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Revised Literature Review Part 3: Organized Annotated Bibliography Entries and Summaries

Topic: Social behaviours in Lynx (*Lynx rufus*, *Lynx pardinus*, *Lynx lynx*, and *Lynx canadensis*) with a focus on communication and kinship.

Description of organization:

The annotated bibliographies are organized in three broad groupings: pre-mating behaviour, post-mating behaviour, and broad influences. They are further organized by relevance, based on the date released, with the newest presented last.

Broad Influences

Article citation

Kleiman, D. G., & Eisenberg, J. F. (1973). Comparisons of canid and felid social systems from an evolutionary perspective. *Animal Behaviour*, 21(4), 637–659. [https://doi.org/10.1016/S0003-3472\(73\)80088-0](https://doi.org/10.1016/S0003-3472(73)80088-0)

Article summary

This review examines the differences in social systems between canids and felids from an evolutionary perspective. It highlights that the understanding of the social systems of known social canids and felids is good, but the social systems among solitary species are less understood, and that the knowledge on the evolution of these behaviours is limited. The objectives of this review were to reconstruct the evolution of the social systems in canids and felids and to compare the social organizations and behaviours present in canids and felids. Methods involved examining literature and previous data on canid and felid phylogeny, comparing preferred habitats, diversity, density, and physical and behavioural specializations. They hypothesized that feeding and hunting habits were the major factors that influenced the evolution of diverse and complex social organization systems in both families. They also hypothesized that the separate social structures in canids and felids are derived from different evolutionary sources, pair bonding in canids and maternal based groups in felids. Both groups found different ways to be successful early on in their evolution. They suggested that group formation likely evolved in response to; high prey density, high mobility to follow migratory species, and cooperative hunting increasing kill success. Felids retained specialized hunting methods early in evolution to hunt live prey, so they did not need to group. While canids switched to a pursuit method and an omnivorous diet that benefitted from pack cooperation and allowed for social tolerance when feeding. These differences are seen in the current diversity of both families. The results of this review are significant because it provides insight into what behaviours were most important in both groups evolution compared to their current specializations. Mechanisms of information and what information is being communicated with certain signals were areas highlighted for future research.

Article contribution

This article is relevant to my review topic because it provides a broad evolutionary context to the felid social behaviours I will be examining. It discusses the roles of different morphological features in communication and social interactions in Felids. It also highlights important differences in social behaviours between canids and felids as well as between different species of felids to highlight unique characteristics. Understanding the larger context of behaviour improves interpretation on a smaller scale.

Pre-mating Behaviour

Article citation

Schmidt, K., Jędrzejewski, W., & Okarma, H. (1997). Spatial organization and social relations in the Eurasian lynx population in Białowieża Primeval Forest, Poland. *Acta Theriologica*, 42, 289–312. <https://doi.org/10.4098/AT.arch.97-30>

Article summary

The spatial behaviour of Eurasian lynx has been studied comparatively less than North American lynx species. Since lynxes are largely solitary animals, their spatial behaviour is important to understanding the overall range of the species and the potential distance of communication signals they use. The goals of this study were to estimate the average size of lynx home ranges and their seasonal dynamics, to construct the spatial structure of the population such as range overlap between sexes, and to evaluate the social relationships among individuals. They also discussed factors that impact the spatial structure of the lynx population. This study took place in the Białowieża Primeval Forest using radio-telemetry tracking data. A total of 18 lynx were observed between February 1991 to March 1996. Locations were recorded 5-7 times a week and generalized by dividing the study area into a grid and noting the grid location of the lynx. A total of 1912 radio locations were recorded. The home-range size was estimated for each individual from this data. The frequency of social contact was determined by measuring the distance between separate individuals' locations on the same day. Overall, the results suggested that home-range size of larger in the fall-winter season than in the spring-summer season. This is likely due to a decrease in prey abundance, requiring more territory to find a sufficient source of food. Adult female home ranges were largest in January-February, coinciding with the mating season. Lynx showed a tendency to avoid each other, most lynx interactions were between adult males and females for short durations, or between mothers and their young offspring. Intra-sexual interactions were rare. The results suggested that the spatial systems in lynx are strongly influenced by territoriality but can still be flexible to population shifts and changing environmental conditions.

