DEMOGRAPHY AND LIFE HISTORY OF THE EURASIAN BEAVER *CASTOR FIBER*

A thesis submitted for the degree
Doctor of Philosophy

To Laic, Hazel and Alistair

Ruairidh D. Campbell **Doctor of Philosophy**
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Demography and life history of the Eurasian beaver *Castor fiber*

Abstract

Long-term studies of animal life histories and demography have been key in advancing our understanding of the processed that shape behaviour and population dynamics of species. The Eurasian beaver *Castor fiber* is a good species in which to study these processes, as it is long-lived, social and territorial. The species is also important to general conservation biology due to its key stone effects on wetland and riparian habitat. In this thesis, I use a 12 year capture-mark-recapture program on a beaver population in Telemark, southern Norway, in conjunction with behavioural, habitat and climate observations to examine life history strategies, demography and territoriality.

I examined growth rates of juveniles and showed, for the first time, that beavers exhibit compensatory growth for body size. Juvenile beavers that were smaller than same-age peers managed to narrow the gap in size by trading-off gain in body condition against gain in size. Examining the effects of body size and condition on survival and dominance, I find for the first time evidence that larger, though not heavier for their size, individuals are more likely to obtain dominant breeding positions. Medium size individuals and those with medium body condition suffer less mortality. The largest of the medium sized animals go on to obtain breeding positions within the population. Thus compensatory size growth in beavers has evolved because selection acts through dominance to increase size, but this size increase is stabilised through selection on survival.

Examining the effects of age on fecundity I show, for the first time, that after an initial increase to 4 – 6 years (minimum age), beavers exhibit reproductive senescence. I also show for the first time that, apart from exhibiting higher fecundity, females in higher quality territories begin reproductive senescence later. I argue that this supports the disposable soma hypothesis of senescence and not the antagonistic genetic pleiotropy hypothesis. I furthermore examine trade-offs in offspring quantity versus quality and show that this trade-off only exists in younger (<7 years minimum age) mothers, indicating support for both the experience and the terminal investment hypotheses.

Investigating the effects of weather on body weight and fecundity I show that that rainfall negatively affected both fecundity and body weight. Examine tree growth-rings, I was able to establish that close to water level (<0.5m) high rainfall suppresses tree growth. Thus higher rainfall can reduce forage availability near water. I also found that cold winters reduced the body weight in young (<2 year old) beavers and rapid phenological advancement associated with warm spring temperatures reduced adult body weight, confirming previous studies on other species. Exploring the effects of weather variability on recruitment and survival, I show that high seasonal amplitude in air temperature and low short-term temperature variability led to an increase in recruitment and low variability in rainfall combined with low short-term temperature variability increased survival. Overall, weather variability may have a greater influence on vital rates in this beaver population than absolute weather conditions.

Investigating territoriality and the propensity of offspring to remain within the natal group, I show that a repacking of territories due to mortality and group fission has reduced a previous imbalance in territory quality. After repacking, territories were more clearly configured around the dispersion of resources. Philopatric tendencies are greater in territories with more resources but their presence results in greater resource depletion.

Statement of contribution

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As the principal investigator on all aspects of this thesis, I contributed primary intellectual input and effort into the design of this study, data analysis and writing. All chapters have been compiled in collaboration with my supervisors Frank Rosell and David Macdonald, chapters 3 and 6 involved further collaboration with Pierre Nouvelette and Chris Newman and chapter 7 with Chris Newman. Frank Rosell instigated the beaver trapping program on which many of the analyses are based. Chris Newman provided comments on chapters 1 and 8. Marco Festa-Bianchet and one anonymous reviewer contributed constructive criticism for chapter 2, Paul Johnson provided constructive criticism towards chapters 4 and Paul Johnson, Atle Mysterud, Chris Newman, Bart Nolet and John Quinn provided comments on chapter 5. Bernadette Allmark drew the artwork for the chapter titles pages.

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Chapter 1

Introduction

Humankind has always needed an understanding of the factors that determine the distribution and abundance of other species, to hunt, to fish, to raise domestic stock and to cultivate the land. The concept of a *"balance of nature"* has been a topic for philosophical contemplation since the time of the ancient Greeks, implicit in the writings of Aristotle, Herodotus and Plato (Egerton, 1968), while the importance of regulation in population ecology has been recognised since the work of Thomas Malthus (1798). The selection of life-history traits befitting extant environmental (niche) conditions was central to Darwin's theory of evolution (1859). The understanding of life-history paradigms, and the fundamental role they play in ecological and evolutionary processes, has advanced over the last century (e.g. Nicholson 1933; Lack 1954; Andrewartha & Birch 1954; Tamarin 1978; Turchin 1990, 1995, 1999; Roff 1992, Stearns 1992; den Boer & Reddingius 1996; Murray 1999; Oli & Dobson 2001). While ecologists continue to debate the mechanisms, most agree that life-history parameters are key to the regulatory mechanisms governing population viability (Murdoch 1970, 1994; Royama 1992; Krebs 1994; Turchin 1995).

An organism’s life history is characterised and defined by schedule of its growth, reproduction and survivorship dynamics until death, shaped by an evolutionary process and mediated by current environmental conditions (Stearns 1992). Life-history dynamics are thus the product of optimisation to the environment experienced by an organism’s ancestors (Roff 1992). Population dynamics and life-history are inextricably linked through the effects of the schedule of life events on population growth rate (Cole 1954; Lewontin 1965; MacArthur and Wilson 1967; Oli and Dobson 2003) and the counter effect of the optimisation of life-history strategies under different population growth rates, age structures and densities (e.g., early reproduction is selected for in populations with many young animals: Charlesworth & Giesel 1972). The vital demographic rates (such as fecundity and survival) that influence population dynamics are then the product of these intrinsic processes plus extrinsic factors, such as variation in the environment (Berryman 2003; Turchin 2003). To return to the fore-fathers of evolutionary ecology, Malthus (1798) determined that resource availability influenced the ability for populations to grow while Darwin (1859) advanced the idea that when resources are limiting, a struggle for existence would ensue in which only those which fit best would survive.

That resources are inevitably limited in natural systems is central to the concept of life histories, either through their availability or by physiological constraints on the ability of an organism to acquire them (Williams 1966). Therefore, trade-offs are expected in life history dynamics, moderated by extrinsic environmental constraints and ontological, physiological and ethological responses. For example to grow larger to achieve a competitive advantage may come at the enhanced risk of predation or cellular damage (Mangel & Munch 2005), or to give birth to many offspring may compromise offspring quality and future fecundity (Williams 1966; Smith & Fretwell 1974).

Climate is an important extrinsic environmental constraint: it is one of the primary controls on species diversity and their distribution, while past climatic changes have had strong influences on the composition and dynamics of natural communities (Root *et al.* 2006). Through impacts on current environmental conditions, anthropogenic climate change is demonstrating significant, but as yet poorly understood, consequences for wildlife. For example projected increases in temperature (IPCC 2007) is anticipated to cause the range of a species to shift to higher latitudes and altitudes or, for species already living at high latitudes and altitudes, species ranges may contract (Hersteinsson & Macdonald 1992; Parmesan *et al.* 1999; Hughes 2000; Parmesan & Yohe 2003). Alternatively, changes in temperature may influence the timing of seasonal resource through changes in phenology resulting in the failure of a population to synchronise a critical life history event with resource supply (Parmesan & Yohe 2003; Charmantier *et al.*

2008; Post & Forchhammer 2008). Ultimately, where species fail to adapt, anthropogenic climate change will cause biodiversity loss (Hughes 2000; McLaughlin *et al.* 2002; Walther *et al.* 2002).

Unless regulated by over-hunting or disease epidemics, populations in stable systems will increase inevitably towards the complete exploitation of the most limiting characteristic of their niche carrying capacity (Krebs 1995). An additional ramification of resource limitation however is that, where resource configuration allows, resources can be monopolised by an individual or a group to the exclusion of other conspecifics through the formation of territories (Kaufmann 1983). Territorial behaviour can have a strong effect on population structure and dynamics (Adams 2001). Where territory boundaries are inflexible to changes in resources and population density, territoriality has the consequence that local populations will be regulated at stable densities (Adams 2001). Inequality in territory size or resource content in populations may furthermore result in variation in growth rates, reproduction and mortality (Adams 2001).

In summary, the schedule of growth, reproduction and mortality of a species interact with resources and the defence of these resources to influence its population dynamics. Thus studying the processes that influence these factors are a fundamental step in our understanding of a species' ecology.

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Investigating life history dynamics

With such a diverse range of life history episodes to consider, and only limited financial and human resources available, trade-offs are also implicit in the research into this subject. This is evidenced by the relatively few studies on life histories, especially in longer lived species (e.g. lifespan > 5 – 10 years).

The principal long term studies (> 10 years) on large and long-lived mammals have been on ungulates such as red deer *Cervus elaphus* (Clutton-Brock *et al.* 1983; 1986), bighorn sheep *Ovis canadensis* (Festa-Bianchet *et al.* 1995, 1998, 2000) and Soay sheep *Ovis aries* (Clutton-Brock *et al.* 1992; Clutton-Brock & Pemberton 2004). Long-term studies on non-ungulate species are fewer (e.g. brown bear *Ursus arctos*, Swendson *et al.* 1994, badger *Meles meles*, Macdonald *et al.* 2002; 2009 and meerkat *Suricata suricatta*, Clutton-Brock *et al.* 1998; Sharp & Clutton-Brock 2010). These studies have provided important insights into life history theory and population biology and further additions to this list may offer new insight into the population dynamics of long-lived species while providing a suitable test of the generality of the theories gained from these previous studies.

In this thesis, I examine life history traits and consequent population dynamics and territoriality in the Eurasian beaver *Castor fiber* using data from a long-term study in southern Norway. After a brief outline of the thesis structure below, I give an introduction to the beaver, the research topics I address in this thesis, the study area and finally the core methods, before providing a brief overview of the thesis structure.

Thesis structure

This thesis is framed front and back by the introduction (current chapter, 1) and a discussion of the general findings at the end (chapter 8). Chapters 2 and 3 examine trade-offs and selection on growth rates, chapter 3 examines the trade-offs involved in reproduction, chapters 5 and 6 examine the effects of weather on body mass and vital rates and chapter 7 examines territoriality. Chapters 2 – 7 were written as independent manuscripts for submission to peer review journals and there is thus inevitable duplication of text between these chapters and the introduction and discussion. To avoid excessive duplication, methods particular to the individual chapters have been left out of this introduction.

The Eurasian beaver as a model species

Beavers display many characteristics that make them an interesting and apposite model species. They are long lived, social and territorial and have a ‘despotic’ monogamous mating system (Wilsson 1971; Novak 1987; Rosell & Pedersen 1999; Műller-Schwarze & Sun 2003). Thus they afford the possibility to address many questions relating to the evolution of life history tactics, and their demographic effects, such as the trade-offs in growth and reproduction. The also have two characteristics in particular that makes them a *good* model species. Firstly, they are highly amenable to observation and trapping from boat (the main technique used in this study, Rosell and Hovde 2001) hence a large proportion of the population, and their behaviours, are visible to observers (though, importantly, not all behaviours are evident). Secondly, there is already a considerable literature on many aspects of beaver ecology (both *C. fiber* and the North American beaver *C. canadensis*) from across their geographic range (see below) and yet no detailed longitudinal study on beaver life histories has ever been conducted. This allows us to address new questions on life-history, population dynamics and territoriality, which would not have been answerable with a cross-sectional study, while benefiting from extensive prior knowledge of the species (see Wilsson 1971; Novak 1987; Rosell & Pedersen 1999; Műller-Schwarze & Sun 2003) to both pose the correct question and assess the answer in relation to the established ecology of the species.

Beavers can also have a significant impact on their environment and on other wildlife due to their river damming and tree-felling activity (Rosell *et al.* 2005, see below), giving the beaver the status of a keystone species (Paine 1995). Furthering our knowledge of the behavioural ecology of the beaver is therefore important in the context of wider conservation because of the implications it has for the management of wetland biodiversity in boreal ecosystems.

A preamble on the model species

Taxonomy

The Eurasian beaver and its phenotypically similar allopatric sister species, the North American beaver *C. canadensis* are large rodents that represent the only extant examples of the diverse family Castoridae that arose in the Oligocene (33.9-23.03 Ma ago) and once included animals ranging from the size of the fossorial 0.8-1.2kg *Palaeocastor* spp. (Late Oligocene – Early Miocene, approximately 25 Ma ago) to the swamp inhabiting 60-100kg *Castoroides ohioensis* (Earliest Pleistocene, approximately 2.6 Ma ago), both found in North America (Korth 2001; Reynolds 2002; Rybczynski 2007). *Castor fiber* appears as a distinct species in the fossil record in the late-Miocene (around 12 Ma ago) and is intermediate in the body-size range for a castorid, with an average adult body weight of ca. 20kg (Wilsson 1971; Pilleri *et al.* 1985; Novak 1987; Műller-Schwarze & Sun 2003). From the fossil record of the Early and Middle Pleistocene (c.2.4-0.13 Ma ago) in Eurasia, this extant beaver appears to have lived alongside, or possibly been locally extirpated by the slightly larger extinct beaver *Trogontherium cuvieri*, since the prevalence of these two beavers at excavation sites shows an inverse relationship (Mayhew 1978) . *C. fiber and C. canadensis* are distinct species with different numbers of chromosomes (48 in *C.f.* and 40 in *C.c.*, Lavrov & Orlov 1973) and some differences in morphology and behaviour (Rosell & Pedersen 1999; Műller-Schwarze & Sun 2003). Despite these minor differences most aspects of their behavioural ecology are indistinguishable.

General ecology and morphology

Beavers are semi-aquatic herbivores that are found across the northern hemisphere (Műller-Schwarze & Sun 2003). They are predominantly crepuscular-nocturnal (Wilsson 1971). Digestion of plant material is aided through hind-gut (caecum) fermentation (Vecherskii *et al.* 2009) with material given additional digestion though the practice of caecotrophy (a type of coprophagy) (Wilsson 1971). Beavers exhibit various adaptations to allow them to succeed in water including a scaly dorso-ventrally flattened tail (used as a propeller and a rudder), large webbed hind feet, fine water-repellent fur protected by longer guard-hairs, lips that can close behind their incisors, a nictitating membrane to protect the eyes underwater and the ability to seal their nostrils (Wilsson 1971; Műller-Schwarze & Sun 2003). Beavers are socially monogamous (but see below) and, as is common in monogamous species, there is little sexual dimorphism, though females have a statistical, though not perceptibly obvious, tendency to weigh more (by approximately 1.5kg) (Wilsson 1971). They live in fresh water, using it as a refuge, to travel and to transport larger food items such as branches and saplings (Wilsson 1971). Eurasian beavers can live for as long as 20 years in the wild (Rosell & Pedersen 1999). Nolet and Baveco (1996) found an adult annual mortality rate of 0.09 in a reintroduced population, indicating that once adulthood has been attained, beavers will live, on average, until the age of 14.

Foraging

Beavers are central place foragers and rarely travel far from water with most foraging occurring within a few meters and generally not more than around 40m from the waters edge (Fryxell & Doucet 1991; Parker *et al.* 2001; Haarberg & Rosell 2006; Margaletić *et* *al.* 2006). Beavers are most renowned for their ability to fell deciduous trees from which they consume the leaves, twigs and bark (cambium) for food while the woody stems may be used in the construction of lodges and dams (Wilsson 1971; Műller-Schwarze *et al.* 2003) (see below). Evidence for wood-cutting in an earlier extinct beaver, *Dipoides* spp. indicates that the behaviour would have been found in a shared ancestor with *Castor* and suggests that the behaviour may have arisen as a response to cold winters in high latitudes in the Castoridae around 24 Ma (Rybczynski 2007). Modern *Castor*, however, appears to be a more efficient wood-cutter than *Dipoides* would have been based on fossil dentition (Rybczynski 2008). Beavers are considered to be 'choosy generalist' herbivores (Jenkins 1979) in that they can eat a wide variety of vegetation including aquatic plants, herbs, forbs and woody vegetation (both deciduous and coniferous) but within this herbivorous remit, they will forage selectively. When foraging on woody vegetation, small saplings (dbh <5cm) are generally preferred over larger trees (Haarberg & Rosell 2006; Margaletić *et al.* 2006). Tree are felled and transported back to the vicinity of water to be consumed, frequently at favoured sites on the river-bank known as feeding stations (Wilsson 1971). Once felled, larger trees may need to be cut into smaller sections before they can be transported to water (Wilsson 1971). Herbs and forbs are usually browsed *in situ* (pers. obs.), plausibly because their smaller size makes ingestion time so short that returning to water is not an energetically efficient strategy. As with other vertebrate herbivores, food selection appears to be mediated by nutrient content and digestibility of the available forage (Ganzhorn & Harthun 2000) with individuals attempting to maximize energy intake over time (Doucet & Fryxell 1993; Nolet *et al.* 1995). Beavers adjust foraging intensity and preference with distance from water, following a central-place-foraging strategy (*sensu* Orians & Pearson 1979): foraging intensity declines while food selectivity and (within limits) size increases with increasing distance from the safety of water (Jenkins

1980; McGinley *et al.* 1985; Fryxell & Doucet 1991; Gallant *et al.* 2004; Haarberg & Rosell 2006; Raffel *et al.* 2009) Beavers show seasonal changes in foraging preferences under some circumstances with shifts from deciduous woody vegetation in winter to herbs, forbs and aquatic vegetation during summer, and occasional consumption of conifers in spring (Jenkins 1979; Műller-Schwarze & Sun. 2003), though preferences between sites and seasons vary (e.g. compare Nolet *et al.* 1994; Urban *et al.* 2008). In general, of the woody tree species available to the beaver in Europe, willow *Salix* spp. is favoured frequently (e.g., Fustec *et al.* 2001; Haarberg & Rosell 2006; O'Connel *et al.* 2008: Urban *et al.* 2008). Nolet *et al.* (1994) found, however, that in an area where willow was dominant, other non-willow species were selected preferentially, indicating that a diversity of species is required to fulfil all the beavers nutritional requirements (Műller-Schwarze & Sun 2003).

Construction behaviour

Beavers dig out nests in burrows, but if bank conditions are not suitable due to the material or height above water, lodges constructed of sticks and mud may be built (Wilsson 1971). The entrance to the nest chamber is underwater (Wilsson 1971). Variation in bank height can result in a range of nest types from complete burrows, through nests that begin as burrows and finish with part of the nest chamber constructed from sticks (bank-dens), to complete lodges with no part of the construction dug out of the bank (Wilsson 1971). In more northern latitudes, particularly where water-ways are likely to ice-over in winter, beavers build a food store, or 'cache', consisting of deciduous woody branches fixed to the substrate under water in front of the chosen wintering burrow or lodge (Műller-Schwarze & Sun 2003; Hartman & Axelsson 2004). Water levels need to be of sufficient depth to cover the entrances of lodges and burrows, cover the food store

(Hartman & Törnlöv 2006) and to provide protection from predation (Wilsson 1971; Zurowski 1992). Areas of slow running water are also preferred as sites for lodges and food stores, to avoid the risk of these investments being washed away (pers. obs.). If these requirements are not met by naturally occurring riverine conditions, beavers can build dams to raise the water levels and reduce the flow. Dam building and repair behaviour appears to be triggered by the sound of running water (Wilsson 1971). Beavers begin to exhibit building behaviour as juveniles at around one year old (Wilsson 1971). As with wood-cutting, lodge building could have evolved as an adaptation to colder high latitudes since their construction allows better insulation than burrows (Rybczynski 2007) and both dam and lodge building behaviour may have arisen with wood-cutting behaviour in the shared ancestor of *Castor* and *Dipoides* (Tedford & Harington 2003; Rybczynski 2007). Beavers may also dig canals from the water inland to access food plants further from the river or lake (Berry 1923; Richard 1967). Canals develop from regularly used feeding trails with digging commencing at the start, where the trail meets the water (pers. obs).

Such building activities require a commitment of effort, and whenever possible beavers prefer slow flowing mature river habitats where damming is not necessary (Slough & Sadleir 1977; Howard & Larson 1985; Hartman 1996). Interestingly, it appears that slow flowing mature rivers were the preferred habitats of the extinct *Trogontherium* beaver, which therefore may have excluded *C. fiber* from using these habitats in the past (Mayhew 1978). Dam building behaviour may thus have facilitated the coexistence of *C. fiber* and *Trogontherium* by allowing *C. fiber* to use smaller tributaries and upland streams.

Territoriality and scent-marking

Beavers are highly territorial, maintaining clearly defined territories through scent-marking and, occasionally, territorial displays and physical conflict (Wilsson 1971; Nolet & Rosell 1994; Rosell *et al.* 1998; Ulevicius & Balciauskas 2000; Thomsen *et al.* 2007). Where agonistic encounters occur, serious and sometimes fatal injuries may be sustained by combatants (Piechocki 1977; Svendsen 1980; pers. obs.). Two excretions are used in scent communication in beavers: the castoreum (a urine based excretion that is flushed through the animals' castor sacks) and anal-gland secretion (AGS) (Rosell & Bergan 1998; Rosell *et al.* 1998). AGS codes for relatedness between individuals (Sun & Műller-Schwarze 1998) and its appearance and smell can be used by humans to distinguish the sexes, as well as between the Eurasian and North American species (Rosell & Sun 1999).

There is evidence that territories are configured economically (*sensu* Brown 1964) to accommodate sufficient resources. For example, Fustec *et al.* (2001) found that territory size on the river Loire was correlated negatively with the richness of the habitat, as defined by the proportion of habitat comprised predominantly of willow. However, a study of two populations in Norway and the Netherlands found a positive correlation between territory size and quality, defined as the proportion of habitat that was wooded (Campbell *et al.* 2005). This counter-intuitive result was due to settlement pattern playing a role in territoriality with earlier settlers retaining larger and better quality territories (Nolet & Rosell 1994; Campbell *et al.* 2005).

Reproduction, development and sociality

Beavers live in family groups that consist of parents and offspring from the current and previous years (Wilsson 1971; Műller-Schwarze & Sun. 2003). Only the dominant adult parents breed (Wilsson 1971; Műller-Schwarze & Sun. 2003). Once paired, beavers tend to remain as a couple until one is displaced by another of the same sex or until one member of the pair dies (Svendsen 1980; Műller-Schwarze & Sun 2003). Copulation occurs in winter (late Jan-Feb) usually in water while swimming (Wilsson 1971). Though socially monogamous, in a population of *C. canadensis* in southern Illinois Crawford *et al.* (2009) found, using microsatellite analysis to examine relatedness, that over half the litters involved multiple paternity, most frequently as a result of mating between neighbouring animals. Winter in southern Illinois is relatively mild however, with a mean daily temperature in February exceeding 0°C (Angel 2008). In colder climates, the prevalence of extra-pair copulation may be lower because ice closure of waterways restricts access to neighbouring animals since swimming beavers require open water to be able to surface and breathe.

Gestation lasts 107 days on average and parturition occurs in the lodge or burrow around mid May in northern latitudes (Wilsson 1971; Parker & Rosell 2001; Nolet *et al.* 2005). Up to five young (known as 'kits') may be born in a litter, but usually there are fewer (Wilsson 1971; Parker & Rosell 2001; Campbell *et al.* 2005). Zurowski et al. (1974) reported six kits being born to a captive Eurasian female while Starikov & Anchugov (2009) quoted a top figure for the Eurasian beaver of nine kits, suggesting that with sufficient nutrition, larger litter sizes can be achieved. Offspring sex ratios have not been found to deviate from parity (Novak 1987; Parker *et al.* 2002). Mothers lactate for two to three months, though kits can consume solid food at the age of just one week (Wilsson 1971; Zurowski *et al.* 1974). The kits remain in the lodge post-partum and do not emerge until approximately 6 weeks to two months of age (Wilsson 1971). Beaver do not reach sexual maturity until 18 months to two years of age and during this time will remain within their natal territory, after which they may disperse (Svendsen 1980; Hartman 1997).

There is no consistent sex difference in dispersal: For example in the Eurasian beaver, Saveljev *et al.* (2002) found males dispersed further than females while in the North American beaver, Sun *et al.* (2000) found females dispersed further than males and McNew and Woolf (2005) found no sex difference in dispersal. Prior to dispersal, individuals commonly make exploratory excursions into neighbouring territories (Hartman 1997; DeStefano *et al.* 2006; Campbell *et al.* 2005). Full adult size is not attained until the age of three (Pilleri *et al.* 1985). Often, and especially at higher population densities, juveniles continue to reside within the natal territory into adulthood (Campbell *et al.* 2005), possibly due to a lack of suitable vacancies in the surrounding area (Boyce 1981; Műller-Schwarze & Schulte 1999). Yearlings and older philopatric offspring will often assist in parenting by provisioning, and interact with kits (Wilsson 1971; Patenaude 1983), though no direct benefit of alloparenting on reproductive success has been recorded (Campbell *et al.* 2005). Yearlings and philopatric individuals also participate in the construction and maintenance of lodges, dams and food stores, as well as territorial behaviours such as scent-marking (Wilsson 1971; Aeschbacher & Pilleri 1983; Rosell & Thomsen 2006). Outside the lodge or burrow, all individuals within a kin group interact socially if they meet with behaviours such as allogrooming and wrestling (fore limb to fore limb pushing), however they do not tend to forage together (Wilsson 1971).

Predators

Aside from humans, the main historical predators of beavers are wolf, *Canis lupus*, and brown bear, *Ursus arctos* (Rosell & Czech 2000), though lynx, *Lynx lynx*, may also prey on beavers (Rosell and Sanda 2006). Smaller carnivores such as fox *Vulpes vulpes* (Kile *et al.* 1996) and possibly pine marten *Martes martes* (Rosell & Hovde 1998) and otter *Lutra lutra* (Tyurnin 1984) can also predate upon beaver kits and yearlings. There is no evidence that mink *Mustela vision* are predators of beaver kits based on analysis of mink scats in beaver lodges (Brzeziński and Żurowski 1992) and I have witnessed several incidences where a mink and beaver kit have been in close proximity without either animal reacting to the presence of the other.

An introduction to the research topics

The topics in this thesis can be divided into four categories covered in six chapters. These are: growth rates and body size (two chapters), reproductive trade-offs (one chapter), environmental effects (two chapters) and territoriality (one chapter). Each topic was chosen because the beaver could provide a test of the hypotheses that arise from the ecological theory.

Body size and growth rates

Amongst mammals 'dominance' is often linked to body size, which may dictate preferential access to resources or afford greater territory holding or mating success (e.g. Jarman 1983; McElligott *et al.* 2001; Iossa *et al.* 2008). In females, greater body-weight may also be associated with greater fecundity (e.g. Festa-Bianchet 1998). Therefore, in females, a strong trade-off may exist between competitive ability (size) and fecundity (weight).

As a consequence of these incremental benefits of selection for larger individuals, Cope's rule, the tendency for species within a lineage to evolve towards larger body size (see Hone & Benton 2005) has been reported widely in the fossil record (e.g. Alroy 1998; Hone *et al.* 2008, but see Jablonski 1997; Kingsolver & Pfenning 2004; Hunt & Roy 2006). Within species, the fact that there is no central tendency to increase size over evolutionary time suggests that directional selection for larger size must be constrained ultimately by scale-laws on morphology, physiology and ecotype (see Schmidt-Nielsen 1984; Hone & Benton 2005) or by koinophilia, the tendency for individuals to seek a mating partner with no unusual, peculiar or deviant features (*sensu* Koeslag 1990).

Factors that influence early development, such as the rate of growth, can affect an individual's fitness in adulthood (Lindström 1999; Metcalf & Monaghan 2001; Newman *et al.* 2001). However, there is evidence that individuals that experience unfavourable conditions in early life - that lead to smaller body size or lower mass - can still attain equivalent size or mass to their same-age conspecifics, or at least narrow the gap, by adulthood if more favourable conditions return (Arendt 1997; Metcalf & Monaghan 2001; Jobling In press). The mechanisms behind growth recovery are thought to involve a combination of two distinct mechanisms. Firstly, through increasing their subsequent growth rate above that of their peers ('compensatory growth') and/or secondly, through following a normal size-dependent growth trajectory (where the growth rate slows as size increases) that results in a convergence in size or mass with same-age conspecifics by a later date ('catch-up growth') (Arendt 1997; Metcalf & Monaghan 2001; Jobling In press). Although the evidence for compensatory growth in particular is equivocal (e.g. Keech et al. 1999; Solberg et al. 2008; Nicieza & Álvarez 2009), this suggests that these early-developmental effects could be reduced greatly in adulthood. However, compensatory growth is likely to incur a fitness cost to the individual (Arendt 1997; Mangel & Munch 2005) else all individuals would follow this higher growth-trajectory. These fitness costs can involve short-term costs such as greater predation risk due to increased foraging activity (Jönsson *et al.* 1996; Gotthard 2000) or long-term (and usually more difficult to measure) costs such as genetic damage associated with elevated growth (Mangel & Munch 2005) that will influence senescence and lifetime reproductive success

(McNamara *et al.* 2009). These posited costs are therefore not always apparent and several studies have been unable to show the existence of specific costs (e.g. Sikes 1998; Johnsson & Bohlin 2005; Walling *et al*. 2007). Overall, it is probable that any costs will also depend on the trade-offs involved in growth, such as the potential incongruity between attaining large size and high body condition.

