

Sociality in a solitary carnivore, the wolverine

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Abstract

The social organizations of animal societies have important implications for several fields of biology, from managing wild populations to developing new ecological and evolutionary theory. Although much attention has been given to the formation and maintenance of societies of group living individuals, less is known about how societies of solitary individuals have been shaped and maintained. Traditionally, the evolution of social organizations in the mammalian order Carnivora has been regarded as a directional selection process from a solitary ancestry into progressively more advanced forms of sociality. In this thesis, I tested this model against an alternative model, assuming radiation from a socially flexible ancestry. I further explored sociality, resource use and dispersal of a solitary carnivore, the wolverine (*Gulo gulo*), in the light of these two evolutionary models. Phylogenetic reconstruction generally supported that carnivore social organizations evolved through directional selection from a solitary ancestor. However, results from captive wolverine females indicated that they may have rudimentary social tendencies, which rather support that sociality in carnivores radiated from a socially flexible ancestry. Wild wolverines in northwestern Brooks Range, Alaska, adhered to the commonly found ecological niche as a largely ungulate dependent generalist carnivore. Lack of sexual asymmetry in dispersal tendencies indicated that resource competition among wolverine females probably was high. I suggest that wolverines have latent abilities to aggregate, but that their phylogenetic legacy in terms of morphology has constrained them into an ecological niche where resource abundance and distribution generally inhibit aggregations. Due to contradictory results, I suggest further research to test evolutionary theory regarding carnivore social evolution, and particularly to explore new avenues into social evolution that better explain intra-specific variation in sociality, as well as formation and maintenance of solitary social systems.



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SOCIALITY IN A SOLITARY CARNIVORE, THE WOLVERINE

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"Do what makes you happy.
It doesn't have to make sense to other people"

W. Zevon (1947-2003)

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Abstract

The social organizations of animal societies have important implications for several fields of biology, from managing wild populations to developing new ecological and evolutionary theory. Although much attention has been given to the formation and maintenance of societies of group living individuals, less is known about how societies of solitary individuals have been shaped and maintained. Traditionally, the evolution of social organizations in the mammalian order Carnivora has been regarded as a directional selection process from a solitary ancestry into progressively more advanced forms of sociality. In this thesis, I tested this model against an alternative model, assuming radiation from a socially flexible ancestry. I further explored sociality, resource use and dispersal of a solitary carnivore, the wolverine (*Gulo gulo*), in the light of these two evolutionary models. Phylogenetic reconstruction generally supported that carnivore social organizations evolved through directional selection from a solitary ancestor. However, results from captive wolverine females indicated that they may have rudimentary social tendencies, which rather support that sociality in carnivores radiated from a socially flexible ancestry. Wild wolverines in northwestern Brooks Range, Alaska, adhered to the commonly found ecological niche as a largely ungulate dependent generalist carnivore. Lack of sexual asymmetry in dispersal tendencies indicated that resource competition among wolverine females probably was high. I suggest that wolverines have latent abilities to aggregate, but that their phylogenetic legacy in terms of morphology has constrained them into an ecological niche where resource abundance and distribution generally inhibit aggregations. Due to contradictory results, I suggest further research to test evolutionary theory regarding carnivore social evolution, and particularly to explore new avenues into social evolution that better explain intra-specific variation in sociality, as well as formation and maintenance of solitary social systems.

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- II. **Dalerum, F., Creel, S. and Hall, S.** Behavioural and endocrine correlates to reproductive failure in social aggregations of captive wolverines.
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- III. **Dalerum, F. and Angerbjörn, A.** 2005. Resolving temporal variation in vertebrate diets using naturally occurring stable isotopes.
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- IV. **Dalerum, F., Kunkel, K., Angerbjörn, A. and Shults, B.S.** Feeding ecology of wolverines in northwestern Alaska: the importance of migrating caribou.
Manuscript
- V. **Dalerum, F., Loxterman, J., Kunkel, K., Shults, B.S. and Cook, J.** Sex-specific dispersal patterns in wolverines: insights from high-resolution microsatellite markers.
Manuscript

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Introduction

The social organizations of animal societies have important implications for the distributions of individual fitness. Knowledge of the ecological and evolutionary mechanisms that underlie and maintain varying forms of social organizations is thus one of the key components for a comprehensive understanding of how evolutionary and ecological processes shape, maintain and restrict animal populations (Clutton-Brock 1988). This, in turn, is fundamental for several fields of biology, from adaptive management of wild populations (Frank and Woodroffe 2001) to developing new theory explaining ecological and evolutionary processes (Pianka 1988).

Carnivora is an intriguing mammalian order, with a wide variety of ecological, behavioral and physiological characteristics. Carnivores have a high position in the trophic hierarchy and often a great influence on large scale ecosystem processes (Ewer 1973; McLaren and Peterson 1994; Noss et al. 1996). They are also often in conflict with human interests (Kellert et al. 1996; Woodroffe 2000; Cardillo et al. 2004). Consequently, research on carnivore ecology has been in the focus for zoologists for decades.

However, research on evolution and maintenance of carnivore social organizations has been heavily biased towards populations living in stable social groups. This is reflected both in developed theory (e.g. Johnstone et al. 1999; Clutton-Brock 2002; Stephens et al. 2005) and in an overwhelming body of research on group living carnivores in the wild (e.g. Mech 1970; Kruuk 1972; Packer et al. 1988; Creel 1996; Creel and Creel 2002). This is quite understandable, since most solitary species are elusive and difficult to study. Nonetheless, this bias hampers our understanding of how ecological and evolutionary processes shape spatial structures and the level of sociality in carnivore populations.

In this thesis, I have explored the evolution and mechanisms behind carnivore sociality, concentrating on a relatively little studied solitary species, the wolverine (*Gulo gulo*). My focus has been threefold. First, using comparative analyses, I tested a generally assumed model of the evolution of carnivore sociality, namely that carnivore social organizations developed through directional selection from a solitary ancestor into progressively more advanced forms of sociality (paper I). Second, using wolverines housed in an artificial captive environment, I tested if dense social aggregations of female wolverines followed predictions from the directional selection model, or if they showed latent social tendencies and adopted to this, for the species novel, social environment (paper II). Third, I studied resource utilization and dispersal patterns in a population of wild wolverines in northwest Alaska, to test if the dispersal patterns in this wolverine population adhere to the general predictions regarding sex-biases in dispersal under relatively homogenous resource distributions for polygynous species, i.e. a male biased dispersal (paper III-V).