Article contribution

This article provided results that suggested that male spatial behaviour depended on the distribution of females, while female spatial behaviour depended on food availability and kitten age. Mutual avoidance was an important factor for the lack of social interactions between individual lynxes.

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When this article was published, this was relatively new knowledge for the field since little research had occurred previously. These findings contributed to my review by suggesting influential factors on the specific social behaviours of lynx.

Article citation

López-Bao, J. V., Rodríguez, A., & Alés, E. (2008). Field observation of two males following a female in the Iberian lynx (*Lynx pardinus*) during the mating season. *Mammalian Biology*, 73(5), 404–406. <https://doi.org/10.1016/j.mambio.2007.10.012>

Article summary

Felids are generally solitary species, where interactions between adults are primarily during mating seasons. Lynx home ranges have been shown to have some overlap with individuals of the opposite sex but very little with individuals of the same sex. The purpose of this article was to report significant observations on the behaviour of two males and one female Iberian lynx (*Lynx pardinus*). No specific hypotheses or goals were presented. The behavioural observations were made between February 16th and 18th, 2006 in Donana National Park. The area contained an established population of lynx that is actively monitored with radio collars. The lynxes were located using radio signals and observed visually from a distance. Location tracking data showed the path of the female and the males following her, as well as the inferred home ranges. The two males were observed following the female while displaying mating behaviours such as grunting and repeated scent-marking. The two males ignored each other for the most part. Their gestures occurred in order, with the older, larger males first, followed by the younger, smaller male. This suggested a potential dominance order. The males were found to not be related. The males both copulated with the female in the same dominance order. These observations suggest that the availability of females has a strong influence on the social behaviour of males. It supports that the main factor of social interactions of non-relatives in solitary felids is for either reproduction and territoriality, and often the purpose of territoriality is influenced by reproduction. More research on monogamy versus polygamy in lynx is needed. More continuous visual observational studies of behaviour are needed. Comparisons of social behaviour at different population densities would also benefit understanding in this area.

Article contribution

This article contributes to my review because it provides a specific observation of social interactions between individual lynx, with the specific function of reproductive competition. It also describes a social structure involving a dominance order, which has not been observed much previously in solitary felids. Overall, it provides a concise discussion on social behaviour in lynx driven by reproduction.

Article citation

Vogt, K., Zimmermann, F., Kölliker, M., & Breitenmoser, U. (2014). Scent-marking behaviour and social dynamics in a wild population of Eurasian lynx (*Lynx lynx*). *Behavioural Processes*, 106, 98–106. <https://doi.org/10.1016/j.beproc.2014.04.017>

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Article summary

The behaviour being studied in this article (scent marking) has been widely observed and generally well described but information is lacking on its function in wild populations. This article explores patterns of scent marking and its role in communication among Eurasian lynx (*Lynx lynx*). Scent marking was defined as spraying, head rubbing, scraping, clawing, or licking at a site. The goals of this study were to describe marking behaviour and gain insight into the function of over-marking in the Eurasian lynx. Observations were made using infrared camera traps triggered by motion detection. The study took place in the north-western Swiss Alps. Marking sites were identified along paths frequented by lynx, identified using snow tracking, radio collar, and visual observation data. Data was collected between December 2009 and July 2012. The results showed patterns of marking activity being highest before and during the mating season. Marking activity was lowest after females gave birth and were lactating. Marking occurred in both sexes but was higher in males. Most visits to marking sites were made by resident individuals, while limited occurrences were by non-residents. For the function of over-marking, three hypotheses were suggested. 'Group odour' to recognize group-living species, 'scent masking' to cover the scent of a conspecific, or a 'chemical bulletin board' to display information about individuals. The results suggested that 'chemical bulletin board' was most likely. In this hypothesis, scent-marking sites are where individuals advertise presence, reproductive state and territory. The significance of this is that over-marking is likely a major method of communicating reproductive state, which is essential for species survival. It also communicates territories, which is required for solitary species to hunt successfully. The article states that further studies are needed to better understand the other functions of over-marking in females and other functions of scent-marking.

Article contribution

This article is relevant to my literature review topic because it provides insight into a specific behaviour in lynx that is involved in communication between individuals of the species. It suggests a specific function that scent-marking and over-making behaviour provides in communication and indirect social interactions in lynx. This communication is important in relaying a variety of signals between individuals and helps understand their social behaviours in general. The article advances knowledge in its field and provides good data on an animal that is relatively solitary and difficult to study in the wild.