Since beavers are monogamous and highly territorial, while not all individuals will secure a breeding position, they should exhibit selection for larger size (explored in chapter 3) with consequences for compensatory growth (explored in chapter 2) and the trade-off between growth and survival (explored in chapter 3). In particular, one would predict that bigger beavers should prove to be competitively superior, that beavers will invest in growth for larger size at the expense of body condition and that this trade off will result in reduced survival.

Reproduction

Understanding the influences on reproduction is crucial to understanding a species' life-history strategy. Fecundity is a product of intrinsic factors (e.g., maternal quality, maternal age and past reproductive effort - Williams 1966; Grafen 1988; Jones *et al.* 2008) and extrinsic factors (e.g., environment and population density - Nussey *et al.* 2005; Balbontín & Ferrer 2008), and thus energetic trade-offs among life-history traits are expected (Williams 1966). Therefore, underlying the above factors, we may find trade-offs that influence an individual's reproductive strategy. Below, I evaluate trade-offs and maternal age as mechanisms for variation in fecundity separately, acknowledging that both mechanisms are inextricably interlinked since the very fact that fecundity changes with age is at least in part due to the trade-offs involved in reproduction.

Trade-offs in reproduction

To reproduce, a mother must expend energy that could have been invested in somatic growth and cellular repair or stored for future requirements (Stearns 1989). Thus reproduction involves a trade-off between current fecundity and growth, survival and future fecundity (Williams 1966; Dijkstra *et al.* 1990). This has implications for the effect of age and past reproductive history on fecundity, elucidated below. In addition, mothers face a trade-off between the number and the quality of offspring (Smith & Fretwell 1974). For example, the best strategy in Soay sheep is generally to give birth to two lambs, but in years with bad weather one lamb will do better, leading to an evolutionary stable strategy (ESS) of producing one larger versus two smaller lambs (Wilson *et al.* 2009).

Since a female beaver may make several reproductive attempts over successive years (iteroparity), we would predict that reproductive output in one year would influence the mother's fecundity in the following year. We would also predict that the number of offspring and their quality would show a negative relationship.

Maternal age and fecundity

In life history theory, the terminal investment hypothesis predicts that reproductive investment will increase with age as an animal's future reproductive value declines (Williams 1966; Pianka & Feener in Smith & Fretwell 1974; Isaac & Johnson 2005). This is because, as mothers age, they are likely to have fewer opportunities for future reproduction. Therefore the trade-off between reproduction and survival (cellular repair and energy storage) should shift away from investment in survival towards higher reproductive effort. Note that reproductive investment may not correlate with fecundity, and therefore a direct positive correlation of fecundity with age is not predicted from this hypothesis. Fecundity may increase with age, however, if maternal experience in acquiring resources and raising offspring improves with age (e.g. Komeduer 1996; Ward *et al.* 2009). An additional influence on fecundity is reproductive senescence, also predicted by life-history theory (Hamilton 1966). Reproductive senescence is a decline in fecundity with age (Jones *et al.* 2008) and can be explained by two hypotheses: the disposable soma hypothesis (Kirkwood 1977; Kirkwood & Rose 1991) and the antagonistic genetic pleiotropy hypothesis (Williams 1957). Under the disposable soma hypothesis, the decline in fecundity with age is due to the interaction between trade-offs in energy allocation to reproduction versus somatic repair and the extrinsic mortality risk. Since no individual of any species will survive indefinitely, in part due to extrinsic factors such as predation, unfavourable environmental conditions or other unfavourable stochastic event, it is advantageous for the organism to not invest in the level of somatic repair that would be required to live a more extended life-span and allocate resources to reproduction instead (Kirkwood 1977; Kirkwood & Rose 1991). Under the antagonistic pleiotropy hypothesis, due to the same extrinsic risk of mortality that leads to the disposable soma, selection acts less on traits that occur later in life (Williams 1957) Therefore any allele that confers an advantage early in life but is pleiotropic for a disadvantageous trait later in life will not be selected against, thus senescence occurs from the expression of deleterious genes later in life (Williams 1957). As a consequence, reproductive output may decline with age despite increasing investment or experience by the ageing parents. These mechanisms lead to the pattern of age related fecundity found in many species where fecundity increases and then declines (e.g. Komdeur 1996; Cichoń 2001; Ericsson *et al.* 2001; Descamps *et al.* 2008; Jones *et al.* 2008; Nussey *et al.* 2009). Distinguishing between the casual mechanisms of senescence patterns is difficult in field studies however, because the predictions are similar and not easily separable. For example, in both the disposable soma and the antagonistic pleiotropy hypotheses, senescence is predicted to occur over a wide range of physiological measures (Kirkwood & Rose 1991; Williams & Day 2003). One point where the predictions of these two hypotheses clearly diverge concerns the interaction between senescence and environment: variation in nutritional history should not influence the timing of senescence under antagonistic pleiotropy (though it may affect its rate), but under the disposable soma hypothesis the trade-off between somatic repair and reproduction will be stronger under poor nutrition. Therefore earlier senescence is predicted in individuals that have experienced lower nutritional intake over their reproductive lives under the disposable soma hypothesis but not the antagonistic pleiotropy hypothesis.

Again, since female beavers breed over several years within the same territory, one can make predictions on the effects of age on fecundity and the interaction between long term resource availability (territory quality), short term resource fluctuations (weather), age and fecundity. In particular, if reproductive senescence is evident in the beaver, one can predict, under the disposable soma hypothesis, that since females in low quality territories will have experienced lower nutrition during their reproductive history; senescence will occur earlier than in females in high quality territories. Conversely, under the antagonistic pleiotropy hypothesis, territory quality is not predicted to influence the timing of senescence. In chapter 4 I test these predictions of reproductive trade-offs and senescence.

Environmental effects on growth, fecundity and survival

Environmental conditions can exert a strong influence on population demographic parameters (Root *et al.* 2006; see examples below). Below I consider the effects of weather (i.e. climate change) on fitness, in particular on herbivores. I begin by exploring the influence of variation in absolute weather conditions and then the effects of changes in the variability of weather.

Absolute variation on weather

Variation in weather may influence fitness directly by changing the physical environment in which the animals live, i.e. the niche characteristics into which the organism “fits”. Mammals, and other homeotherms, incur a greater thermoregulatory cost at lower air temperatures (Wunder 1975), and when exposed to higher wind-chill (Armstrong & Robertson 2000). But Hobbs (1989) also predicted that snow depth would have a strong influence on the energetics of locomotion in mule deer *Odocoileus hemionus*. In addition in terrestrial mammals wetting fur can halve its insulation properties (Webb & King 1984) suggesting that an animal’s energy budget will increase during wet weather.

A potentially more fundamental and significant effect of weather on fitness occurs through the effects on vegetation growth, however, which ultimately affect the resources available to a species. These include effects on forage availability and on seasonal changes in forage quality (plant phenology):

Forage availability:

Within limits, primary productivity increases with both increasing moisture and increasing temperature (Rosenzweig 1968). It has been established that rainfall can benefit aspects of the life histories of various grassland herbivores. For example, increased vegetation growth after high rainfall has been found to increase body condition in red kangaroo *Macropus rufus* while populations of zebra *Equus burchelli*, kudu *Tragelaphus strepsiceros* and kob *Kobus kob leucotis* have been found to increase following above average seasonal rainfall (Fryxell 1987; Owen-Smith 1990; Moss & Croft 1999; Georgiadis *et al.* 2003). Fewer studies have found positive effects of temperature-mediated plant productivity on herbivore populations. In temperate climates, temperature and rainfall are likely to exhibit a negative relationship so that, for example, wet summers tend to be cool and dry summers tend to be warm (Tout 1987) and it is possible that this relationship confounds the indirect effects of temperature on herbivore populations. However, temperature often affects another aspect of plant productivity, namely the timing of growth in seasonal environments (e.g. Cleland *et al.* 2007):

Plant phenology:

In combination with other factors such as photoperiod, variation in weather is also influential on the timing (phenology) of vegetation growth in seasonal environments (Rathcke & Lacey 1985; Cleland *et al.* 2007). In temperate regions, increasing temperatures during spring encourages rapid plant growth after winter dormancy. During the early growth phase, plant tissue generally contains relatively high concentrations of nitrogen (proteins) and digestible energy and relatively low concentrations of structural and defensive compounds such as lignins and phenolics. As tissue growth rate wanes, this situation reverses as nitrogen levels drop rapidly and more energy is allocated to defensive compounds (Mattson 1980; Jones & Hartley 1999; Nolet *et al.* 2005). Therefore, early season vegetation presents a much higher quality food source for herbivores with more energy and higher digestibility, resulting in lower retention rates (i.e. faster digestion) and therefore higher forage intake rates of higher energy per unit time (Demment & Van Soest 1985). Studies on herbivores have shown that either they will feed preferentially on this earlier growth (Wilmshurst *et al.* 1995), or that having access to plants over a greater phenological range improves body condition (Mysterud *et al.* 2001). Thus, for non-migratory animals in seasonal environments, there can be a strong selection pressure to synchronise reproduction with times of peak food availability (Linnell & Andersen 1998; Durant *et al.* 2005; Nolet *et al.* 2005). Temperature may also affect the growth rate of plants, not just the timing of growth, and affect the length of time over which plants are at their peak quality as forage for herbivores. For example, Langvatn *et al*. (1996) suggested that cooler weather enhanced diet quality for red deer by retarding phenological development and slowing the decline in plant digestibility.

Since much of the work that has examined the impacts of weather-mediated effects of resource availability on herbivores has been conducted on ungulates (e.g., Sæther 1985; Wilmshurst *et al.* 1995; Langvatn *et al.* 1996; Post *et al.* 1997; Mysterud *et al.* 2001; Steinheim *et al.* 2004; Nussey *et al.* 2005; Post *et al.* 2008), examining these effect on the beaver provides a test of the generality of the conclusions drawn from ungulate studies. In chapter 5, I examine the effects of annual variation in weather on the body mass and fecundity of the beaver with the prediction that 1) low winter temperatures will reduced body mass though its effects on thermoregulation, 2) high spring temperatures will reduce body mass through its effect on plant phenology and 3) fecundity and both body mass, and fecundity will also increase with total rainfall throughout the growing season due to the effect of rainfall on forage availability.

Variability of weather

Organisms must often make behavioural and life-history decisions based on predictions of future environmental conditions (McNamara *et al.* 1995), such as when to reproduce, how much to invest in reproduction and the amount of resources to defend. Future conditions will be more difficult to predict accurately in fluctuating environments compared with environments that are relative constant, and consequently the degree of stochasticity in the environment can have a significant influence on the optimal phenotype (Tuljapurkar *et al.* 2009). In fluctuating environments, evolution will have honed the decision-making process according to the probability distribution of the environmental conditions experienced by the organism's ancestors (McNamara *et al.* 2001). Therefore, changes in the patterns of fluctuation in the environment can generate changes in the selective pressure on life-histories (Boyce *et al.* 2006; Ruzzante *et al.* 2008). For example, Nouvellet *et al.* (submitted) examined the effects of changes in the unpredictability of the weather (i.e. the deviation in the current weather from historical observations at the corresponding time of year) on fecundity and survival of the badger *Meles meles*. The authors found that temperature unpredictability had increased over time, probably due to anthropogenic climate change, and furthermore that temperature unpredictability reduced both fecundity and survival.

Where some aspect of a species' biology displays a nonlinear response to changes in the environment, such as the asymptotic relationship between the growth rate of many herbivore populations and their resources (Sibly and Hone 2002), there is also the additional implication of Jensen's inequality (Jensen 1906) – a mathematical property of non-linear functions whereby the mean of the response $f(x)$ over the whole range of the predictor x (where the variance of x is greater than zero) is not equal to the response at the mean of x, $f(\bar{x})$. If the function is accelerating (the relationship is convex, e.g. exponential), the mean of $f(x)$ is greater than $f(\bar{x})$ while the opposite holds if the function is decelerating (concave relationship, e.g. asymptotic, see Ruel & Ayres 1999 and Pásztor *et al.* 2000 for reviews). Jensen's inequality has implications for the response of population growth to variation in the environment because it reveals that an increase in the variation of a critical environmental factor, without any change in its mean value, will increase the population growth rate if it displays a convex relationship and decrease it if the relationship is concave. Jensen's inequality is not a hypothesis to be tested *per se*, it is a mathematical artefact that we need to be aware of when examining the response of any non-linear biological system to variability. Thus, in addition to mean values, the variability of weather must also be considered when examining its effects on organisms.

Jarema *et al.* (2009) modelled the effects of predicted climate change on North American beavers in Canada and concluded that population density of beavers should increase in the future. Since potential changes in variability of the weather was ignored in the model (Jarema *et al.* 2009), an examination of the effects of weather variability on beavers will provide additional insight into the potential affects of anthropogenic climate change while extending the work of Nouvellet *et al.* (submitted) from badgers to the beaver. In chapter 6, I examine the effects of temperature and precipitation unpredictability on survival and fecundity in the beaver following Nouvellet *et al.* (submitted), and predict that increase unpredictability of both temperature and precipitation will reduce fecundity and survival.

Territoriality

Maintenance of an area for foraging and breeding to the exclusion of unrelated conspecifics has a very significant impact on a species' population dynamics (Adams 2001). Understanding the mechanisms behind territoriality is thus essential to predict changes in population dynamics and thus aid informed species management. It is generally agreed that the size and shape of the defended areas are dictated by the costs of maintenance (e.g. territory defence) versus the benefits it brings, i.e. exclusive access to a limiting resource such as food, mates and nesting sites (Bekoff and Wells 1982; Davies and Houston 1984; Doncaster and Macdonald 1992; Macdonald 1981, 1983; Macdonald and Carr 1989; Macdonald *et al.* 2004; Stamps 1994). There is less agreement on what form these costs and benefits take, and how they interact with the landscape in which the territory sits (Adams 2001). At its most fundamental, a territory's size would be defined as the defendable area that provides all the needs of the owner at minimum cost, or more accurately, where it gains the greatest net benefit (Brown 1964). Therefore, there is a tendency to find that territory size decreases with a critical resource (Gill and Wolf 1975; Carpenter and MacMillen 1976). Establishing the nature of the resources that provide all the requirements of the territory owner is a critical aspect of the study of territoriality. Resources are rarely distributed evenly in space or time, which has implications for both territory size and the ability of a territory to sustain extra group members. According to the Resource Dispersion Hypothesis (RDH, Macdonald 1983; Carr & Macdonald 1986; Bacon *et al.* 1991), animals maintain the smallest economically defendable area that reliably encompasses sufficient resources for reproduction. Food patches might however be concentrated or widely dispersed. Moreover, food patches will vary in richness. Under the RDH, territory size is determined by food dispersion. When food patches are concentrated spatially and/or temporally, territories will be small, but when food patches are widely dispersed, territories will be large. Group size, on the other hand, is determined by the richness of the most limiting source of key nutrients within the food patches, with territories consisting of rich patches containing larger groups (Macdonald 1983; Carr & Macdonald 1986; Bacon *et al.* 1991). In species that live in groups but forage alone, benefits of group living such as cooperative hunting (e.g. Creel & Creel 1995) or vigilance and defence against predators (e.g. Hass & Valenzuela 2002) do not exist. RDH has been proposed as a mechanism for the sociality of these solitary foraging species, since a territory that is economically configured around spatially or temporally dispersed resources may, in some years or at minimal additional cost, contain sufficient resources for additional individuals (Macdonald 1983; Carr & Macdonald 1986; Bacon *et al.* 1991; Macdonald *et al.* 2004).

In long-lived species with year-round territories, as population density increases, opportunities to expand a territory that has become insufficient for the needs of the resident may decline (Knapton and Krebs 1974). Therefore, a long-term strategy would be to defend a larger area than is required for a single reproductive season. Taking this a stage further for philopatric species, if an owner is able to establish a very good quality territory at high population density, there may be an opportunity to allow offspring to inherit all (territory inheritance), or some part (territory fission) of it and therefore secure a breeding opportunity that may otherwise have been unavailable (Emlen 1996). This long-term strategy is distinct from the discredited concept of super-territoriality (Verner 1977) that involved spite and, more subtly, distinct from the concept of 'empires' (Kruuk and Macdonald 1985).

Beaver are group-living but solitary foragers. Groups are built up through philopatry of offspring, but this build up may actually reduce the reproductive output within the territory (Campbell *et al.* 2005). Although there is likely to be kin selected benefits of group living in the beaver (Hamilton 1964) there are also likely to be costs. In chapter seven, I assess the RDH versus a long-term territorial strategy by examining resource dispersion, territory size, group sizes and territory inheritance and fission in the beaver. Specifically, I predict that under RDH, 1) resource dispersion will dictate territory size but not group size while 2) group size will correlate with resource richness. In contrast, under long-term territoriality, I predict that 3) territory size will not be negatively related to resource richness and 4) reproductive success, group size and the likelihood of territory inheritance or fission will increase with increasing territory richness.

The study area

The study site was centred on three rivers, the Straumen (59°297′ N, 09°153′ E), the Gvarv (59°386′ N, 09°179′ E) and the Sauar (59°444′ N, 09°307′ E), in Telemark, southern Norway (see chapter 5, supplement A for images of the area). The bedrock is granite-gneiss with a thin layer of fluvial (Straumen and Gvarv) or marine (Straumen and Sauar) deposits in valley bottoms. The climate is cool-continental and lies on the boundary of the *Dfb* and *Dfc* classes in the Köppen–Geiger climate classification system (Kottek *et al.* 2006) with a mean annual temperature of 4.6 °C and a mean annual precipitation of 790 mm. Mean monthly 24 hour temperature dips below 0 °C for five months a year between November and March. The rivers flow through a semi-agricultural and populated landscape. Small towns, farms and fields (pasture and arable) are interspersed with riparian woodland dominated by grey alder *Alnus incana* and, to a lesser extent, willow and bird cherry *Prunus padus*, with some dry deciduous and coniferous forest. Where agricultural land is located next to the river, a buffer of riparian woodland or unimproved grass and scrub usually exists. Due to the presence of lakes along their length, which reduce fluctuations in water temperature (Webb & Walling 1996), all rivers exhibit reduced ice cover in winter (though all beaver families in the study area build winter food stores (caches) whether ice-cover occurs or not). All three rivers form part of the catchment of Lake Nordsjø. None of the studied beaver families build dams. Illegal culling is believed to be rare in the area (B Hovde and F Bergan pers. comm.) since few beaver families are in conflict with human land-use. A close relationship is maintained with local hunters, allowing us to keep track of the majority of direct anthropogenic mortality in our population. Hunting pressure is low with 23 of a total of 268 animals shot or kill-trapped during the course of 12 years of study. Predation pressure is also low since wolves have been extirpated from the area for over 100 years, bears only occasionally pass through and lynx are present, but at low densities (Rosell and Sanda 2006). The no figures are available for the otter population in the area, I have only once seen an otter on any of the rivers during >200 nights fieldwork and I would therefore regard the species are rare. Fox, pine marten and mink on the other hand are not uncommon (pers. obs.). Beavers have been in the study area since the 1920s (Olstad 1937).

Population monitoring

Beginning in 1998, this study has monitored beavers through an extensive live-trapping program until 2009, using hand-nets from a motorboat, between March and November (Rosell & Hovde 2001). Captured individuals are immobilized in cloth sacks, sexed based on the colour of the anal gland secretion (Rosell & Sun 1999), tagged with a microchip (Avid or Trovan) and marked with unique colour-plastic (Dalton) and metal (National Band and Tag Co.) ear-tag combinations. All trapping and handling procedures were approved by institutional ethical review committee. Animals were assigned to an age-class (0 years = kit, 1 years = yearling, 2 years = subadult and ≥3 years = adult) based on body-weight (Rosell *et al.* in prep, Appendix 1). Recaptures resulted from either the trapping or sighting of marked animals. An animal was assumed to be resident in a territory if it was trapped or sighted in the same territory more than once >24h apart, or was seen interacting non-agonistically with other known residents. Dominance status was determined by previous trapping sighting history and incidences of lactation in females. For example, individuals dispersing into a territory were posited to have obtained the dominant breeding position, an assumption generally corroborated by data indicating the disappearance (usurpation) of the previous dominant individual of the same sex and, for females, lactation (signified by nipple length > 0.5cm). In the majority of cases, where animals were already present in the territory at the beginning of the study, dominance status was explicit as other same-sex adult group members dispersed, or disappeared, and were not replaced by new animals. On two occasions, where more than one animal was a potential dominant individual, we resorted to the use of body weight to distinguish status, with dominance being assumed for the heaviest individual following Smith *et al.* (1994). Unless there was evidence to the contrary, dominant individuals were assumed to maintain their status until they disappeared or died. Reproduction in each year was determined by counting the number of kits trapped that year plus the number of yearlings trapped the following year that had not previously been trapped as kits. Therefore, our measure of fecundity consists of both reproductive output and mortality prior to emergence at 1.5 – 2 months old, plus any post-emergence mortality prior to the kits being detected. Unmarked kits or yearlings were also included if they were sighted in a territory but not trapped and all other known kits or yearlings were accounted for. In addition, one kit and one yearling shot by local hunters were included in the analyses.

The study population

The study population is typical of a K- selected species with numbers skewed towards the adult age class (Table 1) and low offspring and adult mortality (Table 2). Though there are slightly fewer females than males (Table 1), the sex ration does not deviate from parity in any of the age classes (1999 – 2008: kit, $X^2 = 0.15$, N = 108; yearlings, $X^2 = 0.16$, N = 98; subadult, $X^2 = 0.06$, N = 157; adult, analysed seperatley for each year, $X^2 = 0 – 2.12$, N = 21 – 75, $p > 0.05$ in all cases). A lower recapture rate is evident from age 1 – 2 and 2 – 3 (Table 2), perhaps partially due to the dispersal of many two and three year old individuals out of the study area where there fate is unknown. Philopatry is common in both sexes and individuals frequently do not obtain breeding positions (the within-sex dominant position in a territory) until several years after attaining sexual maturity (see Table 2b). Succesfull reproduction by the dominant pair did not occur every year and younger and older mothers may exhibit lower reproductive output (Table 2a) though females are still capable of reproducing at 10 years old (Table 2b). Most animals lost to the population were simply not recaptured, and thus their fate is unknown (Table 3). A small, but significant, proportion of losses were however due to kill-trapping, shooting or translocation (Table 3). Though there appears to be a peak of these at three years of age, six of the 11 animals lost unnaturally at this age were translocated to Great Britain (Table 3). Unnatural losses appear to be much lower in older individuals however (Table 3), plausibly because older animals survived in territories that came into less conflict with human land-use.

Table 1: Age structure of the population between 1999 – 2008, given as the mean number in each age class alive in the study area each year. Figures are given for each sex together with the combined total, which includes 19 animals (mean two / year) in the kit and yearling age classes that were never trapped and thus not sexed. Numbers in parentheses represent the mean of the proportion of individuals in each year that were in the age class. Years prior to 1999 were ignored as the overall view of the population was incomplete during the initial phases of the project.

	Mean number (proportion) 1999-2008		
Age class	Total	Male	Female
Kit	13 (0.13)	6 (0.11)	5 (0.11)
Yearling	12 (0.12)	5 (0.10)	5 (0.10)
Subadult	16 (0.16)	8 (0.16)	8 (0.17)
Adult	59 (0.60)	32 (0.63)	26 (0.61)

Table 2a: Age specific figures on number of animals, recapture rate, number in breeding positions and numbers successfully breeding. Recaptures at age *x*+n indicates a live recapture at any time in the following years. Breeding positions equate to holding a territory with a member of the opposite sex. The proportion of females reproducing is the proportion of all females, irrespective of their territorial status. Data from individuals between 1 – 2 years old whose age could reliably be determined (see Appendix I) where back-calculated to age 0 (kits). Data is from all animals in the population between 1997 – 2009 and therefore ages from 2 – 12 are the minimum age since it is not always possible to age immigrant adults beyond 2 – 3 years old. Note therefore the increase in the sample at age two and three as new animals arrive in the population (these figures all include adults already incumbent in the area at the beginning of the project).

Age (years) *x*	Number of individuals observed of age *x*			Number (proportion) recaptured at age *x*+n			Number (proportion) in breeding positions at age *x*			N (proportion) of females reproducing at age *x*
	Total	Male	Female	Total	Male	Female	Total	Male	Female	
0	122	54	49	105 (0.87)	52 (0.97)	45 (0.92)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)
1	81	40	34	56 (0.70)	33 (0.83)	23 (0.68)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)
2	148	79	66	114 (0.78)	61 (0.78)	53 (0.81)	50 (0.34)	22 (0.28)	28 (0.43)	1 (0.02)
3	133	70	63	104 (0.79)	56 (0.80)	48 (0.77)	72 (0.55)	32 (0.46)	40 (0.64)	10 (0.16)
4	96	52	44	84 (0.88)	44 (0.85)	40 (0.91)	65 (0.68)	33 (0.64)	32 (0.73)	13 (0.30)
5	66	37	29	55 (0.84)	29 (0.79)	26 (0.90)	49 (0.75)	26 (0.71)	23 (0.80)	8 (0.28)
6	50	28	22	42 (0.84)	24 (0.86)	18 (0.82)	40 (0.80)	21 (0.75)	19 (0.87)	8 (0.37)
7	38	22	16	33 (0.87)	19 (0.87)	14 (0.88)	33 (0.87)	19 (0.87)	14 (0.88)	6 (0.38)
8	32	19	13	28 (0.88)	15 (0.79)	13 (1.00)	30 (0.94)	17 (0.90)	13 (1.00)	6 (0.47)
9	26	14	12	23 (0.89)	13 (0.93)	10 (0.84)	25 (0.97)	13 (0.93)	12 (1.00)	2 (0.17)
10	17	8	9	16 (0.95)	8 (1.00)	8 (0.89)	17 (1.00)	8 (1.00)	9 (1.00)	2 (0.23)
11	12	6	6	11 (0.92)	6 (1.00)	5 (0.84)	12 (1.00)	6 (1.00)	6 (1.00)	0 (0.00)
12	4	2	2	3 (0.75)	2 (1.00)	1 (0.50)	4 (1.00)	2 (1.00)	2 (1.00)	0 (0.00)

Table 2b: Age specific figures on number of animals, recapture rate, number in breeding positions and numbers successfully breeding. Recaptures at age x+n indicates a live recapture at any time in the following years. Breeding positions equate to holding a territory with a member of the opposite sex. The proportion of females reproducing is the proportion of all females, irrespective of their territorial status. Data from individuals between 1 – 2 years old whose age could reliably be determined (see Appendix I) where back-calculated to age 0 (kits). Data is only from animals born in the study area and trapped by two years of age and therefore all ages are exact. Note that despite high recapture rates from seven years, the sample size continues to decrease. This is due to discounting of animals alive when the study period ended in 2009.