The Wolverine

The wolverine is a terrestrial mustelid with a circumpolar distribution, which primarily inhabits tundra and taiga of northern latitudes (Wilson 1982). Our knowledge of ecology, behaviour and social organization of wolverines is still scant in relation to other large carnivores in arctic and boreal areas, although small and fragmented populations, both in the continuous United States and in Scandinavia, recently have generated increased attention to management and research on the species (Weaver et al. 1996; Landa et al. 2000; Rowland et al. 2003; Flagstad et al. 2004).

The wolverine is the largest terrestrial member of the family mustelidae. Wolverines range in size from 10-20 kg, with males approximately 30% heavier than females (Pasitschniak-Arts and Lariviere 1995). It is compactly built, with powerful limbs and a broad head. Colour ranges from brown to black, with a typical pale lateral stripe.

Ecologically, the wolverine has been characterized as an ungulate-dependent carnivore, similar in its ecological role to larger predators such as brown bears (*Ursus arctos*) (Banci 1994). Several studies have emphasized the importance of large ungulates for wolverine populations, particularly as food during winter (Haglund 1965; Rausch and Pearson 1972; Gardner 1985; Magoun 1987; Persson 2003). However, although wolverines have been shown to kill large ungulates (Haglund 1965; Pulliainen 1968; Magoun 1985), they probably mostly feed on them as scavengers (Banci 1994). The diet of wolverines during summer is less well understood, but there are indications that other prey such as microtine rodents may be important (Landa et al. 1997; Paper IV).

The wolverine can be regarded as a typical example of a solitary carnivore. In the wild, it has a social system common among terrestrial mustelids. The territories of males generally overlap territories of both other males and several females, while the territories of reproductive females are exclusive and only overlap with territories of males (Powell, 1979; Hornocker and Hash 1981; Magoun 1985; Banci and Harestad 1990). Social groupings, except for mating pairs and mother and infants, are extremely rarely observed. The mating system is probably polygamous or promiscuous (Banci 1994).

The evolutionary history of sociality in Carnivora (Paper I)

A consensus model of carnivore social organizations assumes directional selection from a solitary baseline into progressively more advanced forms of sociality (e.g. Packer 1986; Gittleman 1989; Creel and Macdonald 1995) (Fig 1a; hereafter referred to as “the directional selection model”). However, the main assumption of this model, i.e. a solitary ancestral state, has never been tested. Further, this conceptual model has been adopted with specific attention to the evolution of group living societies. Evolutionary correlates to solitary societies, as well as species which exhibit a large variation in terms of sociality, are difficult to fit into this framework.

An alternative model would be to assume a socially flexible ancestor to Carnivora (i.e. an ancestor with rudimentary abilities to live in a variety of social organizations), and that present social structures have evolved through radiation from this flexible baseline (Fig. 1b; hereafter referred to as “the radiation model”). This approach may be advantageous for two main reasons. First, the directional selection model assumes directional social evolution from a solitary ancestral state. Hence, it does not well account for evolutionary forces that may act in shaping and maintaining solitary social structures. Second, the radiation model assumes that species are capable of living under a variety of social situations. Since there is no similar inherent assumption of intraspecific variation in the directional selection model, it is less suited to explain species that exhibit large variation in terms of sociality, both within and between populations.

These two models offer testable predictions since they assume competing states of sociality as ancestral for Carnivora. During the past two decades, character traits of extinct ancestors have commonly been reconstructed using data from contemporary species and phylogenetic trees of their relationships (Schultz et al. 1996). These methods have been used to derive the ancestral states of a wide variety of traits; some

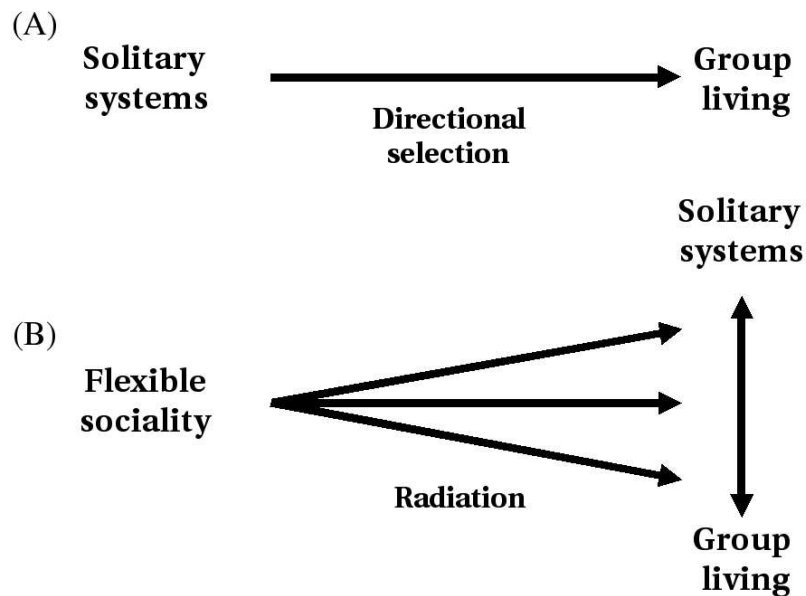


Figure 1. Schematic picture of (A) the traditional model of social evolution in carnivores, based on directional selection from a solitary baseline and (B) an alternative model, based on radiation from a flexible baseline.

of the more innovative uses have included the physiological evolution of enzymes (Jermann et al. 1995) and the evolution of calling behavior in frogs (Ryan and Rand 1995). Two main analytical methods, one based on maximum parsimony criteria and the other on maximum likelihood estimates, have been suggested for phylogenetic reconstructions. Earlier studies typically used maximum parsimony criteria to evaluate the most likely ancestor state at specific nodes (Swofford and Maddison 1987; Maddison 1994). These algorithms simply try to minimize evolutionary change over time, i.e. they find the ancestral states that minimize character transitions throughout the phylogeny. However, although maximum parsimony may be reliable in cases that meet the assumption of equal probability of gains and losses, and in cases that have closely related species, it appears to be unreliable when the rate of character change is high or when there has been much time for evolutionary change (Maddison 1994; Yang et al. 1995; Zhang and Nei 1997). Recently developed maximum-likelihood approaches have been suggested to overcome these shortcomings, and further offer possibilities to quantify the uncertainty of traced ancestral states (Cunningham et al. 1998). These techniques use rates of evolutionary change (either estimated from the data or fixed before analyses) as parameters in evolutionary models that calculate maximum likelihood estimates for the model given specific character states at each node of the tree (Schluter et al. 1997).