Article citation

Allen, M. L., Wallace, C. F., & Wilmers, C. C. (2015). Patterns in bobcat (*Lynx rufus*) scent marking and communication behaviors. *Journal of Ethology*, 33(1), 9–14. <https://doi.org/10.1007/s10164-014-0418-0>

Article summary

Social communication in solitary felids is poorly understood but is a critical part of mate selection and raising of young. Social communication in lynx can be difficult to study, but short and infrequent behaviours like scent-marking can be especially challenging. Patterns of bobcat (*Lynx rufus*) scent-marking and communication behaviours were studied to advance understanding. Four main hypotheses

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were proposed which were that courtship and mating would influence visitation and behaviour, visitation would occur only during nocturnal hours except for in winter when searching for prospective mates, that scraping would be used more than urine spraying for marking behaviour, and that olfactory investigation would be used proportionally to scent-marking. Scent-marking was defined as urine spraying, scraping, defecation, claw marking, or body rubbing at marking sites. Olfactory investigation included lowering of the head and nostril flaring. Motion-triggered video camera traps were used between May 2011 and July 2013 at 48 scent-marking areas called "community scrapes". Occurrence and duration of behaviours were recorded. The results of 496 bobcat visits showed peak occurrence in January but no variation between seasons. This suggested that courtship and mating were significant factors for the occurrence of scent-marking. Olfactory investigation was used more than scent-marking, suggesting that olfactory marking signals were more important than visual signals when receiving information. Scraping and urine spraying was used equally, suggesting both behaviours are useful but are likely used for communicating different signals. There was no significant difference in the time visits occurred among seasons. Areas for further research include the use and function of cryptic behaviours like rubbing and studies which follow marked individuals to distinguish differences in behaviours between males and females and different age groups.

Article contribution

This article contributes to my review because it focuses on a specific social behaviour. It provided detail on the occurrence and duration of these social behaviours. The article also provides new insight into lynx behaviour and challenges results of previous research, suggesting scraping is not used more often than urine spraying. It adds to the understanding of scent-marking as a social behaviour in lynx and provides new overall data on this organism.

Article citation

Vogt, K., Hofer, E., Ryser, A., Kölliker, M., & Breitenmoser, U. (2016). Is there a trade-off between scent marking and hunting behaviour in a stalking predator, the Eurasian lynx, (*Lynx lynx*)? *Animal Behaviour*, 117, 59–68. <https://doi.org/10.1016/j.anbehav.2016.04.004>

Article summary

Visual, auditory, and chemical signals are major methods of social interactions in animals. However, these communication signals can result in a cost to the signaler through eavesdropping. This study investigated the potential trade-off of intraspecific communication through scent-marking and the cost of alerting prey in Eurasian lynx (*Lynx lynx*). Three predictions were made; lynx should scent-mark on conspicuous objects, they should increase scent-marking only when socially beneficial, and they should avoid scent-marking in areas where prey is abundant. Radio-tagging of 15 lynx from 2012 to 2014 was used for GPS tracking. Identification of snow tracks was used to locate scent marks and evidence of hunting behaviour. The data supported that lynx preferred conspicuous objects and that marking was more frequent along linear structures such as roads. This could have been due to the lynx using natural barriers to mark territorial boundaries. It's also possible that track-straightness increased chances of interception by other lynx, increasing scent detection. It was found that lynx marked less in areas where hunting behaviour was displayed. The time since the most recent kill did not impact scent-marking frequency. This could suggest that lynx avoid scent-marking while actively detecting prey, but do not

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choose to mark more or less after a kill. Lynxes maintain expansive ranges, so these behaviours could be due to their ability to easily find areas that have not been marked recently to hunt. Results showed an increase of scent-marking during the mating season, supporting the hypothesis that lynx should scent-mark when it is most socially beneficial. Overall, the authors state that the study supports the hypothesis that lynx do face a trade-off between social communication and hunting success. This suggests that scent-marking is influenced by multiple factors and not only the need to communicate.

Article contribution

This article provides clear evidence of a new factor, eavesdropping, which influences scent-marking behaviour, and therefore contributes to my review. New information is contributed to the field, such as the behaviour of increased marking on straight features. The results of lynx choosing conspicuous objects for scent-marking supports previously done research. Overall, the article contributes to better understanding the costs of social communication in lynx.