Age (years) x	Number of individuals observed of age x			Number (proportion) recaptured at age x+n			Number (proportion) in breeding positions at age x			N (proportion) of females reproducing at age x
	Total	Male	Female	Total	Male	Female	Total	Male	Female	
0	122	54	49	105 (0.87)	52 (0.97)	45 (0.92)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)
1	81	40	34	56 (0.70)	33 (0.83)	23 (0.68)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)
2	63	39	21	45 (0.72)	30 (0.77)	15 (0.72)	2 (0.04)	0 (0.00)	2 (0.10)	0 (0.00)
3	40	28	12	33 (0.83)	22 (0.79)	11 (0.92)	7 (0.18)	4 (0.15)	3 (0.25)	0 (0.00)
4	27	18	9	25 (0.93)	17 (0.95)	8 (0.89)	11 (0.41)	7 (0.39)	4 (0.45)	1 (0.12)
5	19	13	6	15 (0.79)	10 (0.77)	5 (0.84)	8 (0.43)	6 (0.47)	2 (0.34)	0 (0.00)
6	14	10	4	11 (0.79)	8 (0.80)	3 (0.75)	7 (0.50)	5 (0.50)	2 (0.50)	1 (0.25)
7	10	7	3	9 (0.90)	6 (0.86)	3 (1.00)	7 (0.70)	5 (0.72)	2 (0.67)	0 (0.00)
8	9	6	3	9 (1.00)	6 (1.00)	3 (1.00)	8 (0.89)	5 (0.84)	3 (1.00)	2 (0.67)
9	8	6	2	8 (1.00)	6 (1.00)	2 (1.00)	7 (0.88)	5 (0.84)	2 (1.00)	0 (0.00)
10	5	3	2	5 (1.00)	3 (1.00)	2 (1.00)	5 (1.00)	3 (1.00)	2 (1.00)	2 (1.00)
11	1	1	0	1 (1.00)	1 (1.00)	-	1 (1.00)	1 (1.00)	-	-
12	1	1	0	1 (1.00)	1 (1.00)	-	1 (1.00)	1 (1.00)	-	-

Table 3: Causes of losses from the study population at each age. Figures in parentheses are the proportion of losses while sample size is the total number of all animals alive at the start of the age. Most individuals simply disappeared (i.e failure to recapture) but some were recovered dead, either due to disease, unknown causes or from injuries sustained during intra-specific conflict (all classed as natural losses) or due to shooting, kill-trapping or live removal for translocation to the Great Britain (all classed as unnatural losses). Ages are minimum ages.

		Cause of loss: number (proportion of all losses)		
Age (years)	Sample size	Disappeared	Natural death	Unnatural death
0	122	18 (1.00)	0 (0.00)	0 (0.00)
1	81	22 (0.76)	0 (0.00)	7 (0.25)
2	148	25 (0.84)	1 (0.04)	4 (0.14)
3	133	16 (0.58)	1 (0.04)	11 (0.40)
4	96	8 (0.67)	1 (0.09)	3 (0.25)
5	66	7 (0.64)	0 (0.00)	4 (0.37)
6	50	5 (0.63)	1 (0.13)	2 (0.25)
7	38	1 (0.20)	2 (0.40)	2 (0.40)
8	32	3 (0.75)	1 (0.25)	0 (0.00)
9	26	2 (0.67)	1 (0.34)	0 (0.00)
10	17	1 (1.00)	0 (0.00)	0 (0.00)
11	12	1 (1.00)	0 (0.00)	0 (0.00)
12	4	1 (1.00)	0 (0.00)	0 (0.00)

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Size matters: growth trajectories and compensatory growth in the Eurasian beaver

Abstract

Studies of growth trajectories and the pattern growth takes can improve understanding of the effects of environmental conditions experienced during early development and their consequences for a species' population dynamics.

There is evidence that individuals that experience unfavourable conditions early in life that impede growth can recover to attain a similar size or weight to that of their peers by adulthood. Compensatory growth is where this growth recovery is achieved by increasing growth rate above normal levels whereas catch-up growth is where recovery is a result of convergence of normal size-specific growth trajectories as growth rates slow when animals near full size.

We examine specific growth rates compensatory growth and catch-up growth in size and weight in the Eurasian beaver (*Castor fiber*), a large, sexually monomorphic, territorial and herbivorous semi-aquatic rodent. We predicted that beavers would invest in compensatory growth in size over weight because large size, which may provide a competitive advantage, is fixed in adulthood whereas weight is not.

Comparing weight and size of animals between all four age-classes, we found evidence for size recovery from kit (age 0) to older (age 1-3) age-classes and the sub-adult (age 2) to adult age-class and weight recovery from kit to both sub-adult and adult age-classes, suggesting that either catch-up or compensatory growth may have occurred.

Accounting for size-specific growth, we found that animals which were structurally small relative to same–age peers showed a greater rate of size increase between kit to yearling and yearling to sub-adult age-classes. The same pattern was not evident for body weight, suggesting that compensatory growth was occurring in body-size and not weight.

At each transition between consecutive age-classes, individuals that exhibited higher size-growth rates also showed lower body-condition at the end of the transition. Therefore

size was compensated at the expense of body-condition. Beavers that experience poor conditions during early development may trade-off short-term body-condition for greater lifetime reproductive potential.

We suggest that including size in measures of catch-up and compensatory growth will shed new light on the details of the trade-offs involved in growth decisions.

Introduction

Factors that influence early development can affect an individual's fitness in adulthood (Lindström 1999; Metcalf & Monaghan 2001). However, there is evidence that individuals that experience unfavourable conditions in early life - that lead to smaller body size or lower weight - can still attain equivalent size or weight to their same-age peers, or at least narrow the gap, by adulthood if more favourable conditions return (Arendt 1997; Metcalf & Monaghan 2001; Jobling In press). The mechanisms behind growth recovery are thought to involve a combination of two distinct mechanisms. Firstly, through increasing their growth rate above that of their peers ('compensatory growth') and/or secondly, through following a normal size-dependent growth trajectory (where the growth rate slows as size increases) that results in a convergence in size or weight with same-age peers ('catch-up growth') (Fig. 1, Arendt 1997; Metcalf & Monaghan 2001; Jobling In press). Although the evidence for compensatory growth in particular is equivocal (e.g. Keech et al. 1999; Solberg et al. 2008; Nicieza & Álvarez 2009), it suggests that early-developmental effects could be greatly reduced in adulthood by these mechanisms. However, compensatory growth is likely to contain a fitness cost to the individual (Arendt 1997; Mangel & Munch 2005) because otherwise all individuals would follow this higher growth-trajectory. These fitness costs can involve short-term costs such as greater predation risk due to increased foraging activity (Jönsson, Johnsson, & Björnsson1996; Gotthard 2000) or long-term (and usually more difficult to measure) costs such as genetic damage associated with elevated growth (Mangel & Munch 2005). Therefore these posited costs are not always apparent and several studies have been unable to show the existence of specific costs (e.g. Sikes 1998; Johnsson & Bohlin 2005; Walling et al. 2007). Overall, it is likely that any costs will also depend on the trade-offs involved in growth. For example, in many species both body weight and size are important life-history components that may confer an advantage in competition for resources such as mates or territories (e.g. Jarman 1983, Iossa et al. 2008). Yet size and weight are separate, though correlated, components of growth and so presumable a compromise is attained between increasing size and weight.

The Eurasian beaver (*Castor fiber* L.) is a large (> 20 kg at adulthood) herbivorous semi-aquatic rodent (Wilsson 1971; Műller-Schwarze & Sun 2003). Beavers are monogamous (but see Crawford et al. 2008) and highly territorial (Campbell et al. 2005; Rosell & Thomsen 2006) with intra-specific aggression being a major cause of mortality (Piechocki 1977). Beavers live in family groups and only the dominant pair breeds (Wilsson 1971; Műller-Schwarze & Sun 2003). Young (known as 'kits') are born around May and emerge from the natal den or lodge when weaned, approximately two months later (Wilsson 1971). Beavers can attain sexual maturity at two years of age but do not reach full adult size until the age of three (Wilsson 1971; Pilleri, Kraus & Gihr 1985; Rosell, Zedrosser & Parker. In press). In colder climates, particularly where water becomes iced-over in winter and beavers are unable to access land, they build a food cache in autumn which they use to survive until spring (Hartman & Axelsson 2004). Consequently, beavers can experience pronounced variation in nutrient availability between winter, when they are restricted to feeding on their cache or on winter browse, and spring-summer when new plant growth is available. Juvenile beavers may also experience significant cohort variation in body weight between years due to variation in weather (Chapter 5).

We examine specific growth rates, catch-up growth and compensatory growth in body weight and body-length between four age-classes in the Eurasian beaver. We hypothesise that because beavers are monogamous and highly territorial, and because large body-size is likely to carry a significant advantage in territorial contests in both sexes, compensatory size increases will occur in relatively small juveniles. As growth in beavers is likely to involve a trade-off between increasing size and building energy reserves to survive times of nutrient scarcity, we therefore predict that individuals will compensate for size at the expense of body-condition.

More precisely, we predict the following:

1) Evidence for both catch-up and compensatory growth (growth recovery): A commonly used correlative test for the absence of compensatory or catch-up growth is to examine the correlation in size or weight between times t_1 and t_2. However, a statistically significant positive correlation does not demonstrate the absence of compensatory or catch-up growth (compensation may be imperfect, or there may have been insufficient time for the growth trajectories to converge). For example, in Fig. 1, size at point *a* and *b* will correlate under all three scenarios. Only once an asymptote in growth has been attained (usually in adulthood) would we expect that full (as opposed to partial) catch-up or compensatory growth might result in a lack of correlation. We therefore predict that if full catch-up or compensatory growth is occurring in our beaver population, correlations in size and weight between age-classes will disappear only by the adult age-class.

2) Evidence for catch-up growth versus compensatory growth: Gendreau, Cote, & Festa-Bianchet (2005) and Dale et al. (2008) both used the negative relationship of size or weight at time t_1 with the change in size or weight between times t_1 and t_2 as evidence for compensatory growth in, respectively, mountain goats (*Oreamnos americanus,* Blainville) and caribou (*Rangifer tarandus* L.). There are two issues with this method however. Firstly, if we examine size at points *a* and *b* in Fig. 1, we can see that both catch-up and compensatory growth will exhibit this relationship, because growth rate varies with size. Size dependent growth trajectories such as that found in Fig. 1 are widespread (Kaufmann 1981; West, Brown & Enquist 2001). Secondly, analyses that examine the change in a

variable between two points in time are potentially confounded by a statistical artefact commonly termed as 'regression to the mean' (Galton 1886; Healy & Goldstein 1978). Regression to the mean, in the context of measuring the effect of initial size (or weight) on the susequent change in size, may arise because an individual whose size is initially recorded in error as smaller than its true size is less likely to have its size recorded with the same degree of negative error at the next measurement and an individual who is recorded in error as larger than true size is less likely to have its size recorded with the same degree of positive error at the next measurement. As a result, those recorded as small are likely to exhibit an increase in size than those that are recorded as large (who may even show a reduction in size if growth has actually ceased) and thus we expect to find a negative relationship between initial size and the subsequent change in size as a result of regression to the mean. If size (or weight) changes over the year, the same argument will then apply for measurements recorded at different points in different years since an individual that was measured very early in one year is less likely to be measured at such an early point in the next year and vice versa.

The change in size or weight cannot then be used as a prediction for compensatory growth as distinct from catch-up growth due to size dependent growth trajectories (Nicieza & Álvarez 2009) and analyses that use change in a variable need to account for regression to the mean. The size-specific growth rate is however different between a catch-up and a compensatory trajectory. Therefore, we predict:

i. If compensatory growth is occurring, we will see a greater growth rate in individuals that are smaller than other conspecifics of equivalent age only after the effects of regression to the mean and size on growth rate have been taken into account. We make no predictions here of how size differences may have come about. Unfavourable conditions

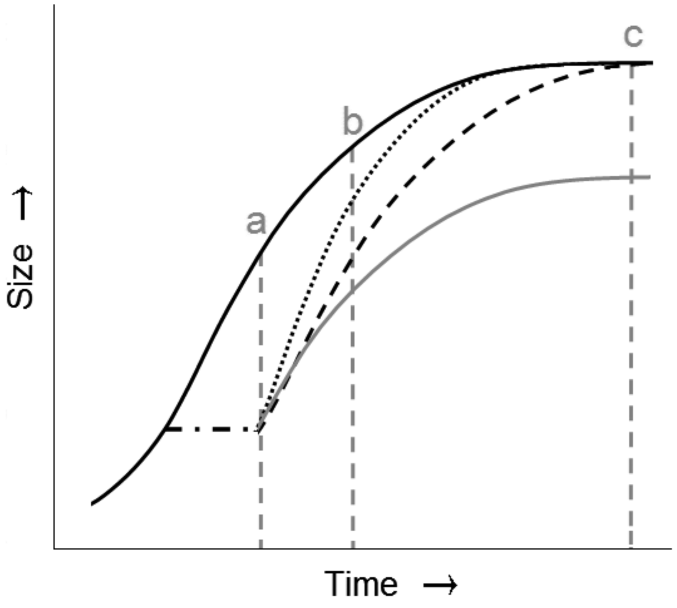

Figure 1. Hypothetical growth trajectories adapted from Jobling (In press). The solid black line follows a typical size-dependent growth trajectory. The horizontal dash-dot line represents a break in the growth trajectory, due to some external factor, which is removed by time *a*. From time *a*, growth restarts and follows one of two trajectories. The dashed black line follows the same size-dependent growth trajectory as before the interruption and represents 'catch-up' growth. The dotted black line follows a more rapid size-dependent growth trajectory and represents 'compensatory growth'. Note that between time *a* and *b*, both catch-up and compensatory growth result in a reduction in the difference in size with the normal uninterrupted growth trajectory. If size were only measured at times *a* and *c*, we would be unable to distinguish between catch-up and compensatory growth. Individuals that have experienced an interruption in their growth may simply be unable to follow their original growth trajectory, perhaps due to seasonal constraints on resources, and therefore never attain their full potential size (solid grey line).

could be specific to an individual or litter (e.g., poor maternal condition or late birth), or specific to a cohort (i.e., environmental stochasticity).

ii. If catch-up growth is occurring, no difference in the size specific growth rates will be visible, while size or weight differences will nevertheless have narrowed by time t_2.

Note that if Fig. 1 is an accurate representation of the alternative growth strategies, these last two predictions may break-down as the animal nears its full size because animals showing growth compensation will attain an asymptote before those that exhibit catch-up growth.

Materials and methods

Study site

The study site was centred on three rivers, the Saua (Nome municipality), the Gvarv and the Sauar (both Sauherad municipality), in Telemark, southern Norway (59°23′ N, 09°09′ E). The mean monthly temperature dips below 0 °C for five months a year between November and March. All rivers contain lakes along part of their length, resulting in only limited fluctuations in water temperature along the main river channels and thus reduced ice cover in winter (though all beaver families in the study area build food stores whether ice-cover occurs or not). All three rivers form part of the catchment of Lake Nordsjø.

Trapping program and sampling

From 1998 - 2008, beavers in the study areas were monitored through an extensive live-trapping program using hand-nets from a motor boat between March and November (spring-autumn, Rosell & Hovde 2001; Campbell et al. 2005). Captured individuals were immobilized in cloth sacks and measured. Measurements recorded were weight (to the nearest 200 g), body-length (cm) following the curvature of the spine from the nose-tip to the base of the tail (where fur gives way to scales), tail-length (cm) from the base to tip of tail and tail-width (cm) from edge to edge of the dorsal surface at the mid-point between base and tip. Animals were sexed by examining the colour of the anal-gland secretion (Rosell & Sun 1999). Individuals were tagged with a microchip (Avid or Trovan) and marked with unique colour-plastic (Dalton) and metal (National Band & Tag Co.) ear-tag combinations to aid repeated identification on recapture.

Animals were divided into four age-classes: 'kits' (0 years), 'yearlings' (1 year), 'sub-adults' (2 year) and 'adults' (≥3 years). For all analyses of compensatory growth and its consequences, we compared growth between these four age-classes. Sample sizes were (*N records, N animals*): kits = 89, 80; yearlings = 101, 77; sub-adults = 69, 51 and adults = 410, 137. Not all animals were trapped in every age-class and therefore sample-sizes for age-class transitions were lower (Tables 2 and 3).

Growth rates

We used Gompertz curves to calculate specific growth rates (SGR) using the equation: SGR = $(ln\ S_{t2} - ln\ S_{t1}) / (t_2 - t_1)$, where S_{t1} and S_{t2} was the body weight (kg) or body-length (cm) on days t_1 and t_2 respectively (Kaufmann 1981). The *ln* geometric mean of S_{t1} and S_{t2} (hereafter called $ln\ gmS_{t12}$) was used as a predictor of SGR to calculate the size-specific growth rate (sSGR) following Kaufmann (1981).

Data analysis

Some individuals were trapped more than once within each age-class potentially creating issues of pseudoreplication during analyses of specific growth rates. These repeated measures were included in the SGR regression analyses. However, general linear models (GLMs) using animal ID were constructed to control for pseudoreplication.

For analyses of compensatory growth, we examined both the effects of prior weight and size ($ln\ S_{t1}$) on later weight and size ($ln\ S_{t2}$), and the effect of prior weight and size ($ln\ S_{t1}$) on the rate of increase in weight and size (SGR) to later age-classes. Where an animal had been measured more than once within an age-class, the geometric mean value of weight, size and day-of-capture was used. Because animals were measured at different times over spring-autumn each year, the effect of $ln\ S_{t1}$ on $ln\ S_{t2}$ was analysed using linear regression with days of capture (t_1 and t_2) being included in the model to control for the confounding effect of the increase in size and weight over spring-autumn. In analysing the effect of S_{t1} on SGR to t_2, it is necessary to account for size-dependent growth (Nicieza and Álvarez 2009). Our prediction is that within each age-class, individuals that are relatively small, given the time of year they were measured, will show a higher growth rate, after accounting for the confounding inverse relationship between size and growth rate. Therefore, we initially constructed sequential (type I) GLMs with SGR between times t_1 and t_2 as the response variable and, in order, gmS_{t12}, t_1 and $ln\ S_{t1}$ as predictor. However, high multicollinearity between all predictors led to model overfitting and it was thus necessary to replace the t_1 and $ln\ S_{t1}$ variables with a date-corrected $ln\ S_{t1}$ variable calculated from the residuals of the regression of t_1 on $ln\ S_{t1}$.

It was also necessary to account for the potentially confounding effect of regression to the mean (RTM) in the analysis of SGR. Since both RTM and compensatory growth predict the same relationship of $ln\ S_{t1}$ on SGR after accounting for sSGR, distinguishing between RTM and $ln\ S_{t1}$ is very difficult in growing animals. Therefore, we constructed a linear regression of t_1 and $ln\ S_{t1}$ on SGR using fully grown individuals of at least four years old. Any effect of $ln\ S_{t1}$ on SGR is likely to be due to RTM alone. The coefficients from the model were then used to calculate the expected difference between S_{t1} and S_{t2} arising from RTM in younger animals. Expected RTM was then subtracted from SGR prior to further analysis of SGR. Since the effects of errors resulting in RTM are likely to be scale dependent, in the initial regression and when used as a correction factor, $ln\ S_{t1}$ was divided by the mean $ln\ S$ for each age-class.

To examine the potential cost of compensatory size-growth on body condition, we used body weight as the response variable while included body-length as an explanatory variable following Freckleton (2002). Therefore, GLMs were constructed with weight at time t_2 as the response variable against days-of-capture at times t_1 and t_2, body-length at time t_2, plus SGR (body-length) between times t_1 and t_2 as the predictors. Again, predictors were added sequentially into the model in the order of day-of-capture at time t_2, body-length, day-of-capture at time t_1 and then the SGR predictor.

All data were analysed in *R* 2.9.2 (R Development Core Team 2009).

Results

Specific growth rates

Specific growth rate of both body weight and body-length exhibited an inverse relationship with body weight and body-length respectively (Table 1). The beavers in our study exhibit seasonal growth, with animals gaining body weight and length rapidly in spring-autumn but loosing body weight (Fig. 2) and increasing body-length more slowly in winter. As a result, sSGR was significantly greater within years than between years for body weight (Table 1, Figs 2 and 3a), though not for body-length (Table 1, Fig. 3b). The within-year sSGR indicated that growth reached a plateau at 22.27kg. There was no difference between the sexes in body weight and body-length, but females exhibited a

Table 1. The effect of ln geometric mean body weight and body-length on specific growth rate. Intercept and slope are from linear regressions, whereas slope (ind), F, df and P values are from GLMs nested within animal ID to control for pseudoreplication. *WBY* is a binary variable where 0 = measurements recorded within the same year and 1 = measurements recorded between years.

Variable		Intercept	Slope		SE	Slope (ind)	F	df	P	
ln mean Body mass (kg)	All	0.0103	-0.0034	±	0.0002	-0.0037	165.92	139, 277	<0.001	***
	Females	0.0111	-0.0036	±	0.0003	-0.0049	67.4	73, 173	<0.001	***
	Males	0.0096	-0.0031	±	0.0002	-0.0026	97.06	65, 103	<0.001	***
	sex (males)		-0.0013	±	0.0010		<0.01	1, 416	0.946	
	sex*mass						17.74	1, 276	<0.001	***
	Within years	0.0168	-0.0054	±	0.0004	-0.0065	73.66	74, 65	<0.001	***
	Between years	0.0065	-0.0021	±	0.0001	-0.0023	564.00	129, 146	<0.001	***
	WBY*mass						57.29	1, 275	<0.001	***
ln mean Body-length (cm)	All	0.0128	-0.0029	±	0.0003	-0.0021	20.27	133, 250	<0.001	***
	Females	0.0112	-0.0025	±	0.0004		7.10	59, 97	0.009	**
	Males	0.0142	-0.0032	±	0.0004		13.57	73, 152	<0.001	***
	sex (males)		0.0024	±	0.0042		0.05	1, 383	0.818	
	sex*length			±			0.34	1, 249	0.558	
	Within years	0.0184	-0.0042	±	0.0008	-0.0023	1.70	71, 51	0.197	
	Between years	0.0099	-0.0023	±	0.0001	-0.0026	264.405	124, 135	<0.001	***
	WBY*length						1.588	1, 248	0.209	

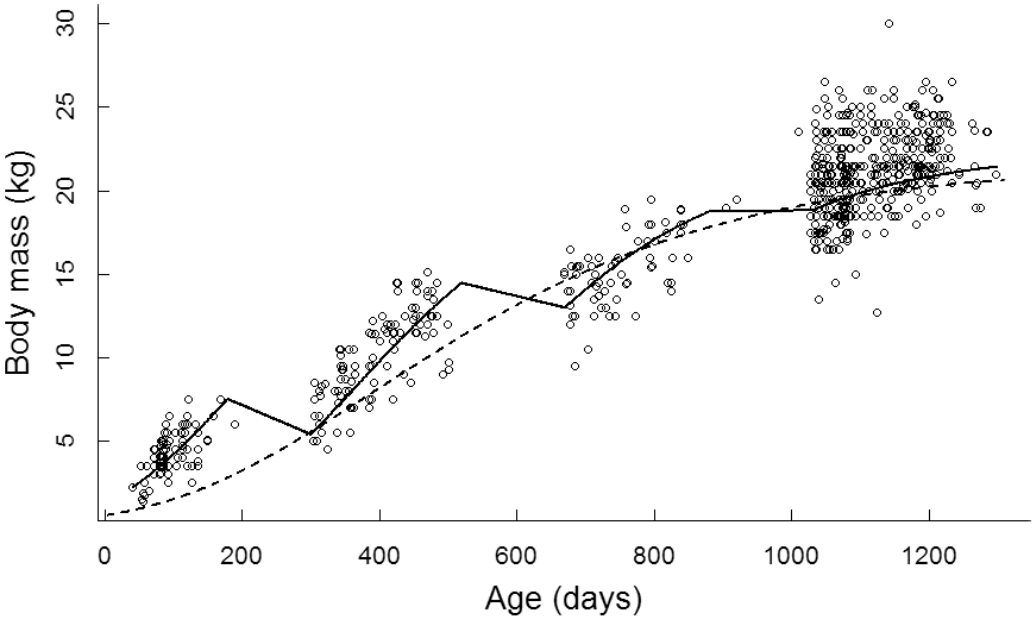

Figure 2. Body weight (kg) if beavers with age in days, assuming a birth date of 13th May. Age-class differences are clearly visible. Gaps in the data correspond to winter. Data from animals >1000 days old includes all animals ≥3 years old and therefore the age in days may be *n*×365 days older than indicated. The dashed line is the Gompertz curve obtained from measurements repeated both within and between years. The solid line is the Gompertz curve obtained from measurements repeated within years only and was broken over periods where no animals were measured (winter), with the curve restarted at the mean weight of all animals captured in March. Winter gaps have been interpolated with a straight line.

steeper relationship between body weight and the SGR of body weight, but not body-length (Table 1, Fig. 3b,d). The Gompertz curve based on within-year data plotted in Fig. 2 (solid line) predicts a birth date of approximately 27th March, assumed a birth weight of 0.525kg (Parker & Rosell 2001). Yet previous work examining foetus development in beavers in the same catchment found a mean birth date of 13th May (Parker & Rosell 2001).

Compensatory growth

Body weights of individuals were significantly positively related to their body weight in the previous age-class from kits to yearlings, yearlings to both sub-adults and adults, and sub-adults to adult, but not for kits to sub-adults or kits to adults (Table 2). The significant results of both yearlings to adult and sub-adult to adult suggest that growth recovery of body weight is weak or does not occur. The non-significant relationship from kits to sub-adults and kits to adults could indicate that growth recovery occurs over longer time periods, sample sizes were however small for these age-class transition. Body-lengths of individuals were significantly positively related to their body-length only from yearlings to sub-adults and yearlings to adults (Table 2), suggesting that some growth recovery of size may occur in kits and in sub-adults, and is weaker in yearlings.

In full grown adults of at least four years of age, the effect of $ln\ S_{t1}$ on the daily change between S_{t1} and S_{t2} was significant for both body weight ($\beta = -0.003$, $r^2 = 0.149$, df = 259, $P < 0.001$) and body length ($\beta = -0.009$, $r^2 = 0.108$, df = 224, $P < 0.001$), indicating that regression to the mean was an issue in the data.

After controlling for sSGR and RTM, there were no significant relationships of SGR between any age-class and the body weight in the preceding age-class - i.e., body weight did not predict the rate of increase in weight in the later age-class (Table 3, Fig. 4a,c,e), indicating that lower-weight individuals did not increase their body weight any more or less than did heavier individuals. Body length was a significant negative predictor of the SGR between kits and yearlings and between yearlings and sub-adults (Table 3, Fig. 4b,d), but not between other age-class transitions (Table 3, Fig. 4f). Four possible outliers in three of the age-class transitions did significantly influence these results (Table 3, Fig. 4a,b,f). These results suggest smaller individuals increased their size more than did larger individuals in the juvenile age-classes at least.

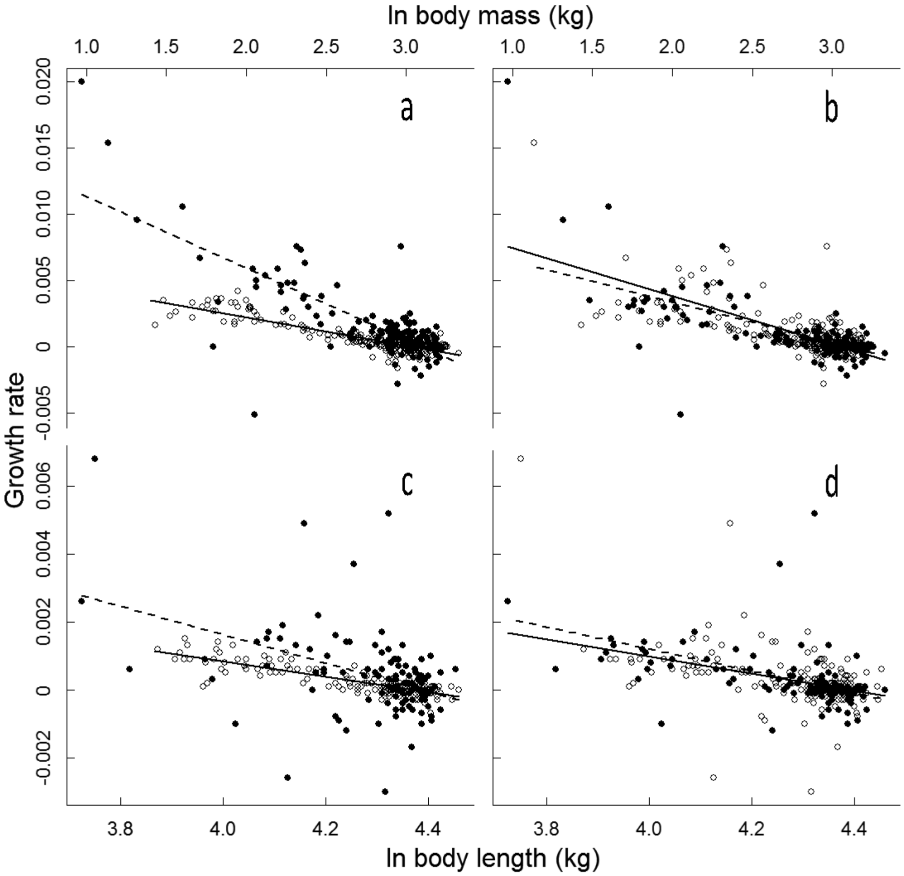

Figure 3. Increase (*ln* day^{-1}) in (a, b) body weight and (c, d) body-length against *ln* geometric-mean body weight and body-length respectively. Open circles and the solid regression line are data repeated between years (a, c) or represent male beavers (b, d) whereas filled circles and the dashed regression line are data repeated within years (a, c) or represent females (b, d). The differences in slopes between within- and between-year data and between males and females were only significant for body weight.