In paper I, I tested the competing predictions of a solitary vs. a flexible social ancestor to Carnivora using phylogenetic reconstruction of published data on carnivore social organizations and a previously resolved phylogeny of Carnivora (Bininda-Emonds et al. 1999). I used two separate maximum likelihood reconstructions; one estimating evolutionary rates of gains and losses of traits to be equal, and one allowing separate rates of change, hence fitting one rate of change for gains of traits (forward rate) and one rate for losses of traits (backward rate). I applied the models to two discrete classifications of social organizations; one binary, in which species were regarded as either solitary or non-solitary, and one multistate. In the binary classification, I classed a species as solitary if only the mother is present at the time of parental care, and as non-solitary if any evidence that any

forms of groupings has occurred. In the multistate classification, I used the previously described definition for solitary species, but classed species as pair living if both parents are present and as group living if more than one adult female or if more than two adults are present. I further incorporated social flexibility as a specific trait by classing species that exhibit more than one of the previous classes as flexible.

Two-rate maximum likelihood models provided significantly better fit than one-rate models. One-rate models failed to provide support for ancestral states for either the binary or the multistate classification. However, a two-rate model provided firm support for a solitary ancestor if a binary classification was used (Fig 2a), although it failed to provide support for any ancestral state using the multistate classification (Fig 2b). Further, two-rate models estimated forward rate of change to be substantially higher than backwards. Hence, phylogenetic reconstruction generally supported the prediction of directional selection.

Social crowding and its consequences for reproductive success among captive wolverines (Paper II)

Under the directional selection model, socially related traits can be predicted to be fixed, so that animals show few tendencies to adapt to novel social environments. In solitary species, this could include high levels of aggression and stress when subordinates are unable to escape direct presence of dominant individuals. The radiation model, on the other hand, assumes social tendencies in most species. Many of the behavioral and physiological traits found in complex social societies might then be present in less well-developed forms even in solitary species. These traits can, in that case, be regarded as reaction norms that may be modulated by the social environment.

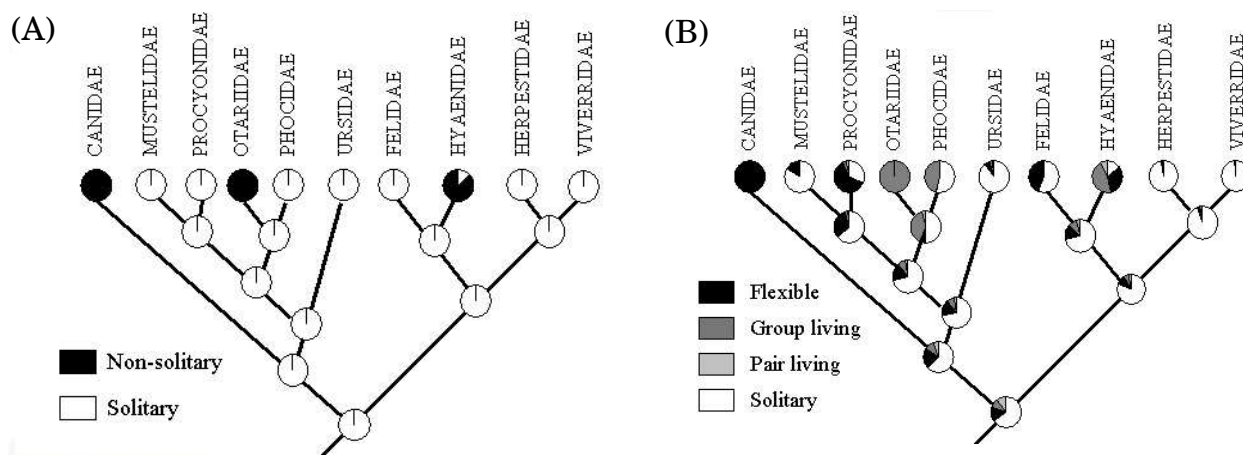


Figure 2. Phylogenetic trees of Carnivora, collapsed to family level, with the ancestral state of social organisations traced with a two-rate maximum likelihood model and a binary classification of social organizations (A), and a multistate classification of social organizations (B). Each node in the trees is represented by a bar graph showing the proportion of total likelihood for each class of social organisations. A higher proportional likelihood for a class indicates a higher probability that that class was ancestral at that node. A likelihood ratio of 7.4:1 approximates a 95 % confidence support for a reconstructed state. The reconstruction using a binary classification and a two-rate model (A) provided statistical support for the ancestral state of social organisations ($10^{11}:1$).

Reproductive suppression of socially subordinate individuals is commonly found among group living mammals (Wasser and Barash 1983; Jennions and Macdonald 1994), and is generally caused by physiological mechanisms that disrupt the endocrine events that control ovulation, implantation, or established pregnancies (Creel 1996; Faulkes and Abbott 1997; Hackländer et al. 2003). Reproductive suppression is rarely observed in solitary societies and is in some cases assumed to be absent (e.g. Creel and Macdonald 1992). However, in dense aggregations the possibility for dominant individuals to interrupt subordinate breeding increases. If a social rank hierarchy is established, one could therefore predict that this will be reflected in reproductive success of individual females. From the standpoint of subordinate reproductive failure, one of two scenarios can then be predicted. If the animals show no pre-adaptations to live in close proximity to dominant individuals, one would expect an elevated stress response that inhibits reproductive function. If, on the other hand, the physiological mechanisms that mediate suppression involves behavioral or physiological traits that can be modulated by the social environment, one would expect mechanisms of reproductive failure to be similar in both solitary and group living species.