Post-mating Behaviour

Article citation

Schmidt, K. (1998). Maternal behaviour and juvenile dispersal in the Eurasian lynx. *Acta Theriologica*, 43, 391–408. <https://doi.org/10.4098/AT.arch.98-50>

Article summary

The reproductive rate and success of lynx are relatively low, as in many species of felids. At the time of this study, there was limited information on the behaviour of wild female lynx and how they raise their young. The objective of this article was to present observations on both the behaviour of female lynx with young and dispersal behaviour and routes of juvenile lynx. Eighteen individual lynxes were radio-tracked from 1991 to 1995 in the Bialowieza Primeval Forest. Five adults and six offspring made up the observational data. Lynx were tracked and observed 5-7 times each with separate periods of focused individual tracking and observing. Dispersal was measured using the radio-collar tracking data. Results on inferred den sites suggested females moved their dens to be near their most recent kill until it was completely consumed. This provides evidence of the importance of food resources to many lynx behaviours. The females were found to leave kittens alone for longer periods as they aged. This was likely due to both the need for more food as the kittens grew and the increasing independence of the kittens. When the kittens reached approximately three months old, they would accompany the mother on hunts, largely increasing interaction time. Juvenile lynxes typically dispersed at 9-11 months old. This occurred suddenly and without any initial phase of separation. Generally, females did not disperse as far as males. This has been suggested to be due to an increased tolerance of female offspring remaining near the mother's territory. Family dispersal coincided with the lynx mating season, suggesting a factor of dispersal could be male competition or a shift in adult female interest to a new litter. The author suggests a larger sample size would be required to make more decisive conclusions about lynx behaviour and dispersal characteristics.

Article contribution

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This article contributed to my review by providing substantial background information on felid behaviour in general. It also discussed specific social behaviours of the mother lynx towards her offspring, such as the variation in the amount of interaction time and when she would provide food, either by nursing or by taking kittens to a kill. The results of this study which suggest dispersal of offspring is sudden contradict later studies which find that dispersal is not always sudden but is instead gradual.

Article citation

Naidenko, S. V. (2001). Aggression in lynx adult-cub relations: Can it be a reason for the dissolution of litters? *Ethology Ecology & Evolution*, 13(3), 283–295.
<https://doi.org/10.1080/08927014.2001.9522777>

Article summary

Eurasian lynx (*Lynx lynx*), like most felids, are mostly solitary. The only relatively long-term social grouping of lynx consists of females and their kittens. The goal of this study was to describe interactions between lynx cubs, their mothers, siblings, and lone adult males at different ages. This was done to clarify possible reasons for litter dispersal. Observations were made periodically between 1989 to 1993 on Eurasian lynx in captivity at a wildlife institute in large enclosures of fenced forest. Observations were made from hidden shelters near the enclosures. Six-hour periods of observations were conducted during maximum lynx activity using a continuous recording method to collect data. Observed behaviours included playing, aggression such as growling, lunging, and blows with and without claws, reproductive behaviours such as mounting, sniffing and flehmen, allogrooming and head "butting". Playing was exclusively observed in kittens. Real aggression among kittens was rare and usually corresponds to the presence of solid food. Results of the observations showed that the most stable social interactions are between females and their litters and are based mainly on friendly interactions. These interactions decrease as the kittens aged and the adults re-entered the mating period again, this was a likely contributor to kitten dispersal. Playful behaviours changed to allogrooming and neutral or greeting behaviours as kittens aged. Aggression decreased as they were weaned and increased again when they were feeding at kills but did not increase during dispersal. These results suggest aggression is not the typical reason for the dispersal of lynx litters. The author suggests it could instead be due to resource availability, primarily food. More studies that have a stronger focus on lynx in the wild with less human interaction would provide more accurate data on their natural behaviours.

Article contribution

This article provides reasonably long-term data on lynx interactions in shared and adjacent enclosures in captivity. It contributes to my review by showing specific changes in social behaviour as family dynamics change. Overall social interactions occur most in family groups. Aggression was found to be a relatively rare social behaviour used in both family groups and non-relatives among lynx in captivity, suggesting it does not play an important role in family group dissolution.