Table 2. The effect of ln body-mass and body-length in the prior age-class on the same variable in the same animal in the later age-class. Values were obtained by using GLMs incorporating day-of-capture (1st Jan = 1) in both the prior and later age-class and the mass or size measure. R^2 values are for the entire model whereas all other values are for the individual predictors. BM = body weight, BL = body-length. Significant relationships are marked with asterisks where * = $P < 0.05$, ** = $P < 0.01$ and *** = $P < 0.001$.

Age-class		Yearling					Sub-adult					Adult				
	Metric	Slope	SE	r^2	df	P	Slope	SE	r^2	df	P	Slope	SE	r^2	df	P
Kit	BM ln(kg)	0.437	± 0.131	0.736	24	0.003**	0.137	± 0.091	0.698	12	0.156	0.127	± 0.235	0.271	9	0.601
	BL ln(cm)	0.252	± 0.113	0.586	22	0.072	0.130	± 0.173	0.412	11	0.468	0.052	± 0.128	0.354	9	0.695
Yearling	BM ln(kg)						0.404	± 0.068	0.739	24	<0.001***	0.312	± 0.145	0.479	17	0.046*
	BL ln(cm)						0.327	± 0.110	0.446	21	0.007**	0.387	± 0.107	0.416	16	0.002**
Sub-adult	BM ln(kg)											0.578	± 0.191	0.440	16	0.008**
	BL ln(cm)											0.070	± 0.082	0.114	14	0.408

Table 3. The effect of prior ln body-mass and body-length on the specific growth rate to later age-classes after accounting for size-specific growth and regression to the mean. Values were obtained using Type 1 GLMs with ln geometric-mean mass or length between times t_1 and t_2, followed by ln mass or length at t_1. BM = body weight, BL = body-length. Figures in italics beneath some age-class transitions result from reanalyses after possible outliers had been removed. Significant relationships are marked with asterisks where * = P < 0.05, ** = P < 0.01 and *** = P < 0.001.

Age-class		To yearling					To sub-adult					To adult				
	Metric	Slope	SE	F	df	P	Slope	SE	F	df	P	Slope	SE	F	df	P
Kit	BM (kg)	-1.8e^{-04}	± 2.7e^{-04}	0.443	1,24	0.512	-1.0e^{-04}	± 7.0e^{-04}	0.017	1,12	0.897	-2.6e^{-03}	± 1.2e^{-03}	5.063	1,9	0.051
		-1.3e^{-04}	*± 2.6e^{-04}*	*0.242*	*1,23*	*0.627*										
	BL (cm)	-2.7e^{-03}	± 7.8e^{-04}	11.524	1,22	0.003**	-1.5e^{-03}	± 1.9e^{-03}	0.593	1,11	0.457	5.9e^{-04}	± 1.8e^{-03}	0.106	1,9	0.752
		-1.7e^{-03}	*± 7.0e^{-04}*	*5.747*	*1,21*	*0.026**										
Yearling	BM (kg)						-4.9e^{-04}	± 5.8e$^{-0.4}$	0.722	1,24	0.404	4.8e^{-05}	± 8.1e^{-04}	0.003	1,17	0.954
	BL (cm)						-1.1e^{-03}	± 4.9e^{-04}	4.635	1,21	0.043*	1.2e^{-03}	± 7.8e^{-04}	2.526	1,16	0.132
Sub-adult	BM (kg)											-3.6e^{-04}	± 7.3e^{04}	0.240	1,16	0.631
	BL (cm)											-1.2e^{-04}	± 9.4e^{-04}	0.016	1,14	0.902
												8.2e^{-04}	*± 1.7e^{03}*	*0.246*	*1,12*	*0.629*

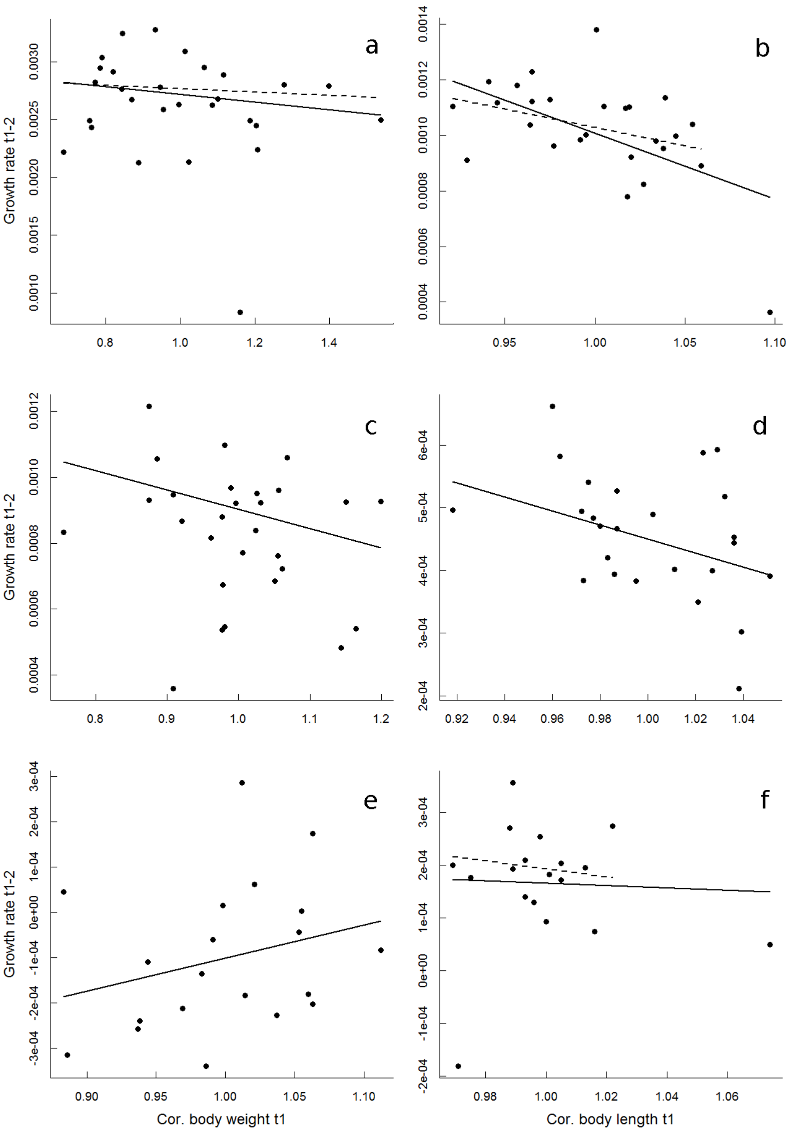

Figure 4. The effect of body weight (*ln* kg: a, c, e) and body length (*ln* cm: b, d, f) at time t_1 on the rate of increase (*ln* day^{-1} correcting for regression to the mean) in the same variable in each animal to the following age-class (time t_2). Shown are transitions from kits to yearling (a, b), yearling to sub-adult (c, d) and sub-adult to adult (e, f). Only fit lines in b) and d) are significant. Dashed fit lines in a), b) and f) result from removal of possible outliers but did not change the significance. Values used in these figures were obtained from residuals of the regressions of *ln* body weight and *ln* body-length with day-of-capture (t_1) and *ln* geometric mean weight or length between t_1 and t_2. However, for statistical analyses, residuals were only used to correct body weight and body-length for variation in day of capture.

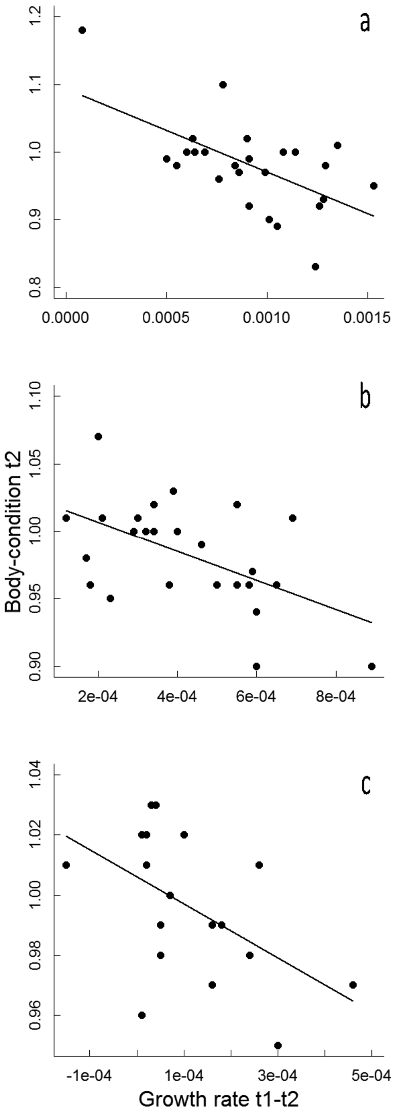

Figure 5. The effect of the rate of change in body-length between times t_1 and t_2 (*ln* cm day^{-1}) on the body-condition of each animal at time t_2. Shown are transitions from kits to yearling (a), yearling to sub-adult (b) and sub-adult to adult (c). All solid regression lines are significant. The dashed regression line in (c) excludes the far-right outlier and is not significant. Values of body-condition used in these figures were obtained from residuals of the regression of *ln* body-length on *ln* weight. However, for statistical analyses, residuals were not used.

Effects of compensatory growth on body condition

For the above age-class transitions where we found evidence for compensatory size growth, GLMs using day of capture, *ln* body-length and SGR on *ln* body weight indicated that the rate of increase of body-length from the previous to current age-class was negatively related to the body-condition of individuals in yearlings (slope = -201.9 ± 70.9, $F_{1,22} = 8.107$, $P = 0.009$, Fig. 5a), sub-adults (slope = -365.8 ± 68.6, $F_{1,21} = 8.107$, $P < 0.001$, Fig. 5b) and in adults (slope = -305.2 ± 99.0, $F_{1,14} = 9.497$, $P = 0.008$, Fig. 5c), suggesting that increases in body size came at a cost to body-condition in all age-classes. Sex did not have a significant effect in any age-class ($P>0.05$ in all cases).

Discussion

We hypothesised that size was important in beavers and may be traded-off against weight. We therefore predicted firstly that individuals would show compensatory size growth but not compensatory growth in weight and secondly that this size compensation would be at the expense of body condition. Our first prediction was, at least partly, met. Weights in all age-classes were dependent on weights in the prior age-class. Though prior size was a positive predictor of later size from yearlings to older ages, kits and yearlings that were smaller than expected given the date they were captured tended to show a more rapid increase in size from one age-class to the next than did larger animals. Thus growth-compensation occurred, but was not perfect in yearlings where smaller animals were still smaller in older age-classes. The opposite was found in animals moving from the sub-adult to adult age-class: There, smaller animals did not increase their size significantly more rapidly than did larger animals, yet their size as adults was not related to their size as sub-adults. This follows our prediction that the growth rate signal of both compensatory and catch-up growth will weaken as animals near adulthood while growth recovery (either catch-up or compensation) may still have occurred, as evident by the lack of between age-class correlations in size. Once growth rates have reached their asymptote, distinguishing between catch-up and compensatory growth is difficult since it is likely that the growth-trajectories associated with each will have converged at that point.

In contrast to the patterns found in size-growth rates, examining the effects of prior weight on later weight, we found no evidence against an absence of compensation growth in weight over most age-class transitions to adulthood. The exceptions were from kits to sub-adults and kits to adults, where it is possible small sample sizes and greater opportunity for stochastic environmental effects over the years between the age-classes could have masked any relationship. Similarly, we found little evidence for compensatory growth when examining the effect of prior weight on growth rates while controlling for size-dependent growth. The exception to this was again from the kit to adult transition and, together with the non-significant effect of prior weight on current weight in this age-class transition, suggests that compensation in body weight may occur over longer time periods. However, this conclusion is cautious since sample-sizes were small for both the kit-sub-adult and kit-adult transitions. This leads to our second prediction: beavers will compensate size at the expense of body-condition. Our results suggest that this prediction was upheld for the three consecutive age-class transitions, where the rate of size increase from the previous year was negatively related to body-condition.

Examining specific growth rates, we found, as expected, that the rate of increase in weight and size was inversely related to weight and size. Beavers display seasonal growth, particularly in body weight which increased significantly more rapidly within years than between years This indicates that, as with North American beavers *C. canadensis* in northern Canada and Alaska (Buckley & Libby 1955; Aleksiuk 1970), but in contrast to those further south in Minnesota and Wisconsin (Smith & Jenkins 1997), juvenile animals in our study site lose body-condition over winter. Based on the within-year Gompertz curves, the rate of body weight increase in beaver kits ranges from 26 g day^{-1} for animals at 2 kg to 44 g day^{-1} at 7 kg. This latter value is in agreement with previous studies on the Eurasian beaver, which range from 38-41 g/day in the first 90 days and 32-40 g/day between days 60 and 150 after parturition (Wilsson 1971; Zurowski et al. 1974; Pilleri et al. 1985). However, the value for animals at 2 kg appears low which, together with the very early predicted birth date based on the same Gompertz curve, suggests that growth rates for beaver kits in the first three months of life (prior to most of our measurements) are actually higher than the Gompertz curve would predict.

Because beavers experience a period of nutritional scarcity over winter, and consequently loose body weight, it is possible that compensatory growth occurs over this period, with animals investing in size growth instead of conserving resources to maintain body weight. This is distinct from convergence of growth trajectories due to catch-up growth since the limit on growth in winter is not size, but nutrients. However, we did not have a large enough sample-size of measurements repeated within years to test whether compensatory growth took place over spring-autumn instead of winter.

Alternatively, the signal of compensatory growth may simply be a by-product of poorer performance of larger individuals during nutritional scarcity, i.e. ‘compensatory conservation of resources’ (Dale et al. 2008). In our study, the compensation in size and not weight suggests that larger beavers are not disadvantaged during lean periods. Such prioritisation of size over weight has also been found in larval damselfly *Ischnura verticalis* (Dmitriew & Rowe 2005) and gull chicks *Larus fuscus* (Royle 2000). In contrast, fish, which exhibit indeterminate growth, tend to show weight recovery before size recovery (e.g. Johnsson & Bohlin 2005; Jobling In press). In species with determinate growth, individuals that are in poor condition may be able to gain body-condition at some future point, whereas individuals that do not manage to attain their full potential size may always be disadvantaged. Therefore, this strategy of increasing size over body-condition may be a trade-off between some positive long-term aspects of larger size, such as competitive ability, against short-term survival.

Conclusions and general implication

Our results show that beavers can limit the influence of conditions experienced during juvenile development by trading off body-condition for a greater rate of size increase. These results highlight the importance of considering structural size as well as body weight when examining compensatory growth. To pick one example, Solberg et al. (2004) found limited evidence for compensatory growth in female moose *Alces alces* and no evidence for compensatory growth in male moose when examining body weight. From these results, the authors argued that females trade-off growth for reproduction while males are already at their maximum growth rate and have no room for compensation. However, Solberg et al. (2004) did not use a measure of body-size in their analyses. Since moose are sexually dimorphic, with adult males being much larger than females, we would predict from our results that male moose would trade-off growth in structural size at the expense of body condition and therefore we would not necessarily expect to see compensation in body weight, particularly if the trade-off was strong enough that the covariance between weight and size was reduced. This by no means changes the main thrust of Solberg et al.'s (2004) conclusions, since male moose would still be maximising size-growth. It does however illustrate the importance of examining both size and weight, while disentangling the covariance between size and weight, in studies of compensatory growth.

Though we examined compensatory growth due to individual variation, the processes involved are likely to be similar for cohort variation, particularly where components of growth such as size and body-condition, can be traded off one another. Our findings that strong positive effects of prior weight on later weight in individual beavers could be found alongside compensatory growth suggests that evidence for a cohort effect is not necessarily evidence against compensatory growth.

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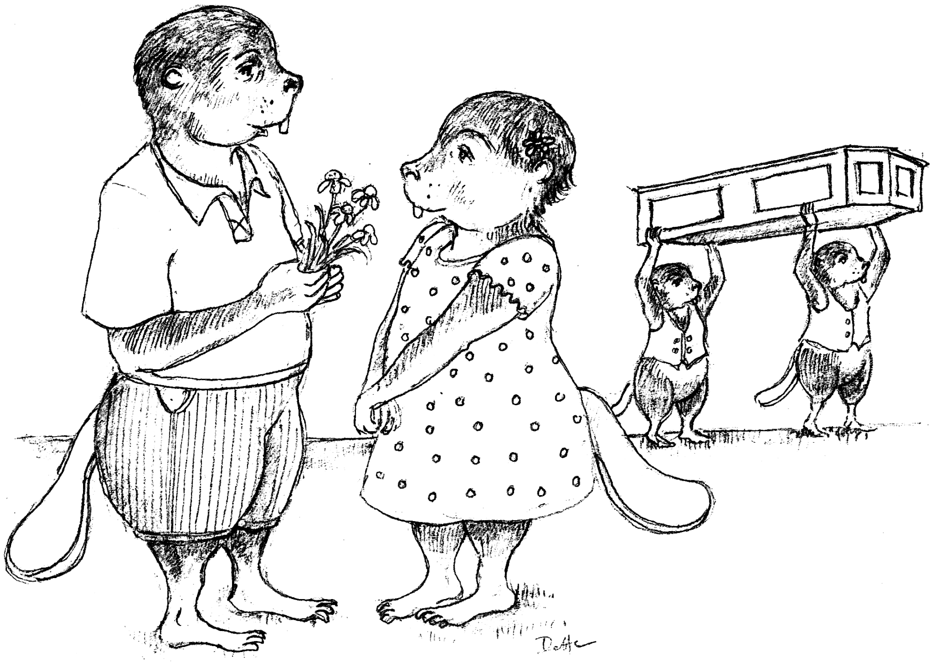
Average, but not mediocre: evidence of stabilising selection for body-size in the Eurasian beaver



Half a league, half a league, Half a league onward, All in the valley of Death, Rode the six hundred.

"Forward, the Light Brigade!

"Charge for the guns!" he said: Into the valley of Death, Rode the six hundred.

Charge of the Light Brigade. Alfred, Lord Tennyson, 1854

Abstract

Darwinian ‘fitness’ and reproductive ‘fitness’ are subtly different measures that describe the action of selection pressure on organisms, in that selective pressures for survival and for reproduction may not be equivalent. In this study we examine the mechanisms that underscore trait selection, in terms of phenotypic survival and heritable genetic perpetuation in the Eurasian beaver. In particular, we examine dominance and survival in relation to body size and condition. There is likely to be selection for large body size in beavers in that it is associated with greater reproductive success, but we find that those beavers that survive best are of average size. We explore hypotheses that might reconcile these observations, and discuss ecological factors which might favour a system in which the breeding population is composed of a *second tier* of “the largest of the medium-sized beavers”. Selection thus operates to stabilise body-size, within a range of normal distribution, such that the competitive advantages accruing to the largest amongst the next generation may be more than offset by disadvantages of rapid growth or large size. The resultant stabilising selection produces the size distribution observed in nature such that those individuals comprising the reproductive proportion of the population are of average, but not mediocre, quality.

Introduction

Over the course of generations natural selection acts on quantitative phenotypic traits to optimize “fitness” (i.e. goodness of fit; Darwin 1859). There is, however, an incommensurability between ‘Darwinian fitness’ and the numerical values associated with reproductive rates (‘reproductive fitness’) as used in population genetics. That is, not all “well fitting” animals will get to breed according to stochastic events and any measure inferring parental fitness based solely on the production of offspring is tautological. While sometimes both inferences are called ‘fitness’, they are distinct concepts coming from distinct explanatory schemes (see Ariew & Lewontin, 2004). The natural properties of an individual organism vary from individual to individual within a species, and the sources of variation are internal to ontogeny. Different individual members of a species then “fit” into – i.e. are adapted to - the environment to different degrees, as a consequence of the variation in their properties, and those that “fit” the best will survive and reproduce more successfully than those whose “fit” was poorer. This metaphorical lock-and-key fitting of the organism into the environment is reflected in the modern concept of the ecological (or environmental) niche that the species is said to occupy (Ariew & Lewontin, 2004).

Where environmental and species-niche conditions are relatively constant, extreme phenotypic characters are selected against, thus stabilizing selection (Mather 1953) occurs as a result of decreasing genetic diversity as the population gravitates towards an optimal trait value. This is probably the most common mechanism of action for natural selection. Stabilizing selection acts to prevent divergence of form and function. In this way the anatomy of some organisms has remained largely unchanged for millions of years (Huxley 1957). Given the continuous process of evolution, the existence of morphologically discontinuous groups, labelled species, whose adult members look extraordinarily similar, and distinctively different from the members of other species, is posited to be as a direct result of such stabilising selection (Koeslag 1995), i.e. selection that favours intermediate phenotypes rather than those at one or both extremes (Schmalhausen 1949).

Within this framework traits closely associated with fitness should generally be under stronger selection pressure than traits more loosely connected with fitness (Mousseau & Roff 1987). Amongst mammals 'dominance' is often linked to body size, which may dictate preferential access to resources or afford greater territory holding or mating success (e.g. Jarman 1983; McElligott 2001; Iossa *et al.* 2008). As a consequence of these incremental benefits of selection for larger individuals, Cope's rule, the tendency for species within a lineage to evolve towards larger body size (see Hone & Benton 2005) has been reported widely in the fossil record (e.g. Alroy 1998; Hone *et al.* 2008, but see Jablonski 1997; Kingsolver & Pfenning 2004; Hunt & Roy 2005). Within species, the fact that there is no central tendency to increase size over evolutionary time suggests that directional selection for larger size must be constrained ultimately by scale-laws on morphology, physiology and ecotype (see Schmidt-Nielsen 1984; Hone & Benton 2005).

Here we consider the role of directional selection on body-size traits in the Eurasian beaver *Castor fiber.* Phyletically and morphologically, the family Castoridae demonstrates the capacity for selection to favour large body sizes (Rybczynski 2007). Fossils of the 'giant' beaver, *Castoroides ohioensis* (also *C. leiseyorum*) of the Pleistocence in North America indicate that this otherwise similar species could achieve body-weights of 60-100kg (Reynolds, 2002). Extant beaver species, however, do not attain these proportions. The Eurasian beaver *Castor fiber* is limited to around 20-30kg (max) once adult (Pilleri *et al* 1985).

The Eurasian beaver is an herbivorous, semi-aquatic rodent (Wilsson 1971;Műller-Schwarze and Sun 2003). As with other herbivorous rodents, beavers digest the plant material in their diet through caecum (hindgut) fermentation and practice caecotrophy (Wilsson 1971; Vecherskii *et al.* 2009). They are monogamous and highly territorial (Wilsson 1971) with intra-specific aggression being a major cause of mortality (Piechocki 1977). Beavers live in family groups within which only the dominant pair breeds (Wilsson 1971; Műller-Schwarze and Sun 2003). Young (known as 'kits') are born around May and emerge from the natal den or lodge when weaned, approximately two months later (Wilsson 1971). Beavers can attain sexual maturity at two years of age but do not reach full adult size until the age of three (Wilsson 1971; Pilleri *et al.* 1985). In colder climates, particularly where water becomes iced-over in winter and therefore beavers are unable to access land, they build a food cache in autumn, which they use to survive the winter (Wilsson 1971; Műller-Schwarze and Sun 2003). Consequently, beavers can experience pronounced variation in nutrient availability between winter and summer.

In chapter 2 I argued that as beavers are monogamous and highly territorial, large body-size is likely to carry a significant advantage in territorial contests for both sexes. In this chapter I also report that juvenile beaver growth involves a trade-off between increasing skeletal size and building energy reserves (body-condition) to survive times of nutrient scarcity, underscoring the implications of larger body-size in this species.

In this study we examine for evidence of directional selection on beaver body-size and body condition within a framework of mechanisms that maintain extant body-size distribution patterns. We predict that, if body size is a corollary of competitive ability, for either sex, dominant individuals will have greater body length than non-dominant individuals. Large body size may confer some other advantage. For example, larger individuals will have reduced heat loss due to a lower surface to volume ratio (*sensu* Bergmann's rule: e.g. Meiri & Dayan 2003) or exhibit increased digestive efficiency (Hume 1989). Larger size may also correlate with individual quality and therefore we also predict that survival will increase with increasing body length. Similarly, we predict that animals with higher body condition will exhibit greater survival.

Materials and methods

Study site and population

The study site was centred on three rivers, the Saua (Nome municipality), the Gvarv and the Sauar (both Sauherad municipality), in Telemark, southern Norway (59°23′ N, 09°09′ E). Mean monthly temperature in this region dips below 0 °C for five months a year between November and March. All rivers include lakes along part of their length, moderating fluctuations in water temperature along the main riverine channels thus reducing freeze over in winter (though all beaver families in the study area build food stores whether ice-cover occurs or not). All three rivers form part of the Lake Nordsjø catchment. None of the studied beaver families built dams. Illegal culling is believed to be rare in the area (B Hovde and F Bergan pers. comm.) since few beaver families are in conflict with human land-use. A close relationship is maintained with local hunters, allowing us to keep track of the majority of direct anthropogenic mortality in our population. Hunting pressure is low with 23, of a total of 268 animals (including floaters: animals that have dispersed from their natal territory but have not established a territory of their own) shot or kill-trapped during the course of the 12 year study interval. Predation pressure is also low since wolves have been extirpated from the area for over 100 years, bears only occasionally pass through and lynx are present, but at low densities (Rosell and Sanda 2006). Beavers have been in the study area since the 1920s (Olstad 1937) and philopatry of individuals beyond dispersing age is frequent (Campbell *et al.* 2005).

Trapping programme and sampling

Between 1998 and 2009, beavers in the study areas have been monitored through an extensive live-trapping program using hand-nets from a motor boat between March and November (Spring-Autumn, Rosell and Hovde 2001). All trapping and handling procedures were approved by an institutional ethical review committee, and met guidelines approved by the American Society of Mammalogists (Gannon et al. 2007). Individuals were tagged with a microchip (Avid or Trovan) on first capture and marked with unique colour-plastic (Dalton) and metal (National Band and Tag Co.) ear-tag combinations to aid repeated identification on recapture. Morphometric measures including weight (to within 0.2kg) and body-length (to within 1cm) following the curvature of the spine from the nose-tip to the base of the tail (where fur gives way to scales) were recorded upon each capture. Animals were sexed by examining the colour of the anal-gland secretion (Rosell and Sun 1999). Recaptures resulted from either the trapping or sighting of marked animals. Dominance status was determined by previous trapping and sighting history and incidences of lactation in females. For example, individuals dispersing into a territory were posited to have obtained the dominant breeding position, an assumption generally corroborated by data indicating the disappearance of the previous dominant individual of the same sex and, for females, lactation (signified by nipple length > 0.5cm). In most cases where animals were already present in the territory at the beginning of the study, dominance status became obvious as other same-sex adult group members dispersed or disappeared and were not replaced by new animals.

Throughout the study we base our analyses on a demographic data base stretching from 1998 to 2009, documenting the capture events of 242 individual beavers with their associated records of body length, body weight and relative body condition indices; each of which was caught between one and 11 times.

Measures of body condition

In order to make comparisons between individuals of different age and sex it was necessary to characterise a standardized index of body condition from measures of body length and weight

Here we first employed a general linear model to examine the interaction / dependency of body length on age and sex, and then used a stepwise procedure to determine the degree of the polynomial linking body length to age. Once the best predictive value of body length as a function of age and sex was determined we tested whether each individual lay above or below that predicted by the equation using residuals from the general linear model (e.g. individual shorter or longer than expected, given its age and sex). For individuals with multiple measurements final standardized body length was calculated as an average of the multiple residuals recorded.