In paper II we used behavioral and endocrine data from captive female wolverines to explore correlates to reproductive failure among females experiencing a crowded social environment. We tested three specific predictions generated by the directional selection model: (i) animals will be badly equipped behaviorally to social aggregations and will show high aggression rates, (ii) females will either show a

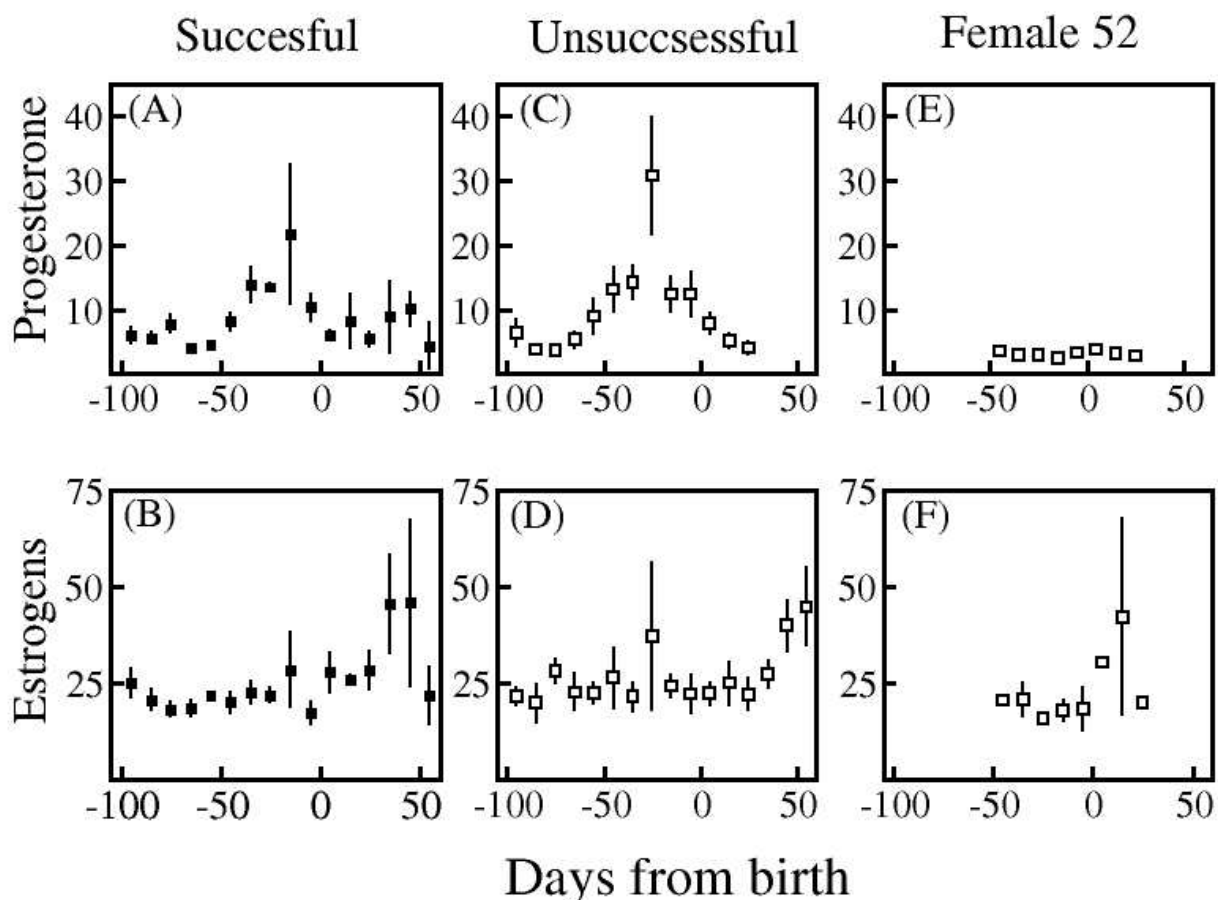


Figure 3: Profiles of fecal progesterone ($\mu\text{g} / \text{g}$ dry feces) and fecal estrogens (ng / g dry feces) during the period of true gestation for successful (A, B) and unsuccessful (C, D) breeding attempts of captive wolverine females, as well as one unsuccessful breeding attempt (E, F) that showed no signs of ovarian activity at time of expected implantation.

strong rank hierarchy with one female monopolizing reproduction, or there will be no socially related difference in reproduction among females at all, (iii) if socially induced reproductive failure occurs, it will be caused by elevated levels of stress hormones in subordinate females that suppress reproductive function.

Behaviorally, the enclosed wolverine females showed low levels of aggression and intermediate levels of social behavior, and reproductive failure seemed to have been related to low social rank. However, none of the females managed to totally monopolize reproduction. Sex hormones generally did not distinguish between successful and unsuccessful breeding, with one exception (Fig. 3a-f). We concluded that reproductive failure seemed to have occurred between ovulation and implantation. Reproductive failure was not detectably related to an increase in glucocorticoid stress hormones. Rather, elevated glucocorticoid levels during the mating season were associated with successful reproduction (Fig. 4). Results from these captive aggregations thus indicate that wolverine females may have latent social tendencies, and that they may possess behavioral and physiological traits that can be modulated by the social environment. This concurs with the radiation model of carnivore social evolution, rather than with directional selection.

