (see Table S2 in Supplementary material 1 for details regarding mixed strategies). NSD: Neighbour–stranger discrimination. Percentages are given in parentheses.

Study implementation did not influence the outcome with regard to neighbour–stranger discrimination (study settings: $P = 0.888$, manipulation: $P = 0.689$; type of confrontation: $P = 0.779$; sex studied: $P = 0.160$) or neighbour–stranger behaviour (study settings: $P = 0.975$; manipulation: $P = 0.533$; type of confrontation: $P = 0.597$, sex studied: $P = 0.146$). However, there was a significant difference ($P = 0.001$) in research methods with regard to type of confrontation, in connection with which order the species belonged to (see also Table S4 for overview of research approaches within orders and Table S5 for pairwise testing). This difference probably reflected that certain study approaches are more suitable for a given order of animals. All studies were conducted on native species or in laboratory settings; thus, no study in the review was undertaken on a non-native species in invaded habitats.

American Mink in Iceland

In total, 66 mink at the three research areas were caught in live traps and tagged. In addition, untagged mink were seen 59 times. Two or more mink, not part of a family during female rearing, were observed directly together on 50 occasions (Supplementary material 3), the majority of these observations being at the coastal area Lonakot, where the density of mink was much higher than at the other two research areas (Table 2). Most interactions (76%) took place during the juvenile dispersal period in autumn (August–October) and the rest (24%) during the mating season in spring (February–April). Three observations involved three mink, all tagged males.

Interactions involved 15 different resident (tagged) males, 40% of them adult, and one resident juvenile female. Fifteen interactions (30%) included at least one stranger (untagged individual) and 35 interactions comprised resident mink only (70%). Most encounters were male pairs (88%). No encounter involved a pair of females, but six cases (12%) involved a male–female interaction, five of them in autumn (dispersal) and one in spring (mating season). The number of distinct pair combinations was 32. The resident/stranger identity of mink involved in social occurrences affected the type of interaction to a great extent (Fig. 1). This effect was highly significant irrespective of whether we tested all encounters ($P < 0.0001$), only distinct pair combinations ($P < 0.0001$) or only distinct male pair combinations ($P < 0.0001$).

DISCUSSION

The findings of the critical literature review and the case study on American mink in Iceland indicate that the ability to differentiate between neighbours and strangers, and to adjust the behaviour accordingly, is widespread among mammal species and there is no evidence that it is influenced by the social system of the species in question. Even highly solitary species, such as the American mink in this study, show strong neighbour–stranger discrimination.

Our results suggest that methodological variation does not significantly influence neighbour–stranger discrimination or behaviour outcomes in studies on mammals. This finding is critical as it allows us to reject with added confidence the hypothesis that the sensitivity of neighbour–stranger discrimination is associated with social system. Furthermore, general trends across species were robust, with consistent patterns observed in all three mammal orders with the largest data sets (Rodentia, Carnivora and Primates). Thus, the inability to test or correct for possible phylogenetic correlations (due to data set limitations) is unlikely to have impacted our conclusions. However, solitary species comprised only 27% of the reviewed species, underscoring the unique contribution of the American mink case study. Notably, this study

Table 2
Comparison of research areas in Iceland where mink were radiotagged for behavioural studies in 1996–2007

Research area	Habitat type	Fieldwork start	Fieldwork end	Active days in the field	Hours in the field	Trap nights	New mink caught	Untagged mink seen (occasions)	Occurrences of 2 or more mink seen together	Length of trapping area (km)	Density index
Lonakot	Coastal	16 Aug 1997	9 Mar 1999	196	1176	793	23	51	45	1.6	18.13
Sog river system	Freshwater	8 Sep 1996	2 Jun 2000	396	2376	2906	37	8	5	5.5	2.31
Kolgrafafjordur	Coastal	27 Aug 2003	19 Mar 2004	102	612	1775	1	0	0	11.4	0.05
Kolgrafafjordur	Coastal	24 Aug 2006	6 Feb 2007	88	528	396	5	0	0	11.4	1.11
Total				782	4692	5870	66	59	50		

The density index was calculated as: number of new mink caught ÷ trap nights ÷ length of trapping area × 1000.