An identical procedure was applied to body weight to determine standardized individual values.

To explore the relationship between variation in body weight relative to length per individual (weight relative to length: Wrel) a predicted log body weight value per body length value was derived from a general linear model . Sex was also included as a factor in the model. These residuals were then used to determine a standardized value of body weight relative to body length - Wrel.

Beavers live in family groups and only the dominant pair breed (Wilsson 1971; Műller-Schwarze and Sun 2003). Using standard t-tests, we tested whether: (1) dominant individuals were longer than expected (given their age and sex); (2) dominant individuals were heavier (given their age and sex); (3) dominant individuals displayed a higher condition index (Wrel).

Body condition (Wrel) and survival

We used the Capture-Mark-Recapture framework to estimate values of survival implemented in the program Mark (White & Burnham 1999). A '*Cormack-Jolly-Seber* ' (CJS) model (Jolly 1965, Lebreton et al. 1992) was applied and checked for goodness of fit using the Bootstrap methods (White 2002), allowing approximation of a corrected variance inflation factor ($\hat{c}$) . This method, using 500 replications, allowed us to deduce that the model satisfied underlying assumptions. Explicitly, the probability of obtaining a deviance equal or greater from that calculated here is 0.12, providing no evidence for any obvious lack of fit. Informed by this corrected variance inflation factor ($\hat{c}$) survival rates were held constant amongst age class but allowed to vary between years, that is, for this model, and all presented below, capture rate was allowed to vary between years and between study sites to reflect differential in trapping effort. In all models presented survival rates were modelled as binomially distributed with a binary response (survived or not/died), and thus modelled using logistic regressions. Note however that in our open population, the apparent mortality of individuals at, or about to attain, dispersing age could also be attributed to dispersal (see Chapter 6).

Indices of body condition (Wrel) were then use as a covariate in a model estimating survival, utilising the information theoretic approach (Akaike information criterion) together with multi-model selection. The difference in the AIC_c between any given model and the most supported model (ΔAIC_c) and Akaike weight W_{AICc} were calculated, expressing relative model compared to the best fit model (Burnham and Anderson 2002, 2004). Models within a $\Delta AIC_c<2$ were considered to be well supported by these data. Each covariate was tested for both a linear- and a quadratic-effect. Firstly, we established a time dependent estimate of survival, $\varphi(t)$, and then as a constant between years, $\varphi(.)$. We then included body condition indices (with and without a squared component) to test whether these increased the fit in the estimation of survival.

We use the annotation: L: standardized body length according to age; W: standardized body weight according to age and sex, Wrel: weight relative to length (standardized body condition relative to sex and body length). These were used to parameterise and test the model:

$$\varphi(L),\ \varphi(W),\ \varphi(Wrel),$$

then:

$$\varphi(L + L^2),\ \varphi(W + W^2),\ \varphi(Wrel + Wrel^2).$$

As a final step we also tested if multiple factors provided a better fit, i.e.:

$$\varphi(L + L^2, W + W^2),\ \varphi(L + L^2, Wrel + Wrel^2),\ \varphi(W + W^2, Wrel + Wrel^2)$$

and

$$\varphi(L + L^2, W + W^2, Wrel + Wrel^2).$$

Results

Population characteristics

Examining recapture rates (Figure 1) indicates mortality peaked in individuals of early dispersing age (1.5 – 2 years) and then declined thereafter. Sample sizes of animals > 10 years old were small and it is therefore difficult to assess mortality at these ages. Mortality exhibits a pronounced dip in four year old individuals before rising again. Of all animals, four of eleven at five years and four of eight at six years were lost in 2002. Of known age

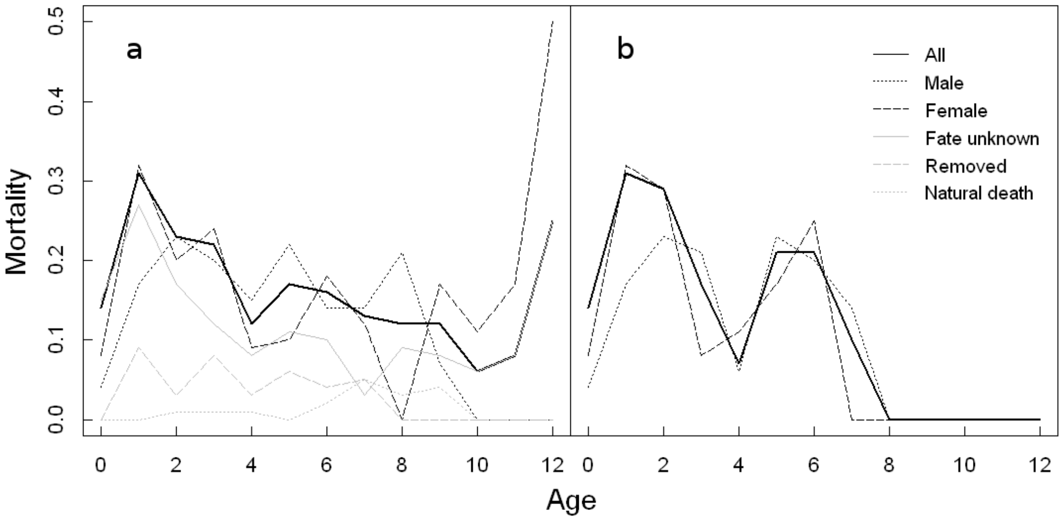


Figure 1: Mortality (proportion of animals not recaptured in following years, *x*+n) with age (*x*). Black solid lines represent both sexes combined, dashed black lines are females and dotted black lines are males. The grey solid line in a) is the proportion of all animals that disappeared (i.e., fate unknown), grey dashed line is the proportion that were removed either by shooting, kill-trapping or translocation (fate known) and grey dotted line is the proportion that died from natural causes, including disease, injuries sustained in fights with other beavers and other unknown causes (fate known). Plot a) is based on all animals in the population between 1997 – 2009 and therefore ages from 2 – 12 are the minimum age since it is not always possible to age immigrant adults beyond 2 – 3 years old, whereas b) is based on animals captured as juveniles in the study area and are of known age (see Table 2 in chapter 1 for sample sizes).

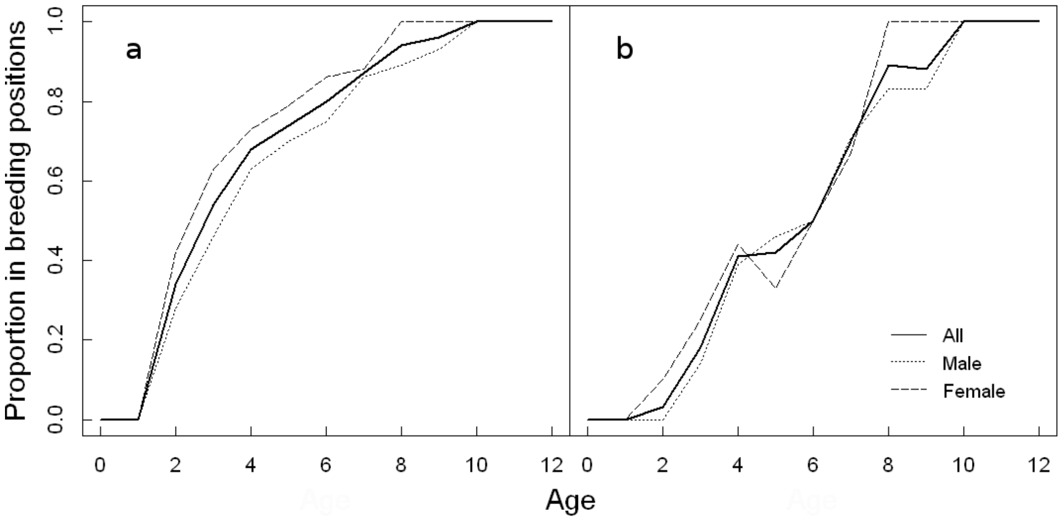


Figure 2: Proportion if animals in breeding positions (i.e., dominant within-sex in the territory). Black solid lines represent both sexes combined, dashed black lines are females and dotted black lines are males. Plot a) is based on all animals in the population between 1997 – 2009 and therefore ages from 2 – 12 are the minimum age since it is not always possible to age immigrant adults beyond 2 – 3 years old, whereas b) is based on animals captured as juveniles in the study area and are of known age (see Table 2 in chapter 1 for sample sizes).

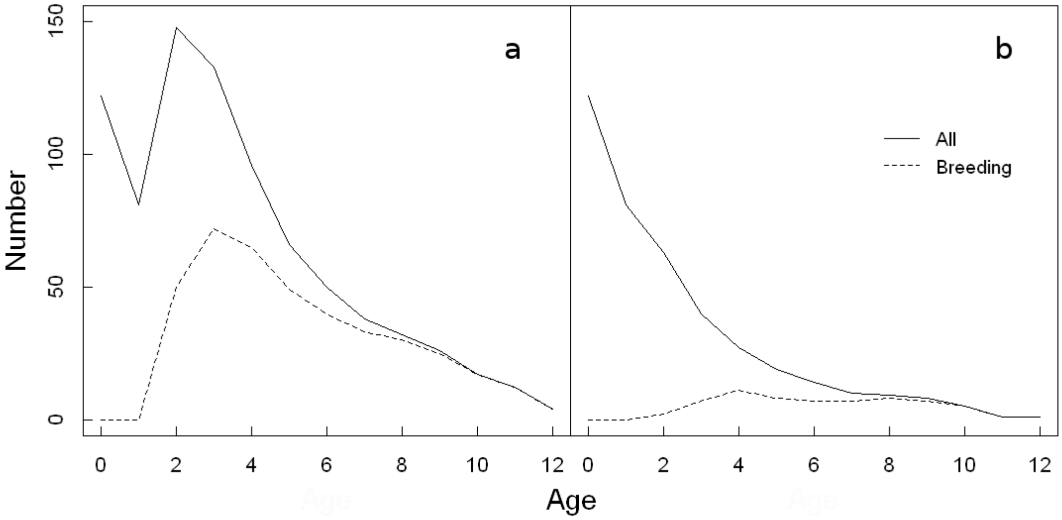


Figure 3: The total number of animals (solid line) and the total number in breeding positions (dominant within-sex in the territory, dashed line) with age, recorded in the population over the entire study period (1997 – 2009). Figures were back calculated for animals that were clearly resident and could be unambiguously aged based on weight (all < 3 years old). Plot a) is based on all animals in the population and therefore ages from 2 – 12 are the minimum age since it is not always possible to age immigrant adults beyond 2 – 3 years old, whereas b) is based on animals captured as juveniles in the study area and are of known age. The age by age drop in numbers is greater than actual mortality rates based on recaptures since individuals of all ages were also 'lost' when the current study period ended.

animals, two of five at five years and one of four at six years were lost in 2002. If you discount data from 2002, mortality = 0.11 and 0.09 for five and six year olds (all animals) and 0.12 and 0.15 for five and six year olds (known age animals). Thus this reduction in mortality at four years may not be a dip but an abrupt drop in mortality that continues into later life. Trap effort (number of nights trapping over two years) was lowest in 2002 – 2003 (19 nights versus a mean of 60 nights over all other two-year periods) but, though recapture rates increased with trap effort, this correlation was not quite significant (Pearson's correlation: r = 0.546, df = 9, $p = 0.082$). Variation in trap effort may not therefore explain the pattern of mortality found here. The year 2002 followed a relatively wet 2001 (rainfall from Apr-Sept was 674mm versus a 1998 – 2008 mean of 597mm) and a relatively cold 2001 – 2002 winter (mean-maximum daytime temperature from Dec-Jan was -2.5C versus a 1998-2008 mean of -1.0C). Both factors may have influenced survival (see chapter five).

Breeding opportunities were restricted in the population (Figure 2) with, based on data from known age animals (Figure 2b), only half of all individuals in breeding positions at the age of six. Indeed, part of the proportionate increase in individuals in breeding positions with age was due to individuals being lost from the population (Figure 3). By age ten, all animals in the study area had either been lost to the population or had obtained a breeding position.

Measures of body condition

Body length was highly dependent upon age but not sex (Figure 4). Body length was influenced most strongly by age in combination with age to the fifth power (e.g. $y = \beta_0 + \beta_1 x + \beta_2 x^5$, with y: body weight, x: age and β's: parameter estimates), resulting in a model explaining 81.9% of the observed variance in body length (R-square, with $p < 0.001$).

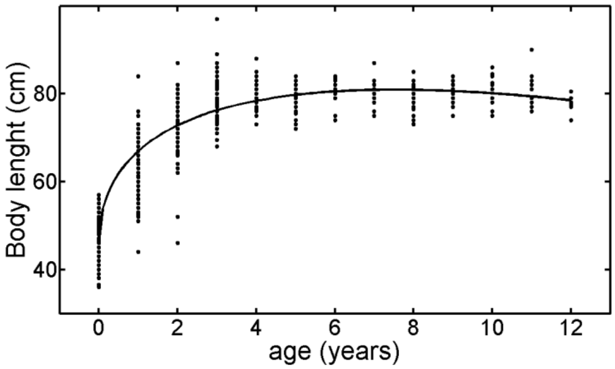


Figure 4: Body length as a function of the age of the beaver. The function, see results section for details, account for 81.9% of the variation in beaver weight. Sex as a factor was initially present but dropped from the model as non significant. The residuals of the model (distances from the observation to the predicted values) were then used to assign a body condition index reflecting body length relative to age.

Body weight was dependent upon both age and sex (Figure 5). Body weight was influenced most strongly by age in combination with age squared, cubed and to the power of four (e.g. $y = \beta_0 + \beta_1 x + \beta_2 x^2 + \beta_3 x^3 + \beta_4 x^4 + \beta_5 s$, with y: body weight, x: age, s: sex and β's: parameter estimates). The resulting model accounted for 85.4% of the variation in body weight (R-square, with $p < 0.001$).

Wrel, derived from a log transformation (e.g. $\log(y) = \beta_0 + \beta_1 x + \beta_2 s$, with y: body weight, x: age, s: sex and $\beta's$: parameter estimates, Figure 6), accounted for 90.3% of the variation in body weight. Using a t-test, $\beta's$ were significantly different from zero (i.e. for β_0 and β_1, $p < 0.001$, and for β_2, $p < 0.05$).

Dominant beavers were longer ($p = 0.001$) and heavier ($p < 0.001$) than expected for their age but not heavier than expected from their body length ($p = 0.19$), i.e. their relative body condition (Wrel) was not superior to subordinate conspecifics.

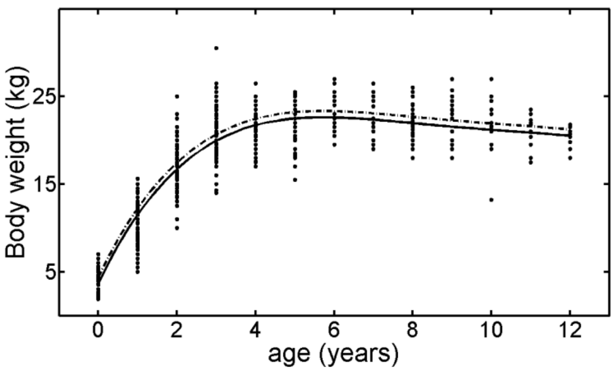


Figure 5: Body weight as a function of age and sex. The function, details in results, account for 85.4% of the variation in body mass. Solid line represent predicted body weight of females while dashed line represent predicted body weight for males The residuals of the model (distances from the observation to the predicted values) were then used to assign a body condition index reflecting body mass relative to age and sex.

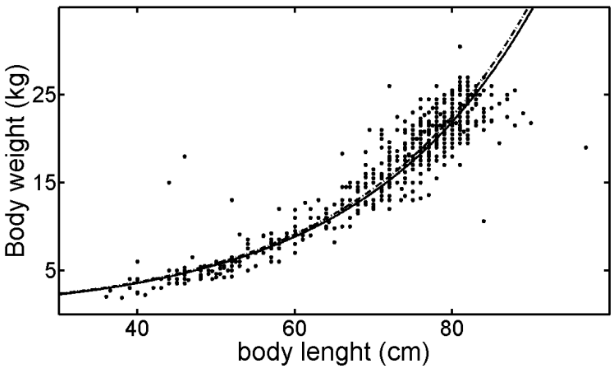


Figure 6: Body weight as a function of body length and sex. The function, detailed in the results, account for 90.3% of the variation in body mass. Solid line represent predicted body weight of females while dashed line represent predicted body weight for males The residuals of the model (distances from the observation to the predicted values) were then used to assign a body condition index reflecting body mass relative to body length and sex.

Effects of body size and condition on survival

Survival rate was highly dependent upon morphometric measures. All covariates included in the most supported model had a quadratic component in addition to a linear component (Table 1). As each quadratic component was negative (e.g. in each estimation), this provides strong evidence of the pre-eminence of medium-sized phenotypes in the population. The most supported model constrained survival rate by both body length (L) and Wrel in a quadratic fashion ($w_{AICc} = 0.59$). The second best model included only body length as covariate ($\Delta AIC_c = 1.94$ and $w_{AICc} = 0.22$). The third best model included all 3 covariates but was only weakly supported ($\Delta AIC_c = 3.54$ and $w_{AICc} = 0.10$). Finally the fourth model, with very weak support ($\Delta AIC_c = 5.66$ and $w_{AICc} = 0.03$), linked survival to body weight relative to age and sex (W) and relative to Wrel. Dominance status (dominant or not) was not a significant factor in the shape of the relationships as the quadratic components of both L and Wrel were similar for both dominant animals and for all animals combined (L^2: 95% CIs for all animals = -0.026 to -0.006 versus, for dominant animals = -0.037 to -0.009 and $Wrel^2$ 95% CIs for all animals = -21.9 to -2.3 versus, for dominant animals = -30.4 to -2.2).

These models highlight that body length, relative to age, had the strongest influence on survival; as it was included in the first 3 models accounting for 91% of the Akaike weight. Wrel had the second strongest effect; included in the first, third and fourth model, accounting for 72% of the Akaike weight. Finally bodyweight relative to age and sex had the least impact, as it was only included in the third and fourth model accounting for 13% of the Akaike weight. We thus deduce that survival rate has a quadratic relationship with body length, relative to age (L) and Wrel; figure 7 illustrates such relationship.

Table 1: Statistical summary of model linking survival and measures of size and body conditions. The fit of the models are given (ΔAIC_c and w_{AICc}) along with estimation of the parameters (with standard errors in parentheses). Parameters are estimates within a logit regression of survival φ. For sake of simplicity only the first four model are presented, models with lower fit can be disregarded as having very low support ($\Delta AIC_c > 7$ and $w_{AICc} < 0.02$).

Model	ΔAIC_c	w_{AICc}	β_L	β_{L^2}	β_W	β_{W^2}	β_{Wrel}	β_{Wrel^2}
$\varphi\left(\begin{matrix}L+L^2,\\ Wrel+Wrel^2\end{matrix}\right)$	0	0.59	-0.009 (0.030)	-0.016 (0.005)			-0.059 (1.013)	-12.14 (5.045)
$\varphi(L+L^2)$	1.94	0.22	-0.015 (0.027)	-0.019 (0.004)				
$\varphi\left(\begin{matrix}L+L^2, W+W^2,\\ Wrel+Wrel^2\end{matrix}\right)$	3.53	0.10	-0.046 (0.057)	-0.014 (0.005)	0.075 (0.097)	-0.015 (0.018)	-0.687 (1.448)	-12.630 (5.089)
$\varphi\left(\begin{matrix}W+W^2,\\ Wrel+Wrel^2\end{matrix}\right)$	5.66	0.03			0.046 (0.049)	-0.034 (0.014)	0.475 (0.945)	-15.262 (4.549)
$\varphi\left(\begin{matrix}L+L^2,\\ W+W^2\end{matrix}\right)$	6.02	0.03	-0.028 (0.038)	-0.017 (0.005)	0.033 (0.071)	-0.010 (0.018)		

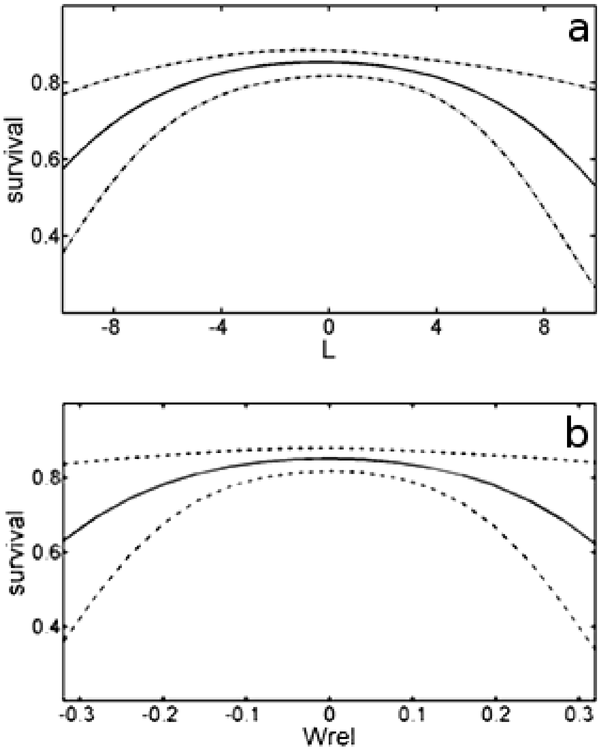


Figure 7: Survival as a function of (a) standardized body length (L: body length relative to age) and, (b) standardized body mass relative to body length (Wrel: body mass relative to body length and sex). The solid curve represents the predicted survival while the dotted curves represent the upper and lower 95% confidence interval on the predicted values as derived from the delta method. In term of representation, it is very important to determine a ‘typical’ range of values of the covariates (L or Wrel). If plotting the relationship between survival and a very large range of value for the covariate, selective pressure might appear stronger (e.g.: one would observe a very thin and narrow peak). Here we chose to represent the relationship between survival and the smallest symmetric range of value for the covariate that include 95% of the values observed.

Discussion

As we predicted, these analyses resolved that dominant animals proved to be larger (longer) than non-dominant conspecifics. Thus, we demonstrate an apparent directional selection pressure towards larger body sizes, where dominance confers breeding status with a trend towards social hypergamy (Buss & Barnes 1986). However, our finding that apparent survival was greater for medium-sized animals and lower for smaller and larger animals was counter-intuitive to our second prediction of greater survival of larger individuals. Similarly, our weaker finding that survival was concurrently highest in animals with medium body condition was only in partial accord with our third prediction that larger body-size should confer superior survival prospects.

These findings define an intriguing paradox in the selection pressures operating on the optimality of genotype and phenotype in this population, with obvious corollaries for continuous vs. discontinuous-discrete mechanisms. Two contradictory observations must be reconciled; the fact that breeding, and thus the heritability of selected traits, is predominantly the preserve of larger- dominant- individuals, while there is simultaneous evidence for the greater survival prospects of the predominant medium sized phenotypes in the population.

Where environmental and species-niche conditions are relatively constant, extreme phenotypic characters are selected against, thus stabilizing selection (Mather 1953) occurs as a result of decreasing genetic diversity as the population gravitates towards an optimal trait value. This evolutionary mechanism is, however, posited on the assumption that the phenotype that is fittest (*sensu* Ariew & Lewontin, 2004) in the environment is most likely, indeed has a realistic probability, of producing offspring; among beavers these optimal, medium-sized, phenotypes are highly unlikely to breed, and so we see a *second tier* of “the largest of the medium-sized beavers” as actual breeders. Simultaneously, those animals that do breed, larger- dominant- individuals, will confer genes for larger body-size to their offspring, and thus there would appear to be a selection for a phenotype with inferior survival dynamics. We concede that ultimately also be an element of directional selection in body size in the beaver since in this study we do not know what portion of disappearances is due to mortality versus dispersal. Our investigations highlight, however the fact that dominance status did not affect the shape of the survival relationship with body size and condition indicating that, since dominant animals are not expected to disperse, it is the signature of survival and not dispersal that we see here. Similarly, this consistency of the survival relationship between all animals and dominant adult animals indicates that the pattern of intermediate survival is not being driven by higher variance in the body weight and condition of juvenile animals.

Higher body-condition and large size are not necessarily better. For example, Dibattista *et al.* (2007) found selection favouring smallness, low body condition and slow growth in juvenile lemon shark *Negaprion brevirostris*. Larger individuals (both longer and with relatively greater body weight) may experience higher travel costs or reduced manoeuvrability in the water due to greater hydrodynamic drag (Schmidt-Nielsen 1990; Lovvorn & Liggins 2002), or may have greater absolute energy demands (Peters 1986) and thus greater risk of starvation during nutrient scarcity (Scharf *et al.* 2009). Moreover, the path to attaining a larger size may carry further risks. For example, increased growth rates post-weaning may expose individuals to greater predation risk (Jönsson *et al.* 1996; Gotthard 2000) or may result in greater genetic damage (Mangel & Munch 2005). Plausibly therefore those individuals with a selected and inherent predisposition for rapid early growth or larger adult size become eliminated from the gene pool prematurely, and thus the breeding population is actually comprised by this *second tier* of "the largest of the medium-sized beavers". The fact that dominant beavers had a statistically significant tendency to be larger, but were not extraordinarily large supports this notion. Selection thus operates to stabilise body-size, within a range of normal distribution, of which those largest amongst the next generation may too over-extend the evolutionary imperative to grow quickly or grow large, at a cost relative to those with average size and more average growth regimes.

The equilibrium of which of these constraints acts most robustly dictates that "strategy" which proves most comprehensive in defining an individual's "fitness", as demonstrated by the capacity of these individuals to leave (more) descendents than their conspecific contemporaries. In a game theoretic sense (Fisher, 1930), here we observe an example of Hamilton's (1967) "Unbeatable Strategy", applied to somatypic selection. The stability of this strategy in an evolutionary context (Maynard-Smith 1974, *inter alia*) will vary over time, with a resilience corresponding with the variability of the overall reproductive capacity of the largest individuals, which will have variable power to exceed that of medium-sized individuals. Thus, individuals that grow more slowly toward average sized phenotypes are maintained within the population, while those that in terms of "absolute" criteria for evolutionary success that grow more quickly, do so at the risk that rapid development will come at the cost of compromised survival likelihood.

Conclusion

In this study we examine the mechanisms that underscore trait selection, in terms of phenotypic survival and heritable genetic perpetuation. We demonstrate the complexity of examining traits for evidence of selectability, in the evolutionary sense. While large body size in beavers militates for greater reproductive success, and thus the numeric values associated with reproductive fitness used in population genetics, we reconcile this with the observation that those beavers which survive best are of average size, according to forces acting on the phenotype originating from a distinct explanatory scheme. That is the "ecological niche" of this species, to which it is evolved to fit, favours those individuals that do not maximise their genetic potential for rapid ontogenic development. The resultant stabilising selection that results from this compromise between inherent genetic capacity and environmental constraints on the phenotype ensures that those individuals comprising the reproductive proportion of the population are of average, but not mediocre, quality. Such observations have implications to both theoretical and practical conservation biology, demonstrating that any extant population is in a continuous state of compromise.

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Chapter 4

Senescence and the offspring quantity versus quality trade-off in the social monogamous Eurasian beaver

Abstract

An increase in fecundity with age is thought to result from increased experience of mothers or increasing investment in reproduction as reproductive value declines ('terminal allocation'). Senescence is hypothesized to result from a build up of damage ('disposable soma', an extension of terminal allocation) or antagonistic pleiotropy. The latter two hypotheses have different predictions in the context of resource availability. Trade-offs are also predicted between offspring number versus quality and current versus future reproduction. We examined the interaction between reproductive trade-offs, age and resource availability in the monogamous Eurasian beaver *Castor fiber* using 12 years of data from a population in Norway. Beavers showed an initial increase in probability of reproduction until minimum age 4 – 6 years, followed by senescence. This pattern was similar to changes in adult body-condition with age, supporting the experience hypothesis. The pattern of reproductive senescence was different depending on resource availability with animals from low quality territories senescing earlier but the amount of rainfall influenced all ages equally, supporting the disposable soma hypothesis. The age of the father did not affect likelihood of reproduction. For younger mothers (<7 years) there was a trade-off between offspring quantity and quality but not for older mothers, supporting either the experience hypothesis or the disposable soma hypothesis. Litter sizes did not change with age and we detected no short-term trade-off between current and future reproduction. Thus, we found evidence for both maternal experience and disposable soma (and by extension the terminal investment) hypotheses but not the antagonistic pleiotropy hypothesis.