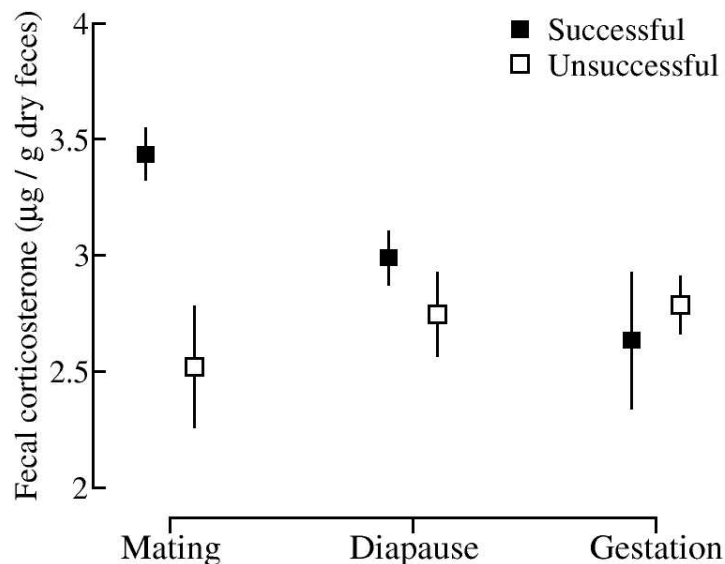


Figure 4: Fecal corticosterone levels during mating, embryonic diapause and gestation in successful and unsuccessful breeding attempts by captive female wolverines. The difference between successful and unsuccessful breeders is statistically significant during the mating season ($p = 0.048$), but not during either the diapause or gestation (diapause: $p = 0.47$; gestation: $p = 0.48$).

Resource utilization and dispersal of wolverines in northwest Alaska

Resource utilization (Paper III and IV)

Macdonald (1983) argued that resource distribution is the central factor determining carnivore spatial organization. Indeed, the spatio-temporal distribution of primarily food resources seems to be one of the most important factors for spacing patterns in carnivores (Sandell 1989), although other factors such as body size and ecological complexity may also be important (Bekoff et al. 1984; Gittleman 1989). Hence, a firm understanding of utilization, availability and distribution of critical resources must

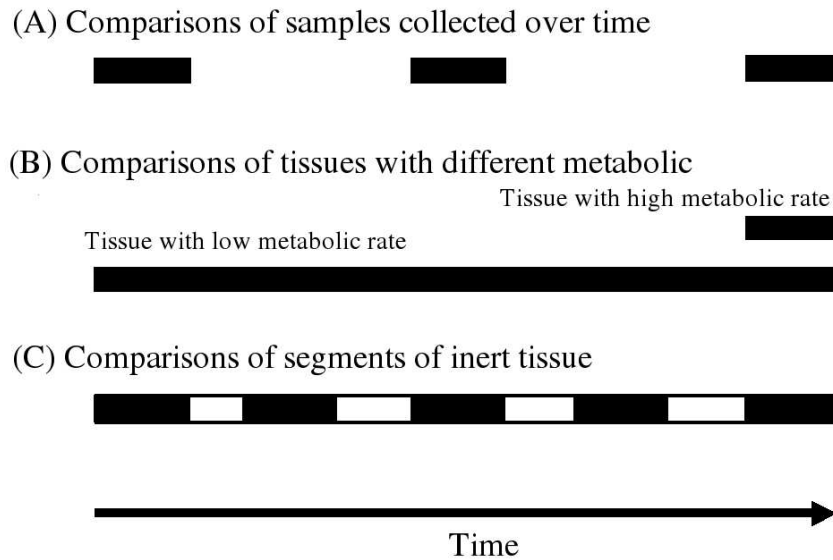


Figure 5. Three different ways of utilizing stable isotopes in animal tissues to resolve temporal diet variation (black boxes reflect measured tissue); (A) comparing samples of the same type of tissues collected repeatedly over time, (B) comparing tissues with different metabolic rates, which means that they will reflect source isotopes over different time spans, and (C) comparing segments of tissues with progressive growth, such as hair, claws or teeth.

be the basis for any research on spatial distribution and sociality in carnivores.

Traditional methods of analyzing carnivore diets, i.e. analyses of content in stomachs and feces, may be prone to shortcomings associated with non-random samples with inherent pseudoreplication (Reynolds and Aebischer 1991; Deb 1997; Darimont and Reimchen 2002). Further, observation on predation events (either direct or through snow-tracking), carcasses for stomach contents or fecal droppings are often difficult to obtain year round for large carnivores in boreal or arctic areas. For carnivores feeding on prey with seasonal variation in availability, there is however a need to understand dietary patterns for all seasons, not only the ones for which data is easy to collect (which normally is during the winter).

In recent years, analyses of stable isotopes have shown to be a powerful complement to traditional diet analyses (Hobson 1999; Kelly 2000). Particularly, since stable isotopes reflect the accumulated diet over time windows specific to the measured tissues metabolic rates, they can be used to address questions related to different time scales than what is possible using traditional analyses. In paper III we suggested three different ways to utilize information in stable isotopes to resolve temporal variation in diets. The most straightforward approach is to compare samples from the same type of tissue that has been collected over time (Fig 5a). This approach is suited to address either long or short-term dietary variation, depending on sample regime and which tissue that is sampled. Second, one can compare tissues with different metabolic rates. Since the elements in a given tissue reflect diet during time spans specific to its metabolic rate, tissues with different metabolic rates will reflect dietary records over different periods (Fig 5b). Third, comparisons of sections from tissues with progressive growth, such as hair, feathers, claws and teeth, will reveal temporal variation since these tissues will retain isotopic values in a chronological order (Fig 5c).