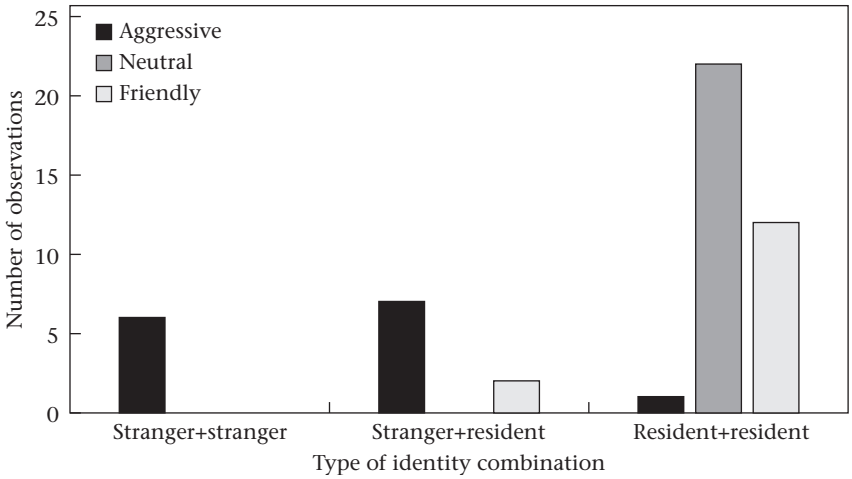

Figure 1. Mink encounters grouped according to type of interaction (aggressive, neutral and friendly) and type of mink identity combinations involved in the encounter. Mink showed clear aggression reduction towards their known neighbours, thus displaying a prominent dear enemy effect. The only aggressive incident between two resident mink was between two juvenile males and took place at the Sog river system research area, where densities were considerably lower than at the coastal Lonakot research area, where the majority of encounters were observed. The only friendly encounters with a stranger+resident combination included two cases of male–female pairs.

employed direct, unmanipulated confrontations, a rare methodology for solitary species that minimizes potential biases and strengthens certainty in the observed behavioural patterns.

Our findings are especially interesting when considered in the context of individual recognition. Recognition systems are fundamental to numerous essential functions in the lives of animals and occur across a wide spectrum of processes (Gokcekus et al., 2021; Tibbetts & Dale, 2007). Kin and mate recognition systems have received particular attention (Sherman et al., 1997) but other noteworthy cases include recognition of self, sex, friend, rival, species, predator and prey (Brecht & Nieder, 2020; Carlson et al., 2020; Ferrari et al., 2008). In line with the social intelligence hypothesis (Johnson-Ulrich, 2018; Speechley et al., 2024), it would not have been surprising to find neighbour–stranger discrimination to a lesser extent in solitary than social species, as the hypothesis proposes that the challenges of social interactions, such as cooperation, competition and social bonding, are main drivers in the evolution of cognitive skills, resulting in social animals being more likely to show greater cognitive abilities (such as higher levels of individual recognition) than solitary species. As we demonstrate that this is not the case with regard to neighbour–stranger discrimination, these results underline the necessity of looking at multiple selective forces to understand evolutionary drivers of cognitive abilities (Holekamp, 2007). Possibly, one such driver is territoriality in itself, irrespective of social system, as evaluating, establishing and maintaining a territory involves many challenging situations (Dugatkin, 2019; Ord, 2021; Sherratt & Mesterton-Gibbons, 2015) that might create selective pressure on cognitive abilities. This might be especially true when it comes to individual recognition. Furthermore, the social environment that even solitary territorial species find themselves within, which shapes their capabilities in an evolutionary perspective (and can be viewed as a kind of social network; Darling, 1952), should not be underestimated. Thus, the findings highlight the adaptative value of individual recognition and aggressive behaviour adjustments based on territory intruder identity, regardless of social systems.

The widespread distribution of neighbour–stranger discrimination among diverse mammal families (Fig. 2) emphasizes and supports the adaptative significance of the behaviour. Every family containing a species included in the review exhibited at least one representative species demonstrating neighbour–stranger discrimination. Thus, even in cases where certain studies within a family reported no evidence of this behaviour, another species within the same family did display it. Although some species groups did not contain any representatives in the review (uncoloured or unincluded species groups in Fig. 2), it should be noted that this does not necessarily mean that these species groups do not show neighbour–stranger discrimination or high levels of individual recognition. All that can be inferred from this lack of presence is that these species have not yet been studied with regard to neighbour–stranger discrimination. If an animal is not territorial, researchers will probably have been unlikely to design a study that tests it for neighbour–stranger discrimination, but that is no reason to infer that it does not have high levels of individual recognition. This might, for example, apply to several species of toothed whales (Au & Hastings, 2008).