Introduction

Life history theory predicts that reproductive investment will increase with age as an animal's future reproductive value declines (the 'terminal investment' hypothesis, Williams 1966; Pianka and Feener in Smith and Fretwell 1974; Isaac and Johnson 2005). This is because, as mothers age, they are likely to have fewer opportunities for future reproduction. Therefore the trade-off between reproduction and survival (cellular repair and energy storage) should shift away from investment in survival towards higher reproductive effort (Williams 1966). In addition, reproductive success may also increase with age due to greater maternal experience (e.g. Komeduer 1996; Ward and Parsons et al. 2009). There is furthermore widespread evidence, also predicted by life-history theory (Hamilton 1966), for reproductive senescence, i.e., a decline in reproductive success with age (Jones and Gaillard et al. 2008). This is likely due to the accumulation of damage (*sensu* the disposal soma hypothesis, Kirkwood 1977) or antagonistic genetic pleiotropy leading to the expression of deleterious genes late in life (Williams 1957). Thus, reproductive output may decline with age despite increasing investment or experience by the ageing parents. More recently, attempts have been made to unite the disparate mechanisms for the observed patterns of age dependent fecundity under the disposable soma hypothesis by proposing that, in long-lived species, both the initial increase and subsequent decline in fecundity are due to a single trade-off between somatic repair and reproduction and its relationship to extrinsic mortality (Cichoń 2001; McNamara and Houston et al. 2009). Under this framework, as with the terminal investment hypothesis, individuals of a long-lived species should invest more in reproduction and less in somatic repair as the likelihood of survival declines with increasing age or damage. Implicit in this strategy is an accumulation of damage with age or with successive reproductive bouts as investment in repair declines and thus senescence occurs as somatic condition declines

(Cichoń 2001). Note that this framework involves neither experience nor antagonistic pleiotropy and is essentially an extension of the terminal investment hypothesis. A characteristic pattern of an initial increase followed by a decline in reproductive success with increasing age is frequently found (e.g. Komdeur 1996; Ericsson and Wallin et al. 2001; Descamps and Boutin et al. 2008; Jones and Gaillard et al. 2008; Nussey and Wilson et al. 2009). Distinguishing between the casual mechanisms of senescence patterns is difficult in field studies however, because the predictions are similar and not easily separable. For example, in both the disposable soma and the antagonistic pleiotropy hypotheses, senescence is predicted to occur over a wide range of physiological measures (Kirkwood & Rose 1991; Williams & Day 2003). One point where the predictions of these two hypotheses clearly diverge concerns the interaction between senescence and environment: variation in nutritional history should not influence the timing of senescence under antagonistic pleiotropy (though it may affect its rate), but under the disposable soma hypothesis the trade-off between somatic repair and reproduction will be stronger under poor nutrition. Therefore earlier senescence is predicted in individuals that have experienced lower nutritional intake over their reproductive lives under the disposable soma hypothesis but not the antagonistic pleiotropy hypothesis. Damage accumulation due to past investment in reproduction and constraints on the energy available for reproduction have the consequence that trade-offs are expected between current versus future reproduction (Williams 1966), and the number of offspring versus their individual quality (Lack 1947; Smith and Fretwell 1974). However, selection on life-history traits may vary with external conditions and consequently the optimal strategy may also vary with these conditions (Wilson and Pemberton et al. 2009). Studies examining the interactions of extrinsic factors with age-specific reproductive output and reproductive trade-offs are few (but see Gillespie, Russell and Lummaa 2008; Wilson and Pemberton et al. 2009).

Examining age specific reproduction with extrinsic factors may allow us to disentangle the various mechanisms behind changes in reproduction with age. For example, by examining factors that influence all individuals in the population simultaneously, such as weather variation, together with factors that vary between individuals, such as available resources within each territory, we should be able to distinguish whether any reduction in fecundity with age is due to prior investment in reproduction (following the disposable soma hypothesis) and not simply a reduced ability to acquire resources in older individuals (following either the disposable soma or the antagonistic pleiotropy hypotheses). In this example, only the disposable soma hypothesis would result in territory quality affecting the onset of senescence while weather variation influences reproductive performance but not senescence.

In monogamous species, both parents may contribute towards rearing offspring. Most studies concentrate on females when examining reproductive output. In the monogamous wood thrush *Hylocichla mustelina*, male age also influences reproductive success of breeding pairs (Brown and Roth 2009), suggesting that the influence of male age is an important consideration in studies of reproductive success in monogamous species. Few other studies have examined the effects of both female and male age on reproduction in monogamous mammals (but see Promislow 1991).

The Eurasian beaver *Castor fiber* is a large (> 20 kg at adulthood) herbivorous semi-aquatic rodent (Wilsson 1971; Műller-Schwarze and Sun 2003). They predominantly forage on deciduous trees, consuming leaves, twigs and bark (Wilsson 1971; Campbell and Rosell et al. 2005). Beavers are highly territorial (Wilsson 1971; Nolet and Rosell 1994; Rosell and Thomsen 2006), live in family groups and only the dominant pair will breed (Wilsson 1971; Műller-Schwarze and Sun 2003 but see Crawford and Liu et al. 2008). Litter sizes usually range from 1 – 5 (Campbell and Rosell et al. 2005). Young (known as 'kits') are born mid May and emerge from the natal den or lodge when weaned, approximately two months later (Wilsson 1971; Parker and Rosell 2001). Number of kits born per breeding female and the body weight of kits and yearlings are all negatively influenced by rainfall (Chapter 5). Sexual maturity is usually attained at 1.5 – 2 years of age (Wilsson 1971), whereupon offspring will disperse (Hartman 1997). Eurasian beavers can live for as long as 20 years in the wild (Rosell and Pedersen 1999). Once paired, beavers tend to remain so until one is displaced or dies (Svendsen 1980; Műller-Schwarze and Sun 2003). Territory borders can remain stable for several years (Campbell and Rosell et al. 2005). Females of the very similar North American beaver *C. canadensis* living in Finland have been found to have smaller litters if they produced larger litters in the previous year (Ruusila, Ermala and Heikki 2000), suggesting that there is an energetic trade-off involved in reproduction in this species. However, though fecundity tends to increase in early adulthood, unambiguous reproductive senescence has not been reported in the North American beaver (Henry and Bookhout 1969; Payne 1984; Welch, Robel and Fox 1993).

Here we examine age-related changes in likelihood of reproduction and in body condition in the Eurasian beaver and the effects that extrinsic factors such as territory quality and weather variation (rainfall) have on age specific reproductive output. Using body condition as a proxy for offspring quality, we furthermore investigate the relationship between offspring quantity and quality and its interaction with both intrinsic factors (parental age) and extrinsic factors. We predict that:

1. Female beavers will exhibit an initial increase followed by a decline in reproductive output with age.
2. The age of male beavers will influence reproductive output with older males showing lower reproductive output after accounting for female age.

3. Resource availability, mediated by weather (negatively) and territory quality (positively), will also influence reproductive output.

4. Following the disposable soma hypothesis, low territory quality will bring forward the onset of senescence but rainfall will not.

5. If any increase in fecundity with age is due to terminal investment and not individual experience, changes in adult body-condition with age will not match changes in fecundity, since under the terminal investment hypothesis body-condition will be maximal in younger animals while reproductive effort is low.

6. Beavers will exhibit a trade-off in current versus future reproduction, and 7) in offspring quality versus quantity.

Materials and methods

Study area

The study site is centred on three rivers, the Straumen (Nome municipality), the Gvarv and the Sauar (both Sauherad municipality), in Telemark, southern Norway (59°23′ N, 09°09′ E). The climate is cold and moderately wet with a mean annual temperature of 4.6 °C and a mean annual precipitation of 790 mm. The mean monthly temperature dips below 0 °C for five months a year between November and March. The rivers flow through small towns, farms and fields (pasture and arable) interspersed with riparian woodland dominated by grey alder *Alnus incana* and, to a lesser extent, willow *Salix* sp. and bird cherry *Prunus padus*, with some dry deciduous and coniferous forest. Where agricultural land is located next to the river, a buffer of riparian woodland or unimproved grass and scrub usually exists. Due to the presence of lakes and hydroelectric dams along their length, all rivers exhibit reduced ice cover in winter (though all beaver families in the study area build food stores whether ice-cover occurs or not). All three rivers form part of the catchment of Lake Nordsjø. None of the studied beaver families build dams. Beavers have been in the area since the 1920s (Olstad 1937). Hunting of beavers in Norway is managed through a system of quotas which are frequently not met (Parker and Rosell 2003) and therefore hunting pressure is low. Predation pressure is also likely to be low since wolf *Canis lupus*, the main predator of beavers (Andersone and Ozolins 2004), have been extirpated from the area for over 100 years, while of the other potential predators, bears *Ursus arctos* only occasionally pass through and lynx *Lynx lynx* are present, but at low densities (Rosell and Sanda 2006).

Animal sampling

Between 1998 and 2008 beavers in the study areas were monitored through an extensive live-trapping program using hand-nets from a motor boat between March and November (Rosell and Hovde 2001). Captured individuals were immobilized in cloth sacks and measurements recorded included weight (to the nearest 200 g) and body-length (cm) following the curvature of the spine from the nose-tip to the base of the tail (where fur gives way to scales). Animals were sexed by the colour of the anal gland secretion (Rosell and Sun 1999), tagged with a microchip (Avid or Trovan) and marked with unique color-plastic (Dalton) and metal (National Band and Tag Co.) ear-tag combinations. An animal was assumed to be resident in a territory if it was trapped or sighted in the same territory more than once >24h apart, or was seen interacting non-agonistically with other known residents.

When trapped for the first time, animals were assigned to an age-class (0 years = kit, 1 years = yearling, 2 years = subadult and ≥3 years = adult) based on weight (Chapter 2, 5; Appendix 1.). For the purposes of analyzes, animals that were ≥3 years old when first trapped were assumed to be three years of age (minimum age), animals that were ≥2 years old when first trapped were assumed to be minimum two years of age, while animals that could be confidently aged to kit, yearling or subadult were ascribed their actual age.

Dominance status of females, and thus the identity of mothers, was determined by previous trapping and sighting history, body weight and incidences of lactation. For example, individuals dispersing into a territory were assumed to have obtained the dominant breeding position, an assumption generally corroborated by the disappearance of the previous dominant female, by higher body weight (compared with same sex group members) and lactation (diagnosed by nipple length > 0.5cm). Unless there was evidence to the contrary, dominant individuals were assumed to maintain their status until they disappeared or died.

Reproduction in each year was determined by counting the number of kits trapped that year plus the number of yearlings trapped the following year that had not been previously trapped as kits. Occasionally, we also found two-year old animals that were also clearly resident in the territory and included these in counts of reproduction. Unmarked offspring (N=19) were also included if they were sighted in a territory but not trapped and all other known offspring were accounted for. We used the first record from each offspring in analyzes of body condition. For each beaver territory, trapping effort was defined as the number of nights spent trapping in the area (either Gvarv river, Straumen river, the northern section of the Sauar river or the southern section of the Sauar river) in the current and following year.

Territory quality

Territory borders were estimated from a combination of firstly, radio-telemetry (see Campbell and Rosell et al. 2005), secondly, behavioural observations of animal locations, thirdly, the location of territorial behaviours such a scent-marking (Rosell and Thomsen 2006), and finally, surveys of beaver scent-mounds. Within beaver territories, deciduous habitat blocks greater than approximately 100 m^2 (corresponding to a minimum of about 10 m of river bank) within 40 m of the shore were delineated into polygons on 1:5000 field maps. On the first instance, blocks were divided into sections containing similar tree species and structure based on visual assessments. The habitat blocks were digitised in 2D onto a geographical information system (GIS: ArcView 3.x or ArcGIS 9.1, ESRI). Rivers were digitized from 1:5000 scanned maps (Sauar and Gvarv rivers) or obtained in digitized vector format (Straumen river). The cut-off point of 40 m was used based on a study of an adjacent population of beavers in southern Norway where the mean maximum distance of beaver-damaged woody plants from the river was found to be 36 m ± 32 SD (Parker and Haugen et al. 2001). This has been confirmed as suitable from research on our own study population where there is a gradual drop in foraging with distance from water with approximately 70% of woody stems being cut by beaver within the first 10 m of the water's edge, compared with just over 20% at 10-20 m dropping to approximately 5% at 30-40 m from the water's edge (Haarberg and Rosell 2006).

Survey transects were carried out in each habitat block containing deciduous vegetation in June-July 2000 (Gvarv and Straumen rivers) and June-July 2006 and 2007 (Sauar river). The first transect was positioned 50m upstream of the downstream border of each block and subsequent transects in the same block were at every 200m. If the block was less than 60m long the transect was taken at the mid-point of the block length. Transects were not walked within 10m of the block edge where possible. Each transect consisted of four points, a point being a 5m radius circle, at 5, 15, 25 and 35m from the shoreline (measured by pacing). At each transect point, we visually estimated the percentage cover of small trees (1-5m) in height. Beavers preferentially forage on smaller trees (dbh <5cm) and woody vegetation represents the largest part of the diet of the beavers in the study area (Campbell and Rosell et al. 2005). It is thus likely that the small trees measured in our survey constitute the main food base of the beavers in our population. We also recorded dominant small tree species, but initial analyzes suggested that there was no simple pattern of species availability on our response variables and, to reduce the ratio of explanatory variables to sample size, we therefore ignored species in further analyzes. Territory quality (q) was therefore defined as:

$$q = \sum_i c_i \times ha_i$$

Where c_i is the mean percentage cover of small trees and ha_i the area in hectares of the ith habitat block in each territory. Based on these values, territories were then divided into four categories so that each category contained approximately the same number of territories. These were: 1, (lowest quality) q < 139; 2, q = 139 – 231; 3, q = 232 – 390; and 4 (highest quality) q > 390. Since territory borders are fairly inflexible (Campbell and Rosell et al. 2005: style), in many cases, territory quality did not change over the residency of a beaver. For example, out of the 38 known females and 36 known males, only five of each sex changed territory quality category, of which one was due the female moving territory and not a shift in the territory borders.

Weather variables

Daily rainfall data between 1997 – 2008 were obtained from the Lifjell weather station (height 354m, E:162249, N:6605878) using *Eklima* (*www.eklima.no*) . These data have been found to correlate well with rainfall measured on rivers in the study area (Chapter 5). For measures of spring-summer rainfall (Apr – Sept) we adjusted values for run-off due to exceptionally high rainfall in July 2007 (see Chapter 5). This adjustment was unnecessary for autumn rainfall (Aug – Oct).

Statistical procedures

All statistical analyzes were conducted in the R environment (v. 2.5.1 and v. 2.9.2; R Development Core Team 2007, 2009). All p values are two-tailed. For analysis of likelihood of reproduction, any territories in areas that were not studies for more than four years were excluded. Sample sizes used were territories = 29, territories where quality assessed = 25, dominant females = 38 (minimum age 2 – 12), mother-years = 150, dominant males = 36 (minimum age 2 – 12), father-years = 149, litters = 71, litters with known mothers = 51, litters with known fathers = 53, litters with know mothers and father = 45, total offspring = 131. Thirty nine of the measured offspring were first trapped as yearlings and 11 as two-year olds with the remainder being first trapped as kits.

Senescence and reproductive output

We investigated the likelihood that a dominant female would reproduce in a year using a generalized linear mixed model (GLMM) with a binomial error structure and a logit-link function that was fitted using the function *lmer* in the R package *lme4* (v. 0.999375-32 in R 2.9.2, Bates and Maechler 2009). We included random terms for *mother* and *year* and used a random slope model following Schielzeth and Forstmeier (2009) with a random intercept and slope for *mother*. Initial data exploration found a potential quadratic relationship between likelihood of reproduction and mother minimum age. Mother minimum age and father minimum age were highly correlated ($r = 0.691$, df = 130, $p < 0.001$) due to the tendency of beaver to pair for life. In order to assess the effects of father age on reproduction in the presence of mother age, we created a young versus old binary variable of father age where 0 = ≤6 years and 1 = ≥7 years minimum age. Previous research has found a significant negative effect of rainfall the previous late-summer and autumn (Aug-Oct) on the number of dominant females that produce litters in each year (Campbell, Rosell and Macdonald submitted). Furthermore, we predict that territory quality will play a role in reproductive decisions in dominant females. Initial data exploration found that the total amount of understory vegetation was a better predictor of reproduction than the amount per unit length of territory. Therefore, we began our analysis by constructing a full model that included mother age and its quadratic term (mother age^2), the binary variable for father age, rainfall in the previous autumn and total understory vegetation plus all possible two-way interactions between these variables (excluding mother age^2). Trapping effort was also included as a control variable as the detection of offspring is likely to be influenced by this variable. We then reduced this full model to its minimum adequate model (MAM) using single-term deletion, starting with the interaction terms and any lower terms not included in the interaction terms. Trapping effort was not considered for deletion. Terms were discarded if they did not improve the explanatory power of the model. Explanatory power was assessed using Akaike’s information criterion (AIC, Burnham and Anderson 2002) and standard likelihood-ratio tests. Following the principle of model parsimony, a model term was considered to be extraneous firstly if its removal resulted in a model with a lower AIC and secondly, in situations where the AIC of the more parsimonious model was higher, if the likelihood-ratio test between the two models indicated that the higher AIC was not significantly different ($p > 0.05$) from the earlier model (Table 1). Models with the same rows of data were always used when comparing AIC and likelihood-ratios. However, once in the model of reproductive senescence, discarding a variable resulted in additional rows becoming available for analysis because the discarded variable was missing in these rows. These new rows were included in further models. The predicted values from the resulting MAM were interpolated to data within the range of the input values and used to create contour plots to examine the interactions between the variables.

For interpreting the results of a GLMM, p values based on the normal z distribution are provided in *lme4*. However, this approach assumes that the distribution of the parameter estimates is symmetric and converges to a normal distribution, both of which are unlikely (Baayen, Davidson and Bates 2008). Therefore, though we provide p values from the z distribution here for easy interpretation, to adequately assess uncertainty in the MAM parameter estimates, we used 95% confidence intervals (CIs) based on the underlying distribution of the model residuals. 95% CIs that do not cross zero are analogous to $p < 0.05$. The 95% CIs were created by firstly generating a Markov Chain Monte Carlo (MCMC) sample (n = 1000) from the posterior distribution of each parameter estimate using the function *mcmcsamp* in *lme4* (v. 0.99875-9 in R 2.5.1, Bates 2007). Secondly, we calculated the Bayesian highest posterior density (HPD) 95% CIs of the MCMC sample for each parameter estimate using the function *HPDinterval* in the R package *coda* (Plummer et al. 2006).

To investigate the relationship between parental age and litter size we constructed a GLMM with a Poisson error structure and a log-link function that was, as before, fitted using the function *lmer* in the R package *lme4* (v. 0.999375-32 in R 2.9.2, Bates and Maechler 2009). We included *year* and *mother* as random terms with a random intercept and slope for *mother* (Schielzeth and Forstmeier 2009). We included trapping effort as a control variable and constructed three alternative models on litter size, which contained firstly both linear and quadratic mother minimum age terms (quadratic age model), secondly a linear minimum age term (linear age model) and thirdly no age term (trapping effort only). Only one litter of >3 offspring (four) was recorded during the study period and we therefore combined litter sizes of three and four. Because there were very few kits born to mothers aged two years (n kits = 1) or mothers with a minimum age >8 years (n kits = 4), we combined mother minimum age two with three and mother minimum ages >8 with minimum age eight.

Physical senescence

We investigated the effect of age on body condition (weight relative to length) in sexually mature beavers (age ≥ 2 years) using linear mixed models (LMM) with a Gaussian error structure with an identity link function, again using the function *lmer* in the R package *lme4* (v. 0.999375-32 in R 2.9.2; Bates and Maechler 2009). To examine body condition, we used *log* body weight as the response variable and included *log* body length as a predictor together with minimum age, minimum age^2, sex and a binary variable that described whether the age data was minimum age (0) or actual age (1). We included random intercepts for *year* and for *subject* within *sex* (Schielzeth and Forstmeier 2009). We reduced each full model to its MAM following the procedure outline above. For each year, dominant females from territories where kits were recorded were excluded from the analysis since reproductive status is likely to influence the relationship between weight and size. Individuals measured only once were excluded from the model. We calculated *p*-values directly from the MCMC 95% CIs instead of from the *z* distribution using the R package *languageR* (v.0.955 in R 2.9.2; Baayen 2009). This procedure is not current available for GLMMs.

Current-future reproduction trade-off

We assessed the current-future reproductive trade-off by examining current versus prior reproduction. Firstly, we examined temporal autocorrelation in the reproductive senescence relationship by repeating the MAM GLMM model of likelihood of reproduction in a penalised quasi-likelihood GLMM using *glmmPQL* in the R package *MASS* (v. 7.3-1 in R.2.9.2, Venables and Ripley 2003) a binomial error structure and a first-order autoregressive correlation (AR1) structure. We specified random intercepts for *mother*. The response variable was reproduction (binary) and fixed effects were age, age^2, rainfall (Aug-Oct) and territory quality, with an age × territory quality interaction. We then repeated this model with the response variable of litter size (0, 1, 2 ≥3 kits) using a Poisson error structure.

Secondly, we included a binary variable if prior reproduction (indicating whether a mother had offspring in the previous year) as a predictor in a GLMM model of likelihood of reproduction in *lme4*. We included all variables that were retained in the original MAM (above) and all possible two-way interactions and reduced the model as above. We then repeated the MAM GLMM for mother age on litter size above but included litter size (0, 1, 2 or ≥3) in the previous year as a predictor in *lme4*. We included a mother age × prior litter size interaction and reduced the model as before. Prior reproduction was not included in the original models of likelihood of reproduction and litter size because it excludes the first records of each female unless we had managed to observe that female's immigration or dispersal into a recent breeding vacancy by trapping (or, with previously marked animals, observing) it in time for parturition. This would bias the data towards older females, for example 22 of 28 three-year olds compared with six of 116 records of older females have missing data for prior reproduction.

Offspring quantity versus quality

We investigated the effect of litter size on the body condition of offspring using a LMM with a Gaussian error structure with an identity link function, using *lmer* in the R package *lme4* (v. 0.999375-32 in R 2.9.2; Bates and Maechler 2009). We included a random intercept for *mother* (Schielzeth and Forstmeier 2009) but did not include a random slope term by *year* due to low correlation between the resulting random slope and intercept for *mother*. However, using a random intercept model instead of a random slope model had minimal effect on the parameter estimates of the MAM.

As above, to examine body condition, we used *log* body weight as the response variable and included *log* body length as a predictor. Models were weighted by trapping effort. Initial data exploration indicated that this measure of body condition in juvenile beaver varied with age and with season with body condition increasing with age and being greatest in spring (Apr-May) and autumn (Sept-Oct) and lower in summer (Jun-Aug) and winter (Nov-Mar). Therefore age and a binary season variable (spring and autumn versus summer and winter) were included in the model as control variables which, along with body length, were not considered for exclusion. As before, due to sample size constraints, we combined litter sizes of three with four, mother minimum age two with three and mother minimum ages >8 with minimum age eight. In the full model, we included a quadratic term for mother minimum age as effects on offspring body condition may follow the same senescence pattern as we predict for likelihood of reproduction. Additional variables we considered were territory quality using the same measure as outlined above and rainfall from Apr - Sept in the year of birth (adjusted for runoff) as this has been found to be inversely related to body weight in beaver kits in the study area (Campbell, Rosell and Macdonald submitted).

We started with a full model with all possible two- and three-way interaction terms between mother minimum age (linear term), territory quality, rainfall and litter size. This full model was reduced to its MAM following the same AIC stepwise selection criteria outlined above (Table 1). Likewise, interactions were assessed and 95% CIs and *p*-values calculated following the same procedures as outlined for the physical senescence LMM above.

Results

Senescence and likelihood of reproduction

Data exploration indicated that the reproductive output of breeding females initially increased and then declined with their minimum age (Fig. 1). A logistic model of territory quality (*q*) on the binary variable of reproduction indicated that territory quality also influences reproductive output with females in higher quality territories more likely to breed ($\beta = 0.003 \pm 0.001$ SE, df = 151, $P(\chi^2) = 0.004$, Fig. 2).

The binary variable describing the age of the male was dropped from the MAM (Table 1a), indicating that male age did not affect reproductive output. Female age had a significant influence on reproduction with the likelihood that a female would give birth increasing until the animal reached a minimum age of between four and six, followed by significant reproductive senescence thereafter (Table 2a, Fig. 3a). Moreover, the pattern of reproductive senescence was influenced by territory quality, but not by rainfall (Table 1a). Females in high quality territories exhibited a higher probability of reproduction at a later age with the peak probability of 0.7 at the minimum age of six (Fig. 3b). In contrast, females in poor quality territories exhibited an earlier and lower peak in reproduction with the peak probability of 0.4 occurring at the minimum age of four years (Fig. 3b).

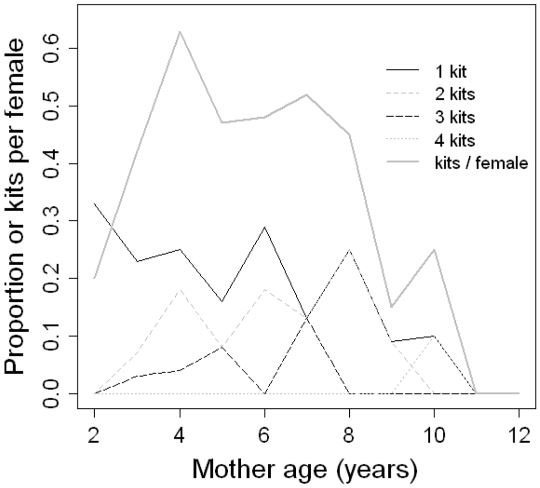

Figure 1: The proportion of females in breeding positions (max one per territory) producing litters of one, two, three or four kits and the total number of kits produced per female (including those in breeding positions that did not produce a litter) with the minimum age of the female.

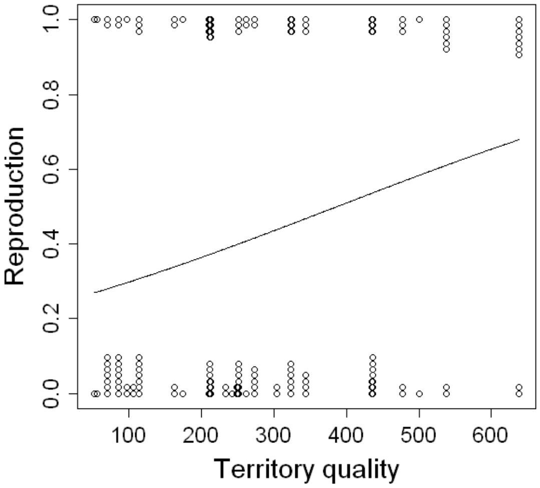

Figure 2: Effect of territory quality (q) on likelihood of reproduction. Stacked points are the numbers that did (top) and did not (bottom) successfully reproduce. The fit line is based on a logistic model of q on reproduction and is statistically significant.

Table 1 (following pages): Selection steps to obtain minimum adequate models (MAMs) for a) the reproductive senescence, b) physical senescence c) current versus future offspring and d) offspring quantity versus quality. At each step, all possible terms were removed singly, starting with the highest order interactions and any lower terms not included in higher order terms. At each step, the term that caused the greatest drop in AIC was selected. Following the principle of model parsimony, if removal of single terms did not result in a drop in AIC, the term that led to the lowest AIC out of all possible single-term deletions was tested against the model from the start of the step using likelihood ratio tests (LRT). If the more parsimonious model was not significantly poorer (p>0.05), it was accepted over the more complex model. d.f.^{1} are the total degrees of freedom taken up by the terms in the model. d.f.^{2} are the degrees of freedom for the χ^2 statistic in the likelihood ration test. χ^2 statistics are only provided when the model AIC increased at a selection step. Eventually, the model became irreducible and the MAM was found (denoted by *†*). Between models a11 and a12 additional rows of data became available due to the removal of a variable with incomplete data and therefore two AIC values are provided. At this point, because additional rows were added, we tested whether adding the last deleted term improved the model. Numbers under LRT indicate which two models were compared in the LRT and model text indentation increases as terms are successfully removed. * indicates whether the proposed deletion of a term was rejected.