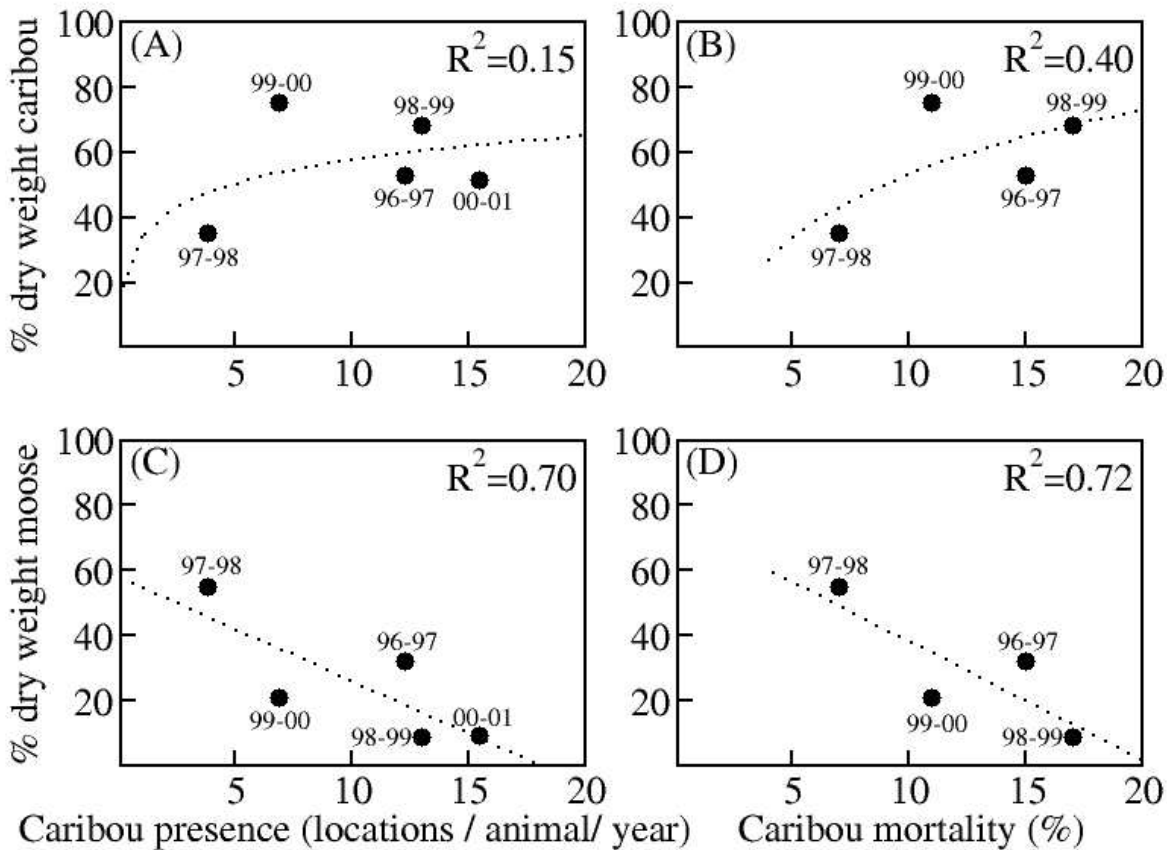


Figure 6. Dietary importance of caribou (A, B) and moose (C, D), expressed as percent of dry stomach content, in relation to annual presence and mortality of caribou from 1996-2000. None of the relationships are significant, but there were trends for negative linear relationships between dietary importance of moose and both caribou presence ($p = 0.107$) and mortality ($p = 0.178$).

In paper IV we combined analysis of stomach content with analyses of the stable isotopes ^{13}C and ^{15}N in wolverine muscle and collagen to investigate annual and seasonal variation in wolverine diets within the migratory range of the Western Arctic Caribou Herd in northwestern Alaska. We compared ^{13}C and ^{15}N values in skeletal muscles collected repeatedly over several winters in combination with analyses of stomach content to investigate annual variation in diet, and compared ^{13}C and ^{15}N values in muscle and collagen collected from the same animals to investigate seasonal diet patterns. We derived the samples from wolverines legally harvested in the drainages of Kobuk and Noatak rivers.

As predicted from previous studies on feeding ecology of wolverines, large ungulates dominated the diet during winter. Wolverines appeared to behave like specialist foragers on caribou, which compensated for a decreased intake of caribou with an increased intake of moose (Fig 6a-d). However, stable isotope analyses of muscle and collagen indicated a seasonal diet shift between winter and summer. This shift seemed to be from a diet dominated by caribou in winter to an increased utilization of other terrestrial herbivores, such as moose, microtine rodents, or arctic ground squirrels, during summer (Fig 7). Hence, the wolverines in Noatak and Kobuk drainages seemed to follow the general pattern among studied wolverine populations, and live as largely ungulate-dependent scavengers, albeit seasonally probably depending on smaller prey.

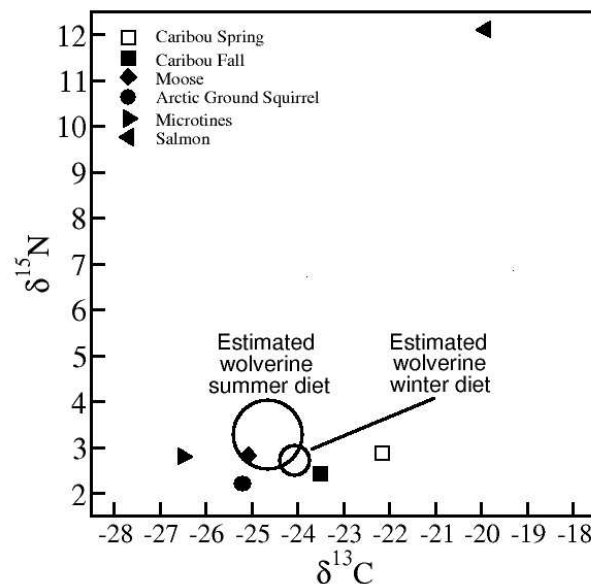


Figure 7. Ninety-five % confidence limits for estimates of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ for wolverine summer and winter diets and average values for potential prey species. Moose and caribou values reflect muscle samples from animals harvested within the study area, while values for other potential prey species are taken from literature (see paper III). Estimates of wolverine winter diets are based on wolverine muscle samples corrected for isotopic fractionation and estimates of wolverine summer diets are calculated from wolverine collagen, corrected for isotopic fractionation, where the signatures for winter diets have been extracted.

Sex-specific dispersal patterns (Paper V)

Patterns of natal dispersal, and particularly of sexual asymmetry in dispersal, are intrinsically linked to the spatial structures and social organizations of animal societies, as well as to local resource distribution and resource utilization (Chepko-Sade and Halpin 1987; Clobert et al. 2001). In polygynous mammals, dispersal is predicted to be male-biased due to biases in resource competition between males and females (Greenwood 1980). If male fitness is determined by mating success and female fitness by resource availability (which has been shown in empirical studies of polygynous mammals, e.g. Clutton-Brock 1988), the amplitude of sexual asymmetry in dispersal can be predicted to increase with an increasing level of mate competition in relation to resource competition (Perrin and Mazalov 1999). Although neither resource competition nor mate competition directly has been quantified for wild wolverine populations, recent data suggesting high rates of male infanticide (Persson et al. 2003) indicate that male mating competition might be considerable. Hence, we could predict that dispersal among wolverines should be male biased.