Assuming that neighbour–stranger discrimination is based on individual recognition and considering that such cognitive abilities might involve an underlying genetic mechanism, the prevalent presence of neighbour–stranger discrimination throughout the mammalian evolutionary tree is particularly interesting when the time since divergences between orders where neighbour–stranger discrimination is present is considered, since a common ancestor would be more than 100 million years old (Graphodatsky et al., 2011). Of course, it would not be surprising if territoriality was this ancient. Whether the discriminatory ability shares a common ancestral origin or has independently evolved on multiple occasions throughout the evolutionary history of mammals is an open question. Finding the genes that underly this capability or directing future research toward taxa where neighbour–stranger discrimination has not yet been studied would offer valuable insights for answering it. The fact that the dear enemy effect, and thus neighbour–stranger discrimination, has been observed in many nonmammalian taxa (birds, amphibians, reptiles, fish and various invertebrates; Christensen & Radford, 2018; Werba et al., 2022) points towards the ability having multiple independent origins among the animal kingdom, but that does not exclude the possibility of common ancestral roots within mammals.

The prominent dear enemy effect that we observed among mink in Iceland was unanticipated, insofar as wild and feral American mink are generally portrayed as aggressive towards competitors of both conspecifics and other species (Dunstone, 1993; Podra & Gómez, 2018; Podra et al., 2013; Previtali et al., 1998; Sidorovich & Macdonald, 2001), so neutral and seemingly amicable