Table 1:

	Model	d.f.^{1}	AIC	LRT	d.f.^{2}	χ^2	*p*	
a)	*Reproductive senescence*							
1	maximal model	19	150.12					
2	∟ *minus* territory quality × rain (Aug-Oct)	18	148.14					
3	∟ *minus* father age × territory quality	17	146.21					
4	∟ *minus* father age × mother age	16	144.49					
5	∟ *minus* father age × rain (Aug-Oct)	15	143.12					
6	∟ *minus* father age	14	143.20	*5 vs 6*	1	2.08	0.150	
7	∟ *minus* mother age × rain (Aug-Oct)	13	143.55	*6 vs 7*	1	2.35	0.125	
8	∟ *minus* mother age × territory quality	12	149.43	*7 vs 8*	1	7.88	0.005	*
9	∟ *minus* rain (Aug-Oct)	12	153.57	*7 vs 9*	1	12.03	<0.001	*
10	∟ *minus* mother age^2	12	152.58	*7 vs 10*	1	11.03	<0.001	*
11	∟ *minus* father (random term)	10	137.55					†
	(with additional rows)		157.84					
12	∟ *add* mother age × rain (Aug-Oct)	11	156.20	*11 vs 12*	1	3.64	0.056	
b)	*Physical senescence*							
1	maximal model	12	-708.38					
2	∟ *minus* sex × age	11	-709.71					†
3	∟ *minus* sex × minimum age vs actual age	10	-703.11	*2 vs 3*	1	8.70	0.003	*
4	∟ *minus* sex	10	-705.82	*2 vs 4*	1	5.89	0.015	*
5	∟ *minus* age^2	10	-666.17	*2 vs 5*	1	45.53	<0.001	*
c)	*Current-future reproduction*							
1	Maximal model	16	128.31					
	∟ *minus* mother age × prior reproduction	15	125.54					
	∟ *minus* territory quality × rain (Aug-Oct)	14	124.02					
	∟ *minus* prior reproduction × rain (Aug-Oct)	13	122.57					
	∟ *minus* prior reproduction × territory quality	12	121.90					
	∟ *minus* prior reproduction	11	119.92					

Table 1 (cont):

	Model	d.f.^{1}	AIC	LRT	d.f.^{2}	χ^2	p	
d)	*Offspring quantity versus quality*							
1	maximal model	20	159.93					
2	∟*minus* mother age × litter size × territory quality	19	158.71					
3	∟*minus* mother age × territory quality	18	157.71					
4	∟*minus* mother age^2	17	159.26	*3 vs 4*	1	3.55	0.060	
5	∟*minus* mother age × litter size × rain (Apr-Sept)	16	160.29	*4 vs 5*	1	3.03	0.082	
6	∟*minus* mother age × rain (Apr-Sept)	15	158.30					
7	∟*minus* litter size× territory quality × rain (Apr-Sept)	14	157.53					
8	∟*minus* litter size × territory quality	13	156.06					
9	∟*minus* territory quality × rain (Apr-Sept)	12	154.39					
10	∟*minus* litter size × rain (Apr-Sept)	11	155.04	*9 vs 10*	1	2.65	0.104	†
11	∟*minus* mother age × litter size	10	161.69	*10 vs 11*	1	8.66	0.003	*
12	∟*minus* rain (Apr-Sept)	10	160.25	*10 vs 12*	1	7.21	0.007	*
13	∟*minus* territory quality	10	167.96	*10 vs 13*	1	14.92	<0.001	*

The proportion of females producing litters with 1, 2, 3 or 4 kits did not show any consistent patterns with age (Figure 1). Litter sizes for each age of mother were (mean±SD) age ≤3 years = 1.4±0.7, age 4 = 1.5±0.7, age 5 = 1.9±0.9, age 6 = 1.4±0.5, age 7 = 2.0±1.0 and age ≥8 = 1.8±1.0 (Fig. 4b). The MAM that described litter size dropped both *age*^{2} and *age* (AIC = 24.61 versus 26.31 and 28.29 for linear age and quadratic age models respectively) indicating that mothers did not adjust the number of kits born per litter with increasing age.

Physical senescence

In sexually mature beavers, the MAM that described the effect of minimum age on body condition dropped the sex × age interaction but included sex, the full quadratic terms for minimum age and a known vs actual age × age interaction (Table 1b). In both sexes, body condition initially increased, peaking at a age of approximately seven years (for animals ascribed a minimum age) or eight – nine years (for animals ascribed an actual age) and declining thereafter (Table 2b, Fig. 5).

Current-future reproduction trade-off

A log-linear model assuming a Poisson distribution with a log-link function of prior reproduction (number of kits born in the previous year) on reproduction (number of kits born in the current year) was not significant ($\beta = 0.112 \pm 0.131$ SE, df = 126, $P(\chi^2) = 0.399$, Fig. 6).

The coefficient of the AR1 correlation structure from the penalised quasi-likelihood GLMMs were low ($\rho = -0.199$ and $\rho = 0.064$ for likelihood of reproduction and litter size respectively). In the GLMM of likelihood of reproduction, the prior reproduction term and its interaction terms were four of the first five terms to be dropped from the model (Table 1c). In the GLMM of litter size, the mother age × prior litter size interaction was the second term to be dropped after mother age^2 (AIC = 23.00 with and 21.04 without interaction term) followed by prior litter size (AIC = 19.07 without prior litter size). These results indicate that reproductive output was not influenced by prior reproductive output.

Offspring quantity versus quality

The MAM that described offspring body condition contained litter size, mother minimum age, rainfall (Apr-Ag) in the year of birth and territory quality as well as a litter size × mother minimum age interaction term (Table 1c, 2c) indicating that the relationship between litter size and body condition of offspring varied with the minimum age of the

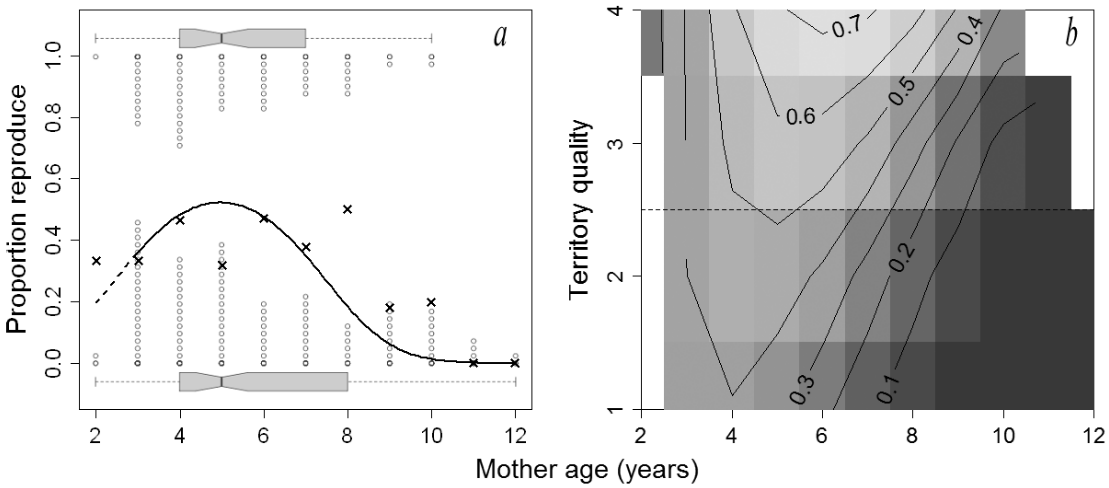

Figure 3: a) The relationship between minimum age on likelihood of reproduction and b) the interaction between minimum age and territory quality on the likelihood of reproduction (contour lines). The shading scheme in b) graduates from dark grey for low probabilities of reproduction to light grey for high probabilities. Predicted probabilities are provided on the contour lines. In a) crosses represent the proportion of breeding females successfully reproducing at each age while the grey open circles are the stacked data points for each female at each age with those stacked from the bottom not reproducing and those stacked from the top reproducing. Horizontal box plots in a) are the 25-75% quartiles with the median of mother minimum age in each group (reproduced or not). The fit line in a) is a cross-section of b) along the dashed line. The dashed line in a) is where no data was available for the age – territory quality combination. The white areas in b) indicates that no raw data were available. The median values of other factors were used to obtain these figures: trapping effort = 20 nights per year, rain = 261mm Apr-Sept and (a only) territory quality = 2.5. Likelihood of reproduction increased to a minimum age of 4-6 years before declining. The curve of the relationship between age and reproduction was lower and peaked earlier for mothers in low quality territories.

Table 2 (following page): Parameter estimates for the MAM for a) reproductive senescence: the effects of age, territory quality and rainfall (in the previous autumn) on the likelihood that a dominant female beaver will give birth, b) physical senescence: the effects of age on body condition (body weight controlling for body length) in females and males from sexual maturity and c) the offspring quality versus quantity trade-off: the effects of litter size, mother age, territory quality and rainfall on the body condition of offspring. Rainfall in c) has been adjusted to account for runoff. In a), this correction was unnecessary. Model a) is a GLMM with a binomial error structure and a logit link function with random terms for *year* and *mother*. Model b) and c) are LMMs with a Gaussian error structure and an identity link function that has random terms for b) *year* and *subject* or c) *mother*. The parameter estimates are obtained using a Laplace approximation to maximum likelihood. 95% CIs are Bayesian HPD 95% CIs of the MCMC sample of each parameter. For models b) and c), *p*-values were obtained directly from the 95% CIs, with * indicating significance at the 95% confidence level, ** at 99% and *** at 99.9%.. For model a), this method was unavailable and statistical significant is best assessed using the 95% CIs (where not crossing zero equates to $p < 0.05$). However, *p*-values based on the normal (z) distribution are provided for ease of interpretation.

Table 2:

		estimate	lower	upper	*z*	*p*
a)	Reproductive senescence (reproduction=)					
	intercept	-0.14	-3.79	3.1	-0.07	0.944
	trapping effort	0.029	0.0086	0.07	1.76	0.078
	mother age (years)	0.69	-0.61	1.53	1.08	0.279
	mother age2	-0.13	-0.23	-0.038	-2.41	0.016 *
	rain (total mm Aug-Oct)	-0.0068	-0.011	-0.0042	-3.35	<0.001 ***
	territory quality (1 – 4)	-0.69	-1.89	0.23	-1.27	0.203
	age × territory quality	0.24	0.13	0.48	2.18	0.029 *
b)	Physical senescence (ln body mass kg =)					
	Intercept	-2.01	-3.88	-1.98	-	<0.001 ***
	ln body length	1.11	1.08	1.53	-	<0.001 ***
	year day	0.0005	0.0003	0.0006	-	<0.001 ***
	sex (male)	-0.039	-0.063	-0.016	-	0.001 **
	minimum aged vs known aged	-0.12	-0.16	-0.06	-	<0.001 ***
	Age (years)	0.074	0.056	0.10	-	<0.001 ***
	age2	-0.0053	-0.0076	-0.0042	-	<0.001 ***
	min aged vs known aged × age	0.014	0.0043	0.024	-	0.005 **
c)	Offspring trade-off (ln body mass kg =)					
	Intercept	-2.88	-5.52	-0.34	-	0.027 *
	ln body length (cm)	1.56	1.08	2.15	-	<0.001 ***
	offspring age (years)	0.25	0.08	0.43	-	0.007 **
	season	-0.18	-0.26	-0.03	-	0.012 *
	mother age (years)	-0.077	-0.19	-0.02	-	0.026 *
	litter size	-0.32	-0.58	-0.14	-	0.003 **
	territory quality (1 – 4)	-0.063	-0.12	0.01	-	0.062
	rain (runoff adj. Apr - Sept)	-0.025	-0.049	-0.005	-	0.014 *
	mother age × litter size	0.052	0.020	0.10	-	0.006 **

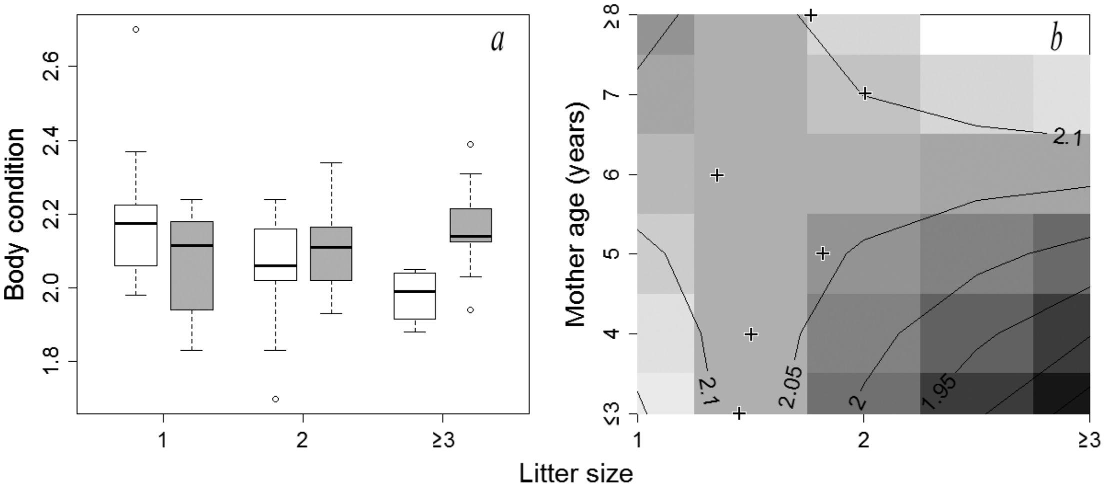

Figure 4: a) Mean body condition of offspring born in different sizes of litters in young (≤4 years old, white boxes) and older (≥5 years old, grey boxes) mothers, and b) the interaction between mother minimum age and litter size on the body condition (represented by contour lines and shading) of offspring. The shading scheme in b) graduates from dark grey for poor body condition to light grey for good body condition. Predicted values are provided on the contour lines. White areas indicate that no or too few raw data were available. Litter sizes of three and four kits, mother minimum ages of two and three years and mother minimum ages of eight years and greater are combined. In a), boxes are the 25-75% quartiles and whiskers represent the most extreme datapoints within 1.5× the interquartile range. Body condition was greatest in offspring born singly to young mothers and those born in larger litters to older mothers. The negative trade-off between litter size and offspring body condition declined in older mothers and was not evident in mothers with a minimum age older than five years. + symbols indicate the mean litter size born to mothers in each age group. The apparent increase in litter size with age is not significant (see results). Body condition was measured as *ln* body weight (kg) controlling for *ln* body length, offspring age and season. The values presented here are weight assuming an age of 0 years, a body length of 48 cm (the mean body length of kits in the population) and a spring/autumn season.

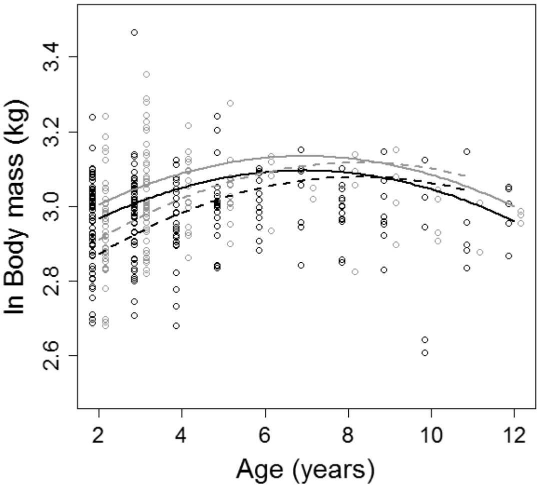

Figure 5: The relationship between body condition (weight controlling for length) and age in sexually mature male (black circles and lines) and female (grey circles and lines) beavers. The fit lines are obtained from a LMM with random intercepts for *year* and for *subject* nested within *sex*. The solid fit lines represent animals which were ascribed a minimum age while the dashed fit lines represent animals whose actual age was known. The circles represent the mean within-age value for an individual. Dominant females which were known to have reproduced that year are excluded. Body condition was measured as *ln* body weight (kg) controlling for *ln* body length. The values presented here are weight assuming a body length of 80 cm on year-day 180.

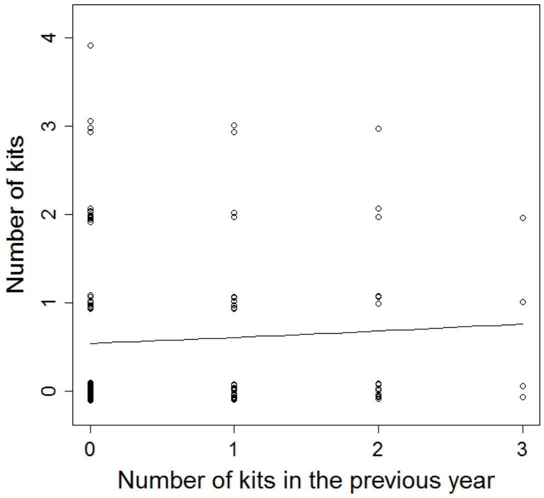

Figure 6: Effect of prior reproductive output on current reproductive output (measures as number of kits in the previous versus current year). The fit line is from a log-linear model assuming a Poisson distribution. The slope was not significant.

mother. In younger mothers, offspring born in larger litters had lower body condition (lower body weight for their size) than those born in smaller litters (Fig. 4). However, this effect disappeared in older mothers where body condition remained similar across litter sizes (Fig. 4). As expected, rainfall had a negative effect on offspring body condition (Campbell, Rosell and Macdonald submitted) while the 95% CIs indicated that the effect of territory quality was not significant.

Discussion

In agreement with out first prediction, likelihood of a female reproducing initially increased, peaked and then declined with her increasing age. However, litter sizes were not influenced by the mother's age. Our second prediction was not met as likelihood of reproduction was not influenced by the age of the male. In agreement with both our third and fourth predictions, territory quality positively, and rainfall negatively, influenced reproductive output, but while the effect of rainfall was independent of female age, fecundity was lower and senescence occurred earlier in females in poor quality territories. Contrary to our fifth prediction, in both sexes, the pattern of age specific body-condition approximately matched the pattern found with fecundity. Counter to our sixth prediction, we found no trade-off between current and future reproduction but, in partial accordance with our seventh prediction, a trade-off was evident between litter size and offspring body-condition, though only in younger mothers.

Senescence

The pattern of reproductive senescence found here is very similar to that found in other bird and mammal species where senescence does not begin immediately after sexual maturity has been attained (Promislow 1991; Jones and Gaillard et al. 2008). Senescence has not previously been reported in studies on North American beavers (Henry and Bookhout 1969; Payne 1984) though low sample sizes in older animals in these studies preclude drawing strong inference from the slight decline in the number of pregnant older females found. There are several potential reasons why we found a much stronger senescence signal in the Eurasian beavers. Firstly, differential mortality, whereby poor quality females that produce fewer offspring tend to die younger and which acts to increase the population mean reproduction with age, may have masked the signal in those cross-sectional studies, whereas our longitudinal study allowed examination of changes within individual animals. Secondly, both North American studies examined pregnancy rates in all females of reproductive age. This may include non-breeding subordinate animals, which would reduce the apparent pregnancy rate in younger animals but not older animals because older animals are more likely to be in dominant positions. Thirdly, both North American studies used kill-trapping. This technique would create breeding vacancies in the populations. If the population density was high enough to contain many non-breeding females, it is possible that some of these would be older animals that had yet to breed. If senescence is cause by the accumulation of damage due in part to the costs of reproduction, then these ageing brides might be expected to have higher fecundity than similar aged females that had bred from a younger age. Our method effectively assumed that any animal that arrived from outside the study area to take a breeding position was three-year old (or occasionally two year old), which may mask similar effects in our population. Fourthly, both North American studies used a combination of corpora lutea, placental scars and embryos to assess pregnancy whereas we used the presence and number of offspring surviving until at least two-months of age. It is feasible that older female Eurasian beavers produce as many embryos as younger animals but are more likely to experience losses prior parturition or emergence of kits at two-months of age (Parker and Rosell 2001).

Due to the high covariance between minim ages of mothers and fathers, our measure of father age was necessarily simple and only distinguished whether he was young or old. Nevertheless, it’s exclusion from the final model of reproductive output suggests that the age of the father has little influence on reproduction in this monogamous mammal. Compared to birds, the proportion of energy invested in reproduction by mammalian fathers is low and so it is perhaps not surprising that father age had no influence, even though beaver fathers aid in provisioning of offspring prior to their emergence (Novak 1987; pers. obs).

The interaction between senescence and territory quality (where senescence began earlier in low quality territories) is, to our knowledge, the first time that senescence patterns have been shown to be influenced by resources in a wild mammal population. Not only was their greater reproductive output in high quality territories, but females in these high quality territories were still exhibiting year-on-year increases in reproductive output at the age that females in low quality territories were senescing. However, females were similarly influenced by rainfall irrespective of age. These results support the disposable soma hypothesis and not the antagonistic pleiotropy hypothesis. However, the interaction between rainfall and mother age was only narrowly dropped from the MAM, which might suggest that older females are also less able to cope with poor nutritional availability, but see further discussion below. An alternative hypothesis that could explain the effect of territory quality is that better quality females might generally acquire the better quality territories. This hypothesis would be difficult to test on incumbent territory owners since we cannot discern the direction of causality between individual quality and territory quality. However, vacancies in territory ownership in our densely populated study area are sufficiently rare (mean = 12% of female breeding positions becoming available per year) and territory loyalty high enough (of 57 breeding females, only two moved territory) to suggest that this hypothesis is unlikely since a prospective owner would do well to take the first territory of adequate quality that becomes available.

The relationship of body condition with age displayed a similar pattern to that of reproductive output. This matching pattern of an initial increase in both reproductive output and body condition supports the hypothesis that the initial increase in reproductive output is due to the accumulation of experience by mothers, as has been suggested in other studies (e.g., Komdeur 1996; Ward and Parsons et al. 2009; Öst and Steele 2010), and does not support the terminal investment hypothesis which predicts that investment in repair and therefore body-condition will be maximal in younger animals. The decline in both body-condition and fecundity in older animals lends further support to the general hypothesis that senescence is due to a physiological decline in late life, but cannot be used to distinguish between the antagonistic pleiotropy and the disposable soma hypotheses.

Current – future reproduction and offspring quality – quantity trade-offs

Our finding of no effect of prior reproductive output on current reproductive output contradict earlier research on carcasses of North American beavers in Finland where the number of foetuses were negatively related to the number of placental scars from the previous year (Ruusila, Ermala and Heikki 2000). However, that study only used mothers between the ages of three and five years whereas we used a wider age range. Our finding that only younger mothers exhibit a trade-off between offspring quantity and quality (here measured as body-condition) suggests that the costs of reproduction are higher in younger animals, which may explain why we did not find a current – future reproductive trade-off in our study. A reduction in the apparent costs of reproduction with age could therefore be explained by the greater experience of mothers, further supporting our earlier suggestion that the initial increase in reproductive output with age is due to experience. Equally, a decline in reproductive trade-offs with age could be explained by the terminal investment hypothesis, whereby older mothers increase investment in reproduction despite increasing costs. Both mechanisms have been previously found to influence the trade-off in reproduction with age in other species. For example, a decline in the apparent cost if reproduction with age was attributed to experience in bison, *Bison bison*, (Green and January 1990) while there is experimental evidence for increasing reproductive investment in older tree swallows, *Tacyhcineta bicolor*, (Ardia and Clotfelter 2007).

Our finding that there is no apparent trade-off in the number and body-condition of offspring in older mothers implies that mothers should invest more in larger litters as they age. However, older mothers were no more likely to give birth to larger litters than younger mothers. Our result matches the finding of Ruusila, Ermala and Heikki (2000) on North American beavers, but disagrees with Henry and Bookhout (1969), Payne (1984) and Welch, Robel and Fox (1993), all of whom found an increase in the number of embryos, placental scars or corpora lutea with age in North American beavers.

The negative effect of rainfall on offspring body-condition matches an analysis on the same population (Chapter 5) in which the reasons why rainfall reduces the body weight of beaver kits and yearlings are discussed. However, rainfall did not influence the trade-off between offspring number and body-condition suggesting that the negative effect of rainfall operates on the foraging efficiency of beaver kits after emergence and not on the foraging efficiency of the lactating mother. Territory quality was dropped from the MAM of offspring body-condition, despite emerging as important for the likelihood of reproduction. Therefore, though greater resource availability resulted in more frequent reproduction, it did not influence offspring body condition. This suggests that females in resource rich territories partition resources towards more offspring but not higher quality offspring. One mechanism for this pattern could be females with greater resources taking shorter breaks between reproductive bouts instead of investing energy in larger litters of high quality offspring. This would appear a sensible strategy in the beaver where offspring are dependent over at least two years and therefore successive offspring can overlap. Increasing litter sizes or investing greater energy in lactation to increase offspring quality would both come at a direct cost to the mother while increasing the frequency of reproduction will increase the pressure on resources in the territory but, particularly if beavers are income breeders, may not increase reproductive costs to the mother.

Though offspring recruitment or offspring life-time reproductive success would ultimately be better measures of offspring quality, such data was not available in sufficient numbers for this analysis. It is worth noting though that of 140 offspring encountered during the study, 125 (89%) are known to have survived until their third year at which age an animals disappearance could be attributed to either dispersal or mortality. There may be a hidden fraction of animals that die before they are detected, but it is nevertheless likely that survivorship until dispersal age is high in the Telemark beavers, as has generally been found in North American beavers (see Novak 1987 for a review). Similarly, reproductive trade-offs may operate on the future survival of the mother and ultimately her lifetime reproductive success. Further research may show whether reproductive investment influences survival.

Using minimum age of mothers instead of actual age allowed us to include a larger sample of females. While we don't believe this invalidates our results (it is more likely to have reduced the probability of detecting senescence for example), it does means that we may have underestimated the age at which senescence begins and the age at which the trade-off in offspring quality versus quantity weakens.

Implications and conclusions

Senescence in highly territorial species with reproductive skew such as the beaver has implications for population regulation. The ageing of incumbent breeding females will result in lower recruitment from beaver territories than would otherwise occur if the turnover of breeding position was higher. Moreover, beavers are philopatric and many territories in our study area contained not just old breeding adults, but also old non-breeding philopatric offspring (Campbell and Rosell et al. 2005) that, when they finally obtain breeding positions, may already exhibit declining reproductive output, assuming that age and not just prior reproductive investment influences senescence. Therefore, a succession of ageing mothers with low reproductive performance could fill the scare breeding positions in the population. This 'Florida effect' (*sensu* Penteriani and Ferrer et al. 2009) has the potential to reduce population growth in high density populations of the beaver.

In conclusion, we found support for both the disposable soma hypothesis and the maternal experience hypothesis, but not the antagonistic pleiotropy hypothesis in Eurasian beavers. In particular, more experienced females were more likely to breed successfully and were able to produce larger litters without any apparent reduction in body-condition of the offspring. Females in lower quality territories that presumable experienced a greater shortage of resources throughout their reproductive lives had lower reproductive output and senesced earlier than females in higher quality territories, suggesting that they had invested a greater proportion of their resources into reproduction at the expense of future reproduction. However this trade-off appears to be in the long-term since current reproductive output was not influenced by reproduction in the previous year. Though paternal age has been found to influence reproductive output in monogamous birds (Emslie, Sydeman and Pyle 1992; Brown and Roth 2009), it appears that the paternal contribution to parental care is not significant enough for paternal age to influence reproductive output in our species of monogamous mammal.

Disentangling the mechanisms controlling age-specific reproduction and reproductive trade-offs are frequently difficult in observational studies on wild populations. However, we have shown here that by examining reproductive trade-offs with age and with environmental variation as part of a longitudinal study, useful insight into these mechanisms can be gained.