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Article citation

Molinari, P., & Molinari-Jobin, A. (2001). Behavioural observations of interactions in a free-ranging lynx *Lynx lynx* family at kills. *Acta Theriologica*, 46, 441–445. <https://doi.org/10.4098/AT.arch.01-49>

Article summary

Eurasian lynxes (*Lynx lynx*) are generally solitary with distinct home ranges. Females give birth near the end of May and generally disperse in February-March in alignment with the next breeding season. This paper describes and discusses the development of interactions between a mother and her two kittens at kills from September 1996 to March 1997. The study took place in the Jura Mountains in Switzerland. The adult female lynx was previously radio-collared. This was used to locate her and her kittens at kills. Visual observations were made from tents located near kills. Feeding presence, succession and aggressive interactions were recorded. Observations occurred from when the kittens were old enough to accompany the mother to kills until the family dispersed. Multiple observations of social interactions were recorded. Generally, a dominance hierarchy was observed between the two kittens and the mother. Initially, the kittens would feed on kills first, followed by the mother. As they aged, the larger of the two kittens displayed aggressive behaviour towards the smaller one in order to feed first. This suggests that social behaviours are strongly influenced by resource availability and physical body condition. Once the kittens were approximately nine months old, the mother began feeding first, followed by the smaller kitten, then the larger one. At ten months, the mother would take the kittens on excursions outside her home range, presumably to aid in the dispersal of the kittens. She appeared to be introducing them to areas with no known resident lynx. The major takeaway the authors discussed was that dispersal in lynx is not caused by female parent aggression. It was suggested that it is instead driven by female abandonment and resource availability. More structured studies involving direct observations but with less human intrusion would be beneficial.

Article contribution

This article contributed to the review on lynx social behaviour because it shows that early in development, age has a strong influence on social behaviours towards relatives, with aggression becoming more common as they age. Resource availability also played an important role and dispersal is generally non-aggressive, but due to female abandonment. This article showed contradictory results to other studies, which suggest that dispersal of young is sudden. While in this study, a gradual increase in kitten independence and roaming away from the mother's home range was observed.

Article citation

Janečka, J. E., Blankenship, T. L., Hirth, D. H., Tewes, M. E., Kilpatrick, C. W., & Grassman, L. I. (2006). Kinship and social structure of bobcats (*Lynx rufus*) inferred from microsatellite and

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radio-telemetry data. *Journal of Zoology*, 269(4), 494–501. <https://doi.org/10.1111/j.1469-7998.2006.00099.x>

Article summary

Social relationships between individual animals are often used to determine the social structure. Relatedness can also have a large influence on the social structure by influencing social interactions, tolerance, dispersal, and territoriality. The goal of this article was to examine the social structure of bobcats (*Lynx rufus*) in southern Texas. Kinship analysis through microsatellites, radiotelemetry, and genetics was used to explore this topic. No specific hypotheses were presented. The study occurred in a wildlife refuge from 1994 to 2001 and included 22 individual cats. Bobcats were temporarily captured, radio collared, blood and hair samples collected, then released. Their location was tracked via GPS for the duration of the study. Genetic material was tested to determine bobcat relatedness in the population. The results of the kinship analysis identified three genetic families among parents and offspring, although full- and half-siblings could not be differentiated. Two of these families were multi-generational. Home-range analysis of the radio-collared cats showed no significant correlation between home-range overlap, home-range proximity, and overall relatedness. However, adult females appeared to tolerate significant home-range overlap with adult female offspring. If there are enough resources, two related females may tolerate a shared home range while raising offspring to increase fitness. This social tolerance for close relatives increases the overall fitness of a specific gene pool. The result also suggested that typically, only individuals with well established/defined home ranges will breed. This also supports hypotheses of male-based dispersal due to intra-sexual competition during the mating season. Juvenile males were found to be the primary dispersers, this resulted in overall higher mean relatedness among females than males since they don't tend to disperse as far. Further studies with a greater number of individuals over a longer period are needed. Comparing social dynamics between related and unrelated individuals would also be beneficial.

Article contribution

This article contributes to my review because it provides indirect data on the occurrence of social behaviours and suggests unique social behaviours used by related individuals. They observed the relationship, distribution, and movement of bobcats within the population. It highlighted the importance of establishing a home range, which requires communication behaviour to form a social structure. Overall, they added knowledge to the field on how relatedness has a strong influence on social structure and behaviour.