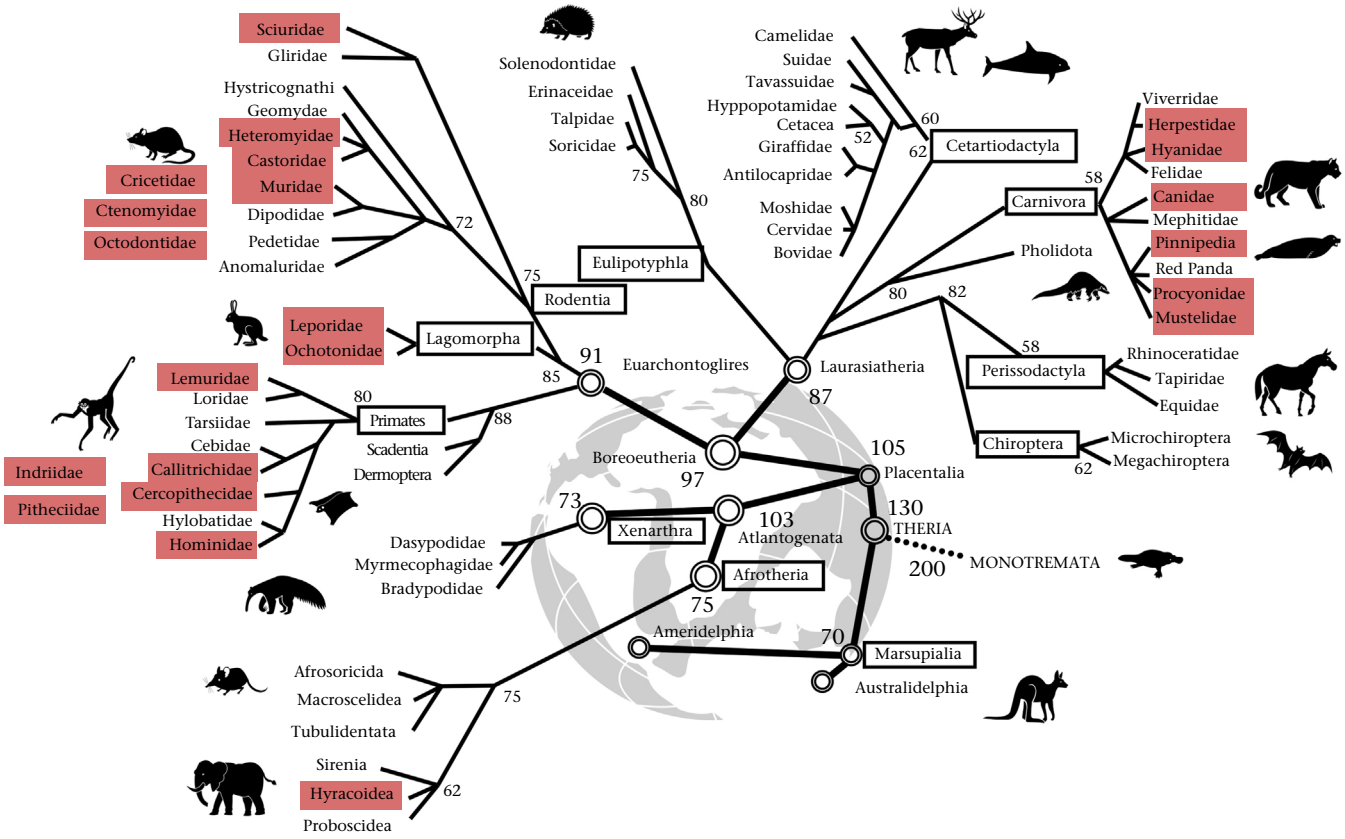

Figure 2. Neighbour–stranger discrimination can be found in diverse species groups among mammals and is widespread throughout the evolutionary tree. Red boxes represent species groups where at least one species displayed neighbour–stranger discrimination in the critical review. Uncoloured or nonincluded species groups represent cases where neighbour–stranger discrimination has not yet been studied. The figure is adapted from Graphodatsky et al. (2011). The tree depicts historic divergence relationships among the living orders of mammals. Double rings indicate mammalian supertaxa, numbers indicate the possible time of divergences (millions of years).

behaviour between both adult+adult and adult+juvenile male pairs was unexpected. As a decidedly solitary, promiscuous species, where both sexes mate with multiple partners during the mating season (Thom et al., 2004; Yamaguchi et al., 2004), male mink do not participate in parental care in spite of overlap of intrasexual territories between the sexes (Dunstone, 1993). It is therefore unlikely that male mink recognize their young, although this has not been tested. Furthermore, the possibility that the male mink involved in the observed interactions were related is minimal due to long-distance dispersals of juveniles in the autumn and to the roaming of males during the mating season in late winter/early spring (Craik, 2008; Dunstone, 1993; Oliver et al., 2016). We would also dismiss the speculation that the reduced aggression we observed could somehow be related to the ancestors of mink in Iceland being farmed. The current feral population is descended from mink that escaped farms in the 1930s, and seems to have mixed little with later escapees (Stefansson et al., 2016). Even though some farmed mink have, in recent years, undergone selective breeding aimed at reducing aggression (Hansen & Moller, 2001), the mink that escaped in Iceland in the 1930s had not experienced such selection.

Field biologists will appreciate that accumulating 50 unmanipulated observations in the wild of encounters between unrelated mink, most of them of the same sex, is exceptional. The vast majority of these observations were made at the Lonakot coastal research area, where mink density was unusually high (Table 2), probably reflecting a very rich and suitable mink habitat (Fretwell & Lucas, 1970; Krivan et al., 2008), and where visibility was good due to limited terrestrial vegetation cover (see Figs. S2–S5) and diurnal mink behaviour (von Schmalensee et al., 2004). Interestingly, the number of observed mink encounters appears to correlate with mink density rather than the time spent observing them (Table 2), suggesting that mink do not actively endeavour to locate one another.

It is noteworthy that the only documented aggressive encounter between two resident mink occurred at the Sog river system, where mink densities were lower than at Lonakot (Table 2, Fig. 1). Thus, it is possible that aggression reduction in mink is density dependent. Although our data are insufficient to support such an analysis, other studies have revealed effects of density and habitat quality on neighbour–stranger discrimination and neighbour–stranger behaviour (Christensen & Radford, 2018). For example, groups of Diana monkeys, *Cercopithecus diana*, in West African primary forest showed nasty neighbour behaviour while those in secondary forest followed the dear enemy strategy. The former lived at high group density, high food availability and low predation pressure, while the latter experienced low group density, low resources and high predation risk (Decellieres et al., 2021). This instance of heightened aggression towards neighbours at high densities is the opposite to our observation of amicable interactions among neighbouring mink at high densities. This raises the caution to be mindful of inter- and intraspecific variation, and behavioural plasticity in neighbour–stranger behaviour (Christensen & Radford, 2018). Nine studies (involving eight species) in our critical literature review demonstrated intraspecific mixed strategies regarding neighbour–stranger behaviour (Table S2) due to differences between the sexes, populations, habitats, seasons or in dominance. Interestingly, we detected no link between social system and

neighbour–stranger behaviour. Thus, underlying causes for an individual to adhere to a specific neighbour–stranger strategy might in many cases be found in other factors than sociality level. Insights derived from inter- and intraspecific variability in neighbour–stranger behaviour unequivocally support the 'relative threat' theory, rather than more simplistic models of reduced aggression being a form of habituation to repeated encounters. Future studies of neighbour–stranger behaviour should first establish whether the species in question discriminates between neighbours and strangers (considering both appropriate situations where animals are likely to display such discrimination and species–specific adaptations for individual recognition), and second distinguish the circumstances and influencing variables under which dear enemy or nasty neighbour strategies manifest, including the relevance of social systems in this regard.