However, recent studies have provided unclear results regarding sex biases in wolverine dispersal patterns. Using direct observations on radio tagged animals in Scandinavia, Vangen et al. (2001) suggested that males may disperse more frequently than females and that females may delay their dispersal relative to males. They did not, however, find any sex differences in terms of dispersal distances. Using population genetic methods, Cegelski et al. (2003) found inconsistent results related to sex-biased dispersal in wolverines from Montana, USA. They found that two separate measures of population differentiation differed for males and females, both supporting male bias in dispersal, but that a third approach failed to provide support for any sex differences in dispersal patterns. Further, both Wilson et al. (2000) and

Tomasik and Cook (2005) found relatively strong evidence for genetic population differentiation using maternally inherited mtDNA. These results have, however, been contradicted by analyses of biparentally inherited microsatellite markers (Kyle and Strobeck 2001). One possible explanation for this contradiction could be female philopatry, which would result in stronger population differentiation for maternally inherited markers (Avice 2004). Chappell et al. (2004) supported this view by analyzing both mitochondrial and nuclear markers simultaneously for Canadian wolverines.

Although male biased dispersal and female philopatry is common in group-living carnivores, such as African lions (*Panthera leo*; Packer and Pusey 1993), grey wolves (*Canis lupus*; Peterson et al. 1984), and meerkats (*Suricata suricatta*; Doolan and Macdonald 1996), empirical evidence for its occurrence in solitary species is relatively sparse. Long-term monitoring programs have found direct evidence for female philopatry in Bengal tigers (*Panthera tigris*) (Smith and Macdougall 1991), Scandinavian brown bears (Swenson et al. 1998) and American black bears (*Ursus americanus*) (Rogers 1987). However, studies like these are expensive and have to be maintained over several years or even decennia (Smith and Macdougall 1991). Further, direct observations of dispersal events are prone to methodological problems (Koenig et al. 1996), which is accentuated in species that disperse over large distances such as most solitary carnivores. The recent explosion in the accessibility of high-resolution genetic data offers a potentially powerful and seductive alternative (Mossman and Waser 1999; Goudet et al. 2002).

This far, three types of analyses have been used to infer sex biases in dispersal from genetic data. First, measures of population differentiation, such as F_{st} values, have been compared between males and females (Goudet et al. 2002). If one sex shows greater dispersal tendencies, indices of population differentiation should be lower for this sex than the philopatric sex. Second, Favre et al. (1997) suggested that if one sex disperses more than the other, individuals of this sex should, on average, have rarer alleles in the population in which they are found than the philopatric sex (providing individuals have been sampled post dispersal). They provided a method to quantify this by calculating an assignment index (AIC) that reflects the probability that a specific genotype has originated in the population in which it was sampled. In the

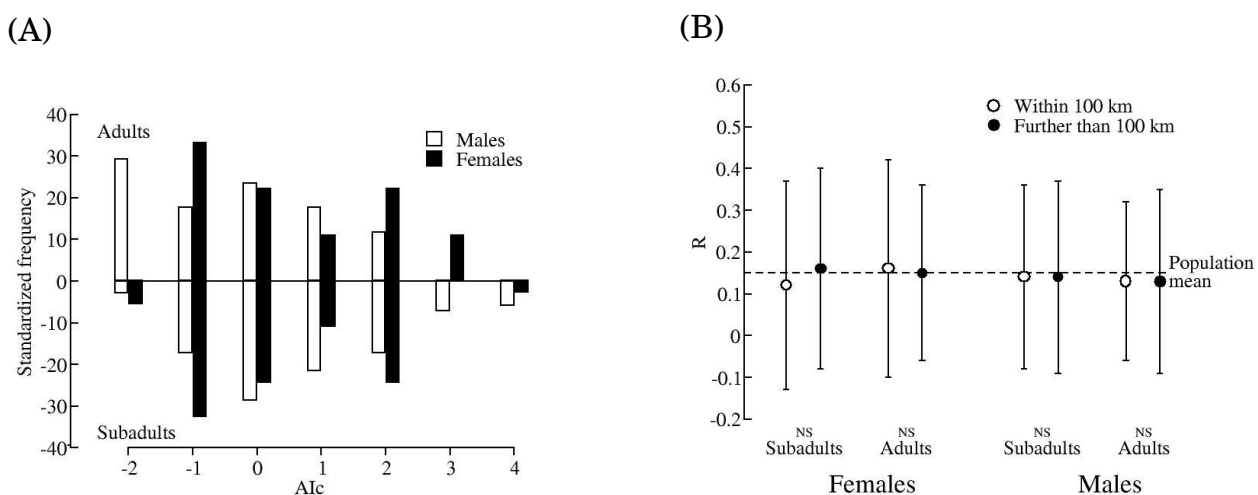


Figure 8. Results from two methods of testing sex biased dispersal in Alaska wolverines using genetic data. There were no differences in assignment indices between males and females, neither in terms of mean index values nor in terms of variance (A). Further, there were no relationship between genetic relatedness and physical distance between harvested individuals, neither for subadult females, subadult males, adult females nor adult males (B).

case of sex biased dispersal, the AIC values of the dispersing sex should be negatively skewed compared to the AIC values of the philopatric sex. Further, since individuals of the dispersing sex will include both residents and immigrants, the variance of assignment indices should be higher for the dispersing than the philopatric sex (Mossman and Waser 1999). Third, there should be a stronger correlation between the genetic and physical distance between pairs of individuals from the philopatric sex compared to the dispersing sex (Prugnolle and de Meeus 2002).

In paper V, we utilized the AIC based method as well as the approach relating genetic and physical distance to test the prediction of male biased dispersal in wolverines from the same population in Brooks Range that I previously have described diet use for. Neither of the two genetic methods provided support for sexual asymmetry in dispersal tendencies, neither in terms of age of dispersal, frequency of dispersal, nor dispersal distances (Fig 8a-b). This study thus adds to the inconsistent picture regarding sex-biased dispersal in wolverines, where some studies have supported male biased dispersal while others have not.