A practical consequence of reduced aggression towards conspecifics at high density could be that non-native invasive species, such as the American mink in Iceland, might achieve even greater densities, and thus do even more damage to local biodiversity, than would otherwise have been expected. A study on the endangered kangaroo rat, *Dipodomus stephensi*, revealed that dear enemy behaviour has positive fitness consequences (Shier & Swaisgood, 2012), suggesting that adopting a dear enemy strategy could also have significant implications for invasive species. Invasive alien species are one of the five most important direct drivers of biodiversity loss worldwide (Díaz et al., 2019) and can cause local and global species extinctions (Pysek et al., 2020; Roy et al., 2023). Invasive species sometimes change their behaviour in novel habitats (Ruland & Jeschke, 2020; Weis & Sol, 2016). The dear enemy effect in invasive mink living in high densities in Iceland might be one such example. None of the studies in our review included an alien species in a non-native habitat. Therefore, potential behavioural shifts in invasive species in terms of reduced aggression towards territorial neighbours merit further investigation.

The widespread ability within mammals to discriminate between neighbours and strangers based on various identification cues, independent of social systems, offers insight into animal individual recognition systems and may have implications for broader aspects thereof, including self-recognition. Traditionally, investigations into nonhuman self-recognition have predominantly relied on the mirror mark (or mirror self-recognition) test (Gallup, 1970), although this has been criticized as being too binary (de Waal, 2019), and too visual and thus unsuitable for species relying heavily on alternative self-recognition stimuli such as odours (Horowitz, 2017) or auditory signals (Brecht & Nieder, 2020). Importantly, only social animals have consistently demonstrated self-recognition by mirror mark test standards, where solitary animals have failed (Lei, 2023). Solitary animals, that rarely see other conspecifics, are however unlikely to depend on visual cues for identifying different individuals, including themselves, and dismissing self-recognition in such species due to failed mirror mark tests should be done with caution, as self-recognition can offer obvious evolutionary advantages (Bekoff & Sherman, 2004; de Waal, 2019). Investigating a possible link between self-recognition and social systems could aid in understanding cognitive evolution and the validity of the social intelligence hypothesis. However, future studies on self-recognition should incorporate methodologies taking account of species-appropriate individual recognition cues, such as those used in neighbour–stranger discrimination studies.

Conclusions

Variable evolutionary forces shape animal cognition. Although the social intelligence hypothesis is receiving growing support (Speechley et al., 2024), other major theories of cognitive evolution are noteworthy and are linked to life history aspects such as mating, obtaining food, innovation, tool use and predation (Cenni & Leca, 2019; van Horik & Emery, 2011; Wooster et al., 2024). Interestingly, territoriality does not seem to have been a focus in understanding the evolution of cognition (Healy & Rowe, 2007; van Horik & Emery, 2011), although Ashton et al. (2020) recently highlighted the importance of considering interactions with conspecific outsiders when investigating cognitive evolution. Given the complexities involved in acquiring and maintaining ownership of a suitable territory, territoriality undoubtedly puts adaptive pressures on cognition as a socioecological driver. As our results indicate that cognitive abilities concerning individual recognition and discrimination are an essential part of being a territorial mammal, even in strictly solitary species, we suggest that territoriality should be given more attention in future research on evolutionary drivers of cognition. This would be in line with the recent call for including to a greater extent the role of natural history in research on animal cognition (Thornton & Truskanov, 2022).

Even though our results appear to contradict the social intelligence hypothesis, which emphasizes the relevance of group size and social interactions within groups or pairs (Dunbar & Shultz, 2007), such an interpretation would be an oversimplification. Instead, our results highlight the social circumstances of being territorial, in solitary and social species alike. Thus, individual recognition and neighbour–stranger discrimination in solitary territorial species has probably arisen due to social pressures from territory neighbours and other territory intruders. This can be viewed as an aspect of social pressures that differs from how these have typically been defined.

Neighbour–stranger discrimination and behaviour in territorial animals offer valuable insights into multiple aspects of animal cognition. Furthering understanding of these behaviours could advance conservation and animal welfare, as well as enhance knowledge of ecological interactions and evolutionary biology.

Author Contributions

Anders Angerbjörn: Writing – review & editing, Conceptualization. **David W. Macdonald:** Writing – review & editing, Conceptualization. **Snæbjörn Pálsson:** Writing – review & editing, Formal analysis, Conceptualization. **Róbert A. Stefánsson:** Writing – review & editing, Investigation, Funding acquisition, Data curation, Conceptualization. **Menja von Schmalensee:** Writing – original draft, Visualization, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Data Availability

Data collected in the critical review on neighbour–stranger discrimination in mammals, and data on mink encounters in Iceland, are available in Supplementary material 2 and 3.

Declaration of Interest

The authors declare there are no conflicts of interest.

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Supplementary Material

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