Discussion

Phylogenetic history and evolution of sociality in Carnivora

The phylogenetic reconstruction presented in paper I supported a directional selection from a solitary ancestry, if a two-rate model and a binary classification of social organizations was used. The failure of providing support for an ancestor using the multistate classification could be caused by a decreased power by a larger number of estimated parameters. However, for both the binary and the multistate classification, the two-parameter models performed better than the one-parameter ones. Further, the two-rate model estimated a faster forward rate of change than backward, both for the binary and multistate classifications. This agrees with a directional selection approach, where reversal of evolved traits can be expected to be rare (Futuyma 1998).

The directional selection model regard a solitary life as a phylogenetic legacy that persists in species that has not been exposed to selection pressures to develop pair or group living. However, there is evidence that a solitary life may generate specific adaptations, such as induced ovulation (Lariviere and Ferguson 2003), indicating that maintenance of solitary social structures may have been under active selection. Further, although it is generally assumed that resource distribution dictates the level of sociality for most carnivore species (Johnson et al. 2002), studies specifically testing whether the level of sociality is constrained by resources are rare.

In paper II, the study of captive wolverine females contradicted the predictions given by the directional selection model. Among these females, reproductive failure was not related to an endocrine stress response, females did not show high levels of aggression, and although reproductive success appeared to be related to social rank none of the females managed to monopolize breeding entirely. Hence, when ecological constraints to aggregate were released, these females showed rudimentary abilities to live in complex social groups.

These two fundamentally different approaches to test predictions regarding the evolutionary background of carnivore sociality thus provided contradicting results. Although a large body of research has focused on social evolution within Carnivora, little or no attention has been given to the underlying evolutionary theory that has been used. The contradicting results given by these studies emphasize that we still have no clear understanding of how different social structures developed, and from

what level of sociality present carnivores have evolved. I thus encourage future research to test evolutionary theory regarding carnivore social evolution, and also to explore new avenues in which present social organisations might have evolved.

Why are wolverines solitary?

Many carnivore biologists have asked why animals live in stable social groups, and how these social units are maintained (see reviews in Ewer 1973; Eisenberg 1983; Gittleman 1989; Macdonald and Creel 1992). However, there is not an equal amount of studies addressing why solitary species does not live in social groups. In the studies that have been done, explanations can be generalized into two categories; (i) animals has maintained a solitary social organisation in the lack of selection pressure to evolve more elaborate social structures, and (ii) resource distribution generally prevent animals from aggregating. While the first explanation only is possible under the direction selection model, the second is possible under the radiation model as well. The results in the papers presented here provide at least crude abilities to differentiate between these two alternatives for wolverines.

Two main hypothesis have been provided to explain how critical resources may induce formations of social groups; (i) cooperative hunting often increases hunting success of group living individuals (Creel and Creel 2002), and (ii) the defendability of patchy resources increases if animals aggregate and cooperate in defending them (Macdonald 1983). Wolverines appear to depend on large ungulates throughout its range, including the population studied in paper IV and V. In many carnivores feeding on large ungulates, cooperative hunting groups has been suggested to increase hunting success over solitary hunters (see review in Creel and Creel 2002). Therefore, it would be reasonable to postulate that wolverines could benefit from cooperative hunting as well. From the basis of a fundamental resource, it's main prey, wolverines may thus live under ecological conditions that could favour formation of social groups to increase hunting success.

However, wolverines mainly seem to scavenge carcasses from large ungulates, rather than hunt them down as prey. This scavenging is likely caused by morphological constraints to hunt efficiently. Since morphological traits are more heritable than behavioral (Stirling et al. 2002), it is likely that wolverines' evolutionary past constrain them morphologically into an ecological niche as a scavenging generalist predator. In this niche, the spatial distribution of resources is not patchy enough to favour aggregation to defend them. Wolverines also appear to cache food rather than to stay and defend a carcass, which would further decrease the need to aggregate to defend food resources. This would support that wolverines mainly live a solitary life due to ecological constraints to aggregate.

Theory predicts that male biased dispersal will develop when the intensity of mate competition (among males) exceeds the intensity of local resource competition (among females) (Dobson 1982). Although different studies (summarized in paper V) have provided somewhat different results regarding sex bias in dispersal among wolverines, none has provided clear evidence for a strong sexual asymmetry in dispersal tendencies. Therefore, it can be assumed that male mate competition is low or local resource competition among females high. Studies in Scandinavia have shown that females appear to be food limited and that male infanticide, which usually occurs in systems with strong mate competition (see Ebensberger 1998), is common (Persson 2003; Persson et al. 2003). Both of these results indicates that the low level of sexual asymmetry in wolverine dispersal probably is due to a strong competition for resources among females, rather than by weak mate competition among males.

This further accentuates that resources and ecological factors likely dictates the social structures among wolverines.

When ecological constraints to aggregate were released, as in paper II, both behavioural and physiological mechanisms in wolverine females appeared to have been modulated by the social environment. Although many of the social tendencies shown during the study was rudimentary compared to group living species, wolverines may carry both behavioral and physiological pre-adaptations to form different social structures in wild populations. Such social flexibility is relatively common among carnivores, for instance in badgers (*Meles meles*) (Revilla and Palomares 2002) and several species of canids (Moehlman 1989). However, many of these species are much more generalistic in their feeding habits than wolverines, and it is likely that the ecological niche as an ungulate dependent scavenger, in combination with low resource availability in arctic and boreal areas, inhibit social aggregations of wolverines in the wild.

Conclusions

Phylogenetic analyses generally supported that carnivore social organizations evolved through directional selection from a solitary ancestor. However, results from captive wolverine females indicate that they have rudimentary social tendencies, which rather support that sociality in carnivores radiated from a socially flexible ancestry. Wild wolverines in northwest Alaska adhered to the commonly found ecological niche as an ungulate dependent generalist carnivore, and lack of sex bias in dispersal tendencies indicates that resource competition among wolverine females was high. I suggest that wolverines have latent abilities to aggregate, but that their phylogenetic legacy in terms of morphology has constrained them into an ecological niche where resource abundance and distribution generally inhibits aggregations. Due to contradictory results, I suggest further research to test evolutionary theory regarding carnivore social evolution, and particularly to explore new avenues into social evolution that better explain intra-specific variation in sociality, as well as formation and maintenance of solitary social systems.

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