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Freeze, flush and overwater: multi-scale effects of weather on a temperate sedentary herbivore

Abstract

Understanding the impact of weather on vertebrates will inform management of the consequences of anticipated climate change. Previous studies on ungulates have found that, indirectly, low spring temperatures benefit herbivores by reducing the rate of spring-flush and high rainfall can benefit herbivores by increasing forage. Cold winters can harm herbivores by directly increase the thermoregulatory burden. We examined the effects of weather variation on body weight and reproduction in a non-ungulate, the Eurasian beaver *Castor fiber*, in southern Norway from 1998-2008 and predicted they would follow similar patterns to those found in ungulates. As expected, cold winters were related to lower body weight in both yearlings and two-year olds and higher spring temperatures resulted in a more rapid spring green-up and reduced body weight in adults, but not in other age-classes. The effect of rainfall was wide-ranging and ran contrary to predictions: Rainfall over spring−summer was inversely related to the body weight of adults, yearlings and newborns. Similarly, rainfall during the summer−autumn was inversely related to reproductive success the following year. The effect of rainfall was not direct via beavers avoiding higher predation risk or higher energetic costs in wet weather since they did not change the time invested in foraging or in sheltering on wet nights. We found that the growth of 68 gray alder *Alnus incana* trees, the main food of the beavers in the study area, was affected differently by rainfall depending on the tree's proximity to water: Trees growing <0.5m above water showed reduced growth while trees >0.5m above water showed increased growth in wet years. Thus temperature influences beavers at the landscape scale via direct effects on thermoregulation and indirectly through spring phenology. In contrast, rainfall may influence beavers at smaller spatial scales through its effects on plant growth on low ground. Unlike other herbivores, beavers are tied to living

near water and are less able to take advantage of better growth further from water in wet years. We suggest that accounting for topographic variation in other herbivore studies will improve understanding of the interaction between weather and topography.

Introduction

Knowledge of the impact of weather variation on vertebrate populations will add to understanding, and inform the management, of the consequences of anticipated climate change (IPCC 2007; Root *et al.* 2007). Studies on the impacts of climate change frequently concentrate on either the effects of temperature changes on species' ranges (e.g. Hersteinsson and Macdonald 1992; Parmesan *et al.* 1999), or the effects of temperature changes on species' synchrony with phenological changes in temperate systems (e.g. Charmantier *et al.* 2008; Post and Forchhammer 2008). With the exception of climate induced changes in phenology, there is a tendency to assume that populations that exist away from their range edges are likely to be less affected by climate change. Additionally, the potential impacts of changes in precipitation as opposed to temperature have received less attention in the literature, particularly for temperate species (but see Mysterud *et al.* 2001a)

Weather can influence organisms in a number of ways that are direct or indirect. Homeotherms generally incur a greater direct thermoregulatory cost at lower air temperatures (Wunder 1975) and wet fur can lose halve its insulating properties (Webb and King 1984). The energy budget of terrestrial homeotherms is therefore likely to increase during cold and wet weather. Also, prey species may not be able to detect predators as easily in wet weather, with consequent impacts on the trade-offs between predator avoidance and other behaviours such as foraging (e.g. Hilton *et al.* 1999).

Indirectly, weather can influence vegetation growth and consequently the resources available to herbivores. Within limits, plant primary productivity increases with temperature and moisture (Rosenzweig 1968). Thus high rainfall has been associated with greater body weight and condition or increased population growth in many ungulate herbivores (e.g. Sæther 1985; Owen-Smith 1990; Georgiadis *et al.* 2003) though for northern temperate herbivores, this trend is not as clear (Steinheim *et al.* 2004). There is less evidence of the effect of temperature variation on total plant productivity and consequent impacts on herbivore populations.

In seasonal environments, variation in climate can influence the phenology of vegetation growth (Cleland *et al.* 2007). In temperate regions, warmer spring temperatures encourage the rapid growth of plants that have been dormant over winter. Plant tissue during the early growth phase has higher concentrations of nutrients, and lower concentrations of tough structural and defensive compounds, than plant tissue later in the season (Mattson 1980; Veraart *et al.* 2006). Therefore, early season vegetation provides herbivores with higher quality food (Demment and Van Soest 1985). Herbivores are consequently likely to feed preferentially on this earlier growth (Wilmshurst *et al.* 1995), in mountainous regions may achieve better body weight when they are able to follow the new growth as it moves up-slope (Mysterud *et al.* 2001b) and exhibit increased reproduction after cool springs which slow the rate phenological development (Sæther 1985; Nolet *et al.* 2005).

When examining the effects of weather variation on vertebrate herbivores, most studies have used ungulate herbivores as the system. Here we use the Eurasian beaver *Castor fiber*, a non-ungulate semi-aquatic herbivore, as our system. The Eurasian beaver, a large rodent (> 20kg), is distributed across most of northern Eurasia between 35°N and 70°N (Halley and Rosell 2002; Műller-Schwarze and Sun 2003). Beavers are territorial and live in fresh water, using it as a refuge and to transport larger food items (Wilsson 1971). They are central place foragers and mostly forage within a few meters, and generally not more than around 40m, from the water's edge (Parker *et al.* 2001; Haarberg and Rosell 2006; Margaletić *et al.* 2007). This foraging pattern combined with their territoriality means that beavers are much less mobile than most ungulates. They predominantly forage on deciduous trees from which leaves, twigs and bark will be consumed (Wilsson 1971) but will also take herbs, forbs and aquatic vegetation in summer (Jenkins 1979; Műller-Schwarze and Sun 2003). Small saplings (dbh <5cm) are generally preferred over larger trees (Haarberg and Rosell 2006; Margaletić *et al.* 2007). Beavers are monogamous and only the dominant adult pair breeds (Wilsson 1971). Copulation occurs around late January to early February (Wilsson 1971). Kits are born around mid-May (Parker and Rosell 2001), are weaned at approximately 1 – 2 months of age and emerge from their lodge around mid-July (Wilsson 1971). Both sexes are sexually mature at two years of age, though not quite fully grown (Wilsson 1971; Műller-Schwarze and Sun 2003). The main natural predators of beavers are wolf, *Canis lupus*, and brown bear, *Ursus arctos* (Rosell and Czech 2000), though lynx, *Lynx lynx*, may also prey on beavers (Rosell and Sanda 2006).

This study examines the effects of weather variation on the body weight and reproduction in a population of Eurasian beavers. Based on the hypothesis that these semi-aquatic rodent herbivores will respond to climate in the same ways as ungulates, we test the predictions that both high food availability due to wet growing seasons and a slower rate of phenological development due to cool spring temperatures will benefit beavers through increased body weight and higher reproductive output. We furthermore predict that cold winters will have a negative influence on body weight and reproduction due to greater thermoregulatory costs. We examine the potential mechanisms behind these climate effects by analyzing the impact of rainfall on tree growth and the effect of temperature on plant-productivity. The results provide insight into how climate change could impact species living around wetland environments and provides a test of the generality of the theories gained from ungulate herbivore studies.

Ignoring other potential causes of variation may lead to erroneous interpretation of the effects of climate (Krebs and Berteaux 2006). We therefore also examine the effects of non-climatic factors that could potentially influence body weight and reproductive success.

Materials and methods

Study site

The study site is centred on three rivers, the Straumen (Nome municipality), the Gvarv and the Sauar (both Sauherad municipality), in Telemark, southern Norway (59°23′ N, 09°09′ E, Supplement A). The bedrock is granite-gneiss with a thin layer of fluvial (Straumen and Gvarv) or marine (Straumen and Sauar) deposits in valley bottoms. The climate is cold and moderately wet with a mean annual temperature of 4.6 °C and a mean annual precipitation of 790 mm. The mean monthly temperature dips below 0 °C for five months a year between November and March. The rivers flow through small towns, farms and fields (pasture and arable) interspersed with riparian woodland dominated by grey alder *Alnus incana* and, to a lesser extent, willow *Salix* sp. and bird cherry *Prunus padus*, with some dry deciduous and coniferous forest. Where agricultural land is located next to the river, a buffer of riparian woodland or unimproved grass and scrub usually exists. Due to the presence of lakes along their length, all rivers exhibit reduced ice cover in winter (though all beaver families in the study area build food stores whether ice-cover occurs or not). All three rivers form part of the catchment of Lake Nordsjø. None of the studied beaver families build dams. Hunting pressure is low and predation pressure is also likely to be low since wolf have been extirpated from the area for over 100 years, bears only occasionally pass through and lynx are present, but at low densities (Rosell and Sanda 2006).

Trapping program and sampling

Since 1998, beavers in the study areas have been monitored through an extensive live-trapping program using hand-nets from a motor boat between March and November (Rosell and Hovde 2001). Captured individuals were immobilized in cloth sacks and measurements including weight (to the nearest 100g) were recorded. Animals were sexed (Rosell and Sun 1999), tagged with a microchip (Avid or Trovan) and marked with unique color-plastic (Dalton) and metal (National Band and Tag Co.) ear-tag combinations. An animal was assumed to be resident in a territory if it was trapped or sighted in the same territory more than once >24h apart, or was seen interacting non-agonistically with other known residents.

Animals were assigned to an age-class (0 years = kit, 1 years = yearling, 2 years = two-year and ≥3 years = adult) based on weight (Supplement B). Since body weight increases over the year in all age classes, weight was corrected for by trapping date (Supplement B).

Dominance status was determined by previous trapping and sighting history, body weight and incidences of lactation in females. For example, individuals dispersing into a territory were posited to have obtained the dominant breeding position, an assumption generally corroborated by data indicating the disappearance of the previous dominant individual of the same sex, by higher body weight (compared with same sex group members) and, for females, lactation (signified by nipple length > 0.5cm). Unless there was evidence to the contrary, dominant individuals were assumed to maintain their status until they disappeared or died.

Reproduction in each year was determined by counting the number of kits trapped that year plus the number of yearlings trapped the following year that had not been previously trapped as kits. Unmarked kits or yearlings (N=17) were also included if they were sighted in a territory but not trapped and all other known kits or yearlings were accounted for. In addition, one kit and one yearling shot by local hunters were included.

To minimize noise in the weight and reproduction data, all animals deemed as non-residents plus animals in territories that had been monitored for less than four of the 11 years were excluded in the analyses. For the analyses, a total of 198 animals was used from an annual mean of 15 territories; 65 animals as kits, 64 as yearlings, 38 as two-year olds and 112 (mean 25/year) as adults. If an individual was trapped more than once in any one year, its mean corrected body weight was used.

Climate variables

Local weather data between 1975 – 2007 were obtained from *Eklima* (*www.eklima.no*) in the form of air temperature from the town of Gvarv (Gvarv weather-station from 1975-1989, height 26m, UTM Zone 33, E:169812 N:6597179, Gvarv-Lindem 1989-1994, height 71, E:170906 N:6597475, Gvarv-Nes 1994 to present, height 93m, E:170832 N:6597089) and precipitation from the Lifjell weather station (height 354m, E:162249, N:6605878). Minimum and maximum temperatures were recorded four times per 24 hour period. Rainfall was available as monthly values prior to 1980 and daily values thereafter. During night-time observation sessions on the river, temperature and rainfall was recorded at regular intervals. In this situation, rainfall was recorded as a binary variable and the variable ‘rain’ expressed as the percentage of observations with rain each night. To validate the *Eklima* data as a measure of weather experienced on the rivers, we compared temperature and rain variables obtained at night on the Straumen river near Lunde (height 60m, E:0505-0511, N:6572-6574) in 2000 with the *Eklima* data. The temperatures at Gvarv-Nes were strongly correlated with those on the river (Pearson’s $r^2 = 0.924$, $n = 69$, $P < 0.001$) as was the rainfall over Lifjell (Spearman’s $r = 0.670$, $n = 62$, $P < 0.001$).

Total rainfall may not be a realistic representation of the amount of water that is retained in the soil and thus available for use by plants. Therefore a separate rain variable (effective rainfall, *w*) was created from the rainfall measure that took into account direct soil run-off, evaporation and drainage:

$$\text{Effective rainfall } w = \frac{\log(1+r)}{(1+m)}$$

Where *r* is the rainfall that day and *m* is a negative exponential regressive function that sums up the $\log(1+r)$ of the previous nine days (i.e., log rain at t-1 × 0.5 + log rain at t-2 × 0.33 + log rain at t-3 × 0.25…). Therefore, as rainfall increases, more of it will be lost to the rivers as runoff (hence the log functions). The rest of the rain will go into the soil if the soil is dry and either drain away or evaporate, at first swiftly but then more slowly as the moisture content drops (hence the negative exponential function). Finally, the more water there is already in the soil, the larger the proportion of rainfall will go straight to run-off (hence r/m; dividing current rain with soil moisture).

Plant productivity

We used a satellite derived dataset on fAPAR (fraction of Absorbed Photosynthetically Active Radiation), obtained from the European Communities Joint Research Centre (http://fapar.jrc.it/), to estimate plant productivity. fAPAR is a more accurate measure of vegetation phenology and productivity than NDVI (Verstraete *et al.* 2008). Monthly measures of fAPAR across the study site were obtained from April – October in 1998 – 2005 and April – June in 2006, (between 59°18'-59°30' N and 09°00'-09°24' E) with a pixel resolution of approximately 2km^2 (10 × 14 pixels). Only one measurement is used to define fAPAR in each pixel in each month. Therefore, variation in sample dates between pixels could introduce noise, necessitating the correction of pixel values for sampling date. This was achieved by applying a NIST Hahn regression (where: $y = (a + b*x + c*x^2 + d*x^3) / (1 + e*x + f*x^2 + g*x^3)$ with x = day where 1st Jan = 1; we found that a =1.8E+33, b =-23.6E+30, c =83.4E+27, d =93.3E+24, e =250.8E+27, f =-2.8E+27, g =9.1E+24) in Python Equations 3.0 (Phillips 2007) to the pixel data with fAPAR as the dependent variable and sampling date as the predictor. We then used the unstandardised residual values from this regression plus the monthly mean fAPAR over all years as the corrected measure of fAPAR. The rate of phenological development in spring was defined as the increase in fAPAR between April and June.

Tree cores

To estimate tree growth over the study period and the potential effects of proximity to water, we collected tree-cores for tree-ring analysis from small to medium ($5 \leq DBH \leq 20$cm) examples of grey alder, the most common deciduous riparian tree species and also the most commonly utilized food tree for beavers in the study area (Haarberg and Rosell 2006). Within woody deciduous habitat in each of the three rivers, 24 transects (eight per river) were assigned randomly on paper maps so that they were evenly spread along the length of each river. Transects began at the riverbank and ran perpendicular to it for 40m, or until they left woody deciduous habitat. The length of each transect was then divided into eight sections: 0-2.5m, 2.5-5m, 5-10m, 10-15m, 15-20m, 20-25m, 25-30m and 30-40m from the riverbank. The sections nearest the riverbank were shorter and the section furthest was longer in order to weight the samples because beavers forage less further from water (Haarberg and Rosell 2006) and rivers will have the greatest influence on the local water table in areas nearest the river edge. In each section, the nearest tree was located, height at base above local water level was recorded and two cores were extracted at chest height using an increment borer. The second core was extracted opposite the first and areas of the trunk with reaction wood were avoided (Copenheaver *et al.* 2007). If no grey alder was found within 20m of the transect line, no cores were extracted.

Cores were measured on a Lintab 4 measurement table and logged using TSAP-Win 0.53 (both RinnTech, Rinn 2003) where the ring widths were measured to the nearest $^{1}/_{100}$ mm. Ring widths were visually cross-dated within tree and between trees to identify any missing, false, or partial rings (Yamaguchi 1991). To ensure accuracy of ring dates, only trees where tree-ring could be unambiguously measured and where at least one of the cores still contained cambium were used. Furthermore, cores without cambium were only used if growth patterns matched that of their sister cores (cores with cambium from the same tree). Ring widths were averaged within trees. Cores from 68 trees in 20 transects were used in the final analysis.

Data analysis

All analyses were conducted in *SPSS* v13.0 (SPSS 2004) and *R* 2.8.0 (R Development Core Team 2008). When examining the effects of climate on body weight and reproduction, we used annual mean body weight (corrected for trapping date). Reproduction was defined as the number of offspring per territory and it was assumed that only one female (the breeding female) was able to breed per territory. Weighted least squared regression was weighted by sample size - which was either the number of animals sampled (body weight regressions), or the trapping effort over the current plus previous year (reproduction regressions). For adults, sex (and pregnancy) may influence weight, therefore a Type 3 GLM was used with sex as a random factor and climate variables as covariates (again, using least squared regression weighted by sample size).

To examine the effects of rainfall and height above water on grey alder growth, a linear mixed-effects model was created with *nlme* in R using a random slope model, following Schielzeth *and* Forstmeier (2009). Year and Tree were included as a random effect and a first-order autoregressive (AR1) correlation structure was used to account for repeated measures within trees. A fitted *varPower* function was used for weighting variables in the model to control for heteroscedasticity. To examine the effects of height above water-level, trees were grouped into one of two height categories with the cut-off being 0.5m above water as this was the median height above water of all trees used in the analysis. Fixed effects and covariates were Age, Transect ID, Height category and Total rainfall over April-July. An interaction between Height category and Rainfall was specified. We used rainfall over April-July instead of April-September because trees tend to lay down the bulk of their wood in spring and early summer (Schweingruber 1988) and therefore rainfall over this period is likely to be a better predictor of ring-width than rainfall over the entire growing season.

Results

Inter annual variation in body weight and reproduction

Body weights of kits and yearlings varied significantly between years (ANOVA: Kits; $F_{9,55} = 3.451$, $P = 0.002$, Yearlings; $F_{10,53} = 2.196$, $P = 0.032$, Supplement C), but those of older animals did not (2 year olds; $F_{9,28} = 1.460$, $P = 0.211$, adults; $F_{10,261} = 0.861$, $P = 0.571$ – adult males $P = 0.533$, adult females $P = 0.734$, Fig. 1, Supplement C). The number of females successfully breeding varied significantly between years (Logistic regression: Cox & Snell $r^2 = 0.112$, chisq = 20.46, df = 9, $P = 0.015$, Fig. 2, Supplement C). Yearling body weight positively correlated with adult male body weight (Pearson correlation, $r = 0.624$, $N = 11$, $P = 0.040$). Despite all age classes showing similar patterns of variation over the course of the study (Fig. 1), no significant correlation was found between any of the other age-classes or between reproductive success and body weight in any age-class ($P>0.05$ in all cases).

Weather effects on body weight

A table of the effects of all weather variables tested on beaver body weight and reproductive success is provided in Supplement D. Temperature did not influence annual mean body weight in kits, and rainfall did not influence the body weight of two-year olds (weighted LS regressions, $P > 0.05$ in both cases, Supplement D). Though the relationship

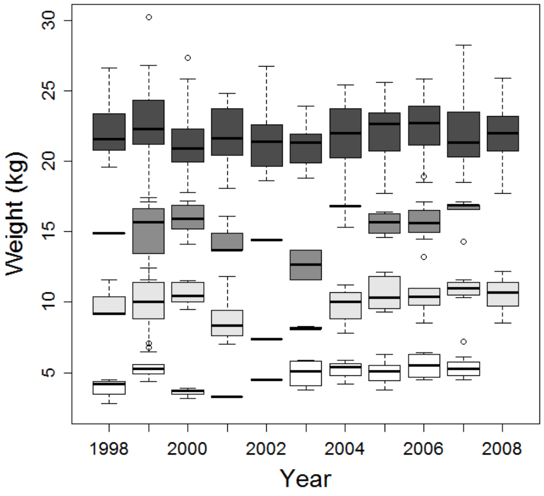


Figure 1: Variation in mean body weight with year in kit (white), yearling (light grey), subadult (medium grey) and adult (dark grey) beavers. Boxes around the mean represent the 25-75% interquartile range and whiskers extend to the most extreme data points within 1.5× the interquartile range. The variation between years was significant for kit and yearling, but not older, age classes.

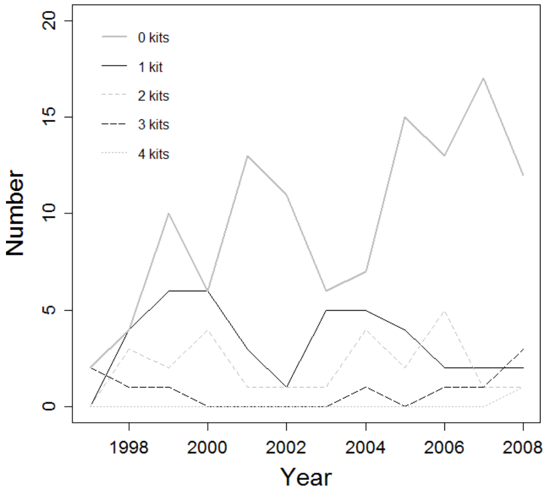


Figure 2: Variation with year in reproduction (number of litters with 1, 2, 3 and 4 kits or number of breeding females that did not reproduce).

between total rainfall between April – September and kit weight was not significant (weighted LS regressions, $P > 0.05$, Supplement D), this was due to 2007 which was an outlier (Supplement E): July rainfall in 2007 was exceptionally heavy and as a result, 2007 had the highest rainfall while also among the heaviest kits. When 2007 was excluded, kit weight was inversely related to rainfall ($r^2 = -0.647$, df = 8, $P = 0.009$). The effective-rainfall model discounted heavy rainfall over short periods of time, and therefore kit weight was also inversely related to effective rainfall (April – September) over all years ($r^2 = -0.735$, df = 9, $P = 0.002$, Fig. 3a). A significant positive relationship between kit weight and effective rainfall in the preceding July – September was found ($r^2 = 0.402$, df = 9, $P = 0.049$, Supplement F), however this result is likely to be spurious.

The combined total rainfall between April – September of the sample year and the previous year did not explain yearling weight ($r^2 = -0.145$, df = 9, $P = 0.247$, Supplement G). The heavy July rain in 2007 again may have exerted an influence on the rainfall measure for 2007 and 2008. The same variable excluding 2007 and 2008 was a significantly negative predictor of mean yearlings weight ($r^2 = -0.580$, df = 8, $P = 0.017$) and effective rainfall over all years was also a significant negative predictor ($r^2 = -0.468$, df = 10, $P = 0.020$, Fig. 3c).

The mean of the maximum daytime temperatures during the previous winter (Dec-Jan) was associated with greater yearling weight ($r^2 = 0.546$, df = 10, $P = 0.009$, Fig. 3d). Combining effective rain over two years and winter temperature in a multiple regression resulted in a highly significant model ($r^2 = 0.779$, df = 10, $P = 0.002$).

Two-year old body weight showed a positive relationship with the mean maximum daytime temperature in December – January over the previous two years ($r^2 = 0.759$, df = 9, $P = 0.001$, Fig. 3b).

Preliminary correlations indicated that total rainfall between April – September and the mean maximum daytime temperatures in December – January and March – June all may influence adult body weight. A GLM found a negative effect of rainfall ($F_{1,17}$ = 6.04, P = 0.025), a non-significant positive effect of Dec – Jan temperature ($F_{1,17}$ = 4.28, P = 0.054) and a non-significant negative effect of Mar – Jun temperature ($F_{1,17}$ = 1.44, P = 0.246). However, using effective rainfall in the model changed the outcome with both rainfall and Mar – Jun temperature having significant negative effects ($F_{1,17}$ = 9.68, P = 0.006, Fig. 3e; $F_{1,17}$ = 6.16, P = 0.024 ,Fig. 3f) while Dec – Jan temperature remained non-significant ($F_{1,17}$ = 3.43, P = 0.081). The best model based on lowest Akaike's information criterion (AIC) was the model containing effective rain (=33.96 versus 37.18 for rain). There were no interactions with sex for any variable.

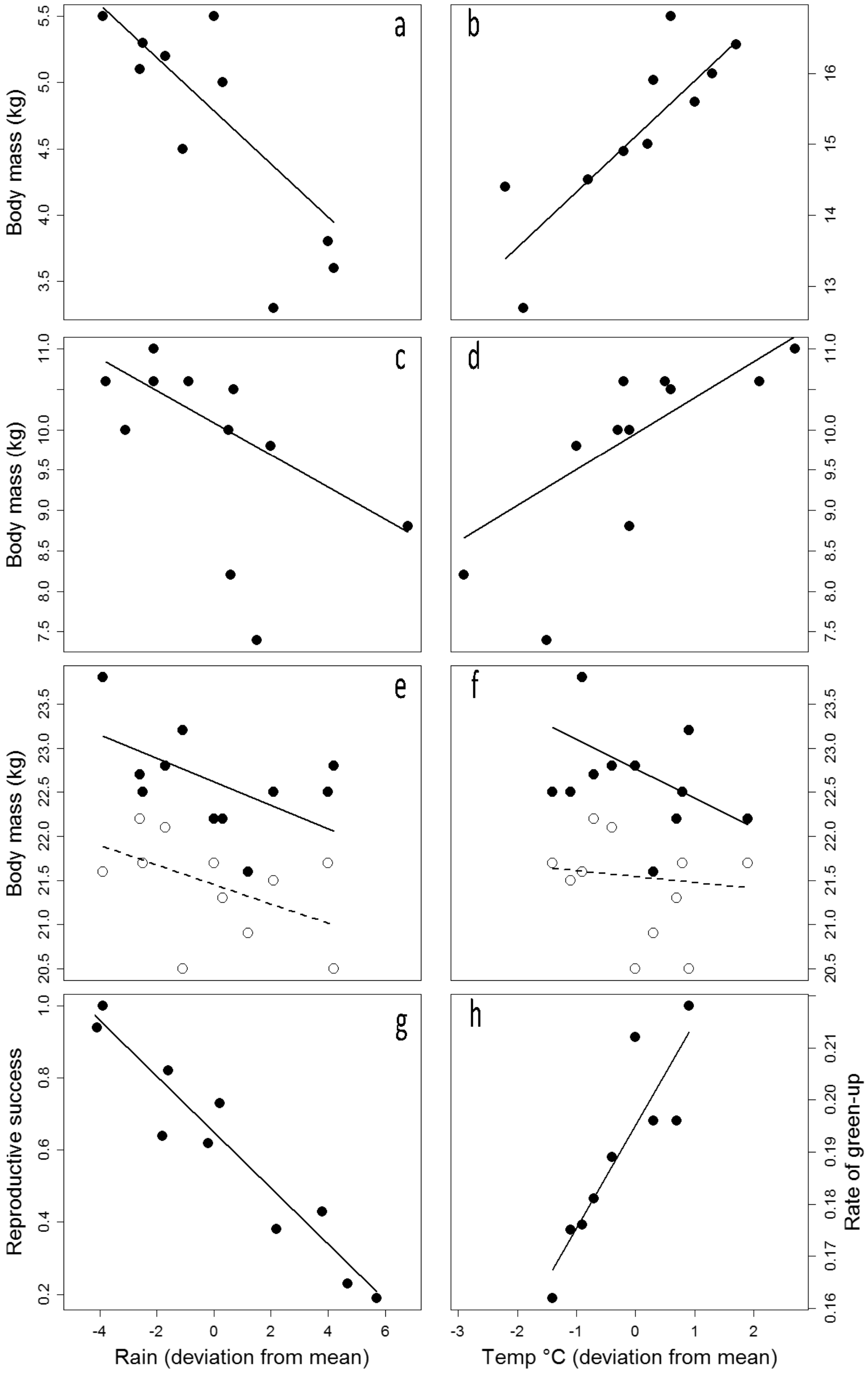
Adult body weight was significantly inversely related to the rate of phenological development as indicated by fAPAR (Type 3 GLM with Weighted LS regression $F_{1,15}$ = 5.50, P = 0.033, Supplement H).

Weather effects on reproduction

Temperature in December – January and March – June did not influence the number of kits born per family (weighted LS regressions, P > 0.05 in both cases, Supplement D). However, the total rainfall over the previous late summer and early autumn (August – October) was inversely related to the number of kits born per breeding female (weighted LS regression r^2 = -0.771, df = 9, P = 0.001). Using effective rainfall instead of total rainfall over August - October improved the fit of the relationship further (r^2 = -0.922, df = 9, P < 0.001, Fig. 3g). Similarly, the proportion of breeding females that successfully reproduced (i.e., the number of litters per territory) was significantly influenced by August

Figure 3 (following page): Effects of weather on annual mean body weight, reproduction and phenology, where a) is the relationship between body weight of beaver kits with rainfall in Apr-Sept, c) body weight of yearlings with rainfall in Apr-Sept over two years, e) body weight of adults with rainfall Apr-Sept, g) reproduction (number of kits born peer breeding female) with rainfall in the preceding Aug-Oct, b) is body weight of two-year olds with temperature in the preceding Dec-Jan over two years, d) is yearling body weight with temperature in the preceding Dec-Jan, f) is the body weight of adults with temperature in Mar-Jun and h) is the rate of spring green-up (measured as the difference in fAPAR from Apr-Jun) with temperature in Mar-Jun. In e) and f), closed symbols and solid regression lines represent females and open symbols with dashed regression lines represent males. All regression lines are weighted by sample size except for h). Rainfall measurements were adjusted for soil run-off. All body weight variables were corrected for measurement dates to avoid bias due to within-year seasonal trends. Both rainfall and temperature are presented as deviations from the mean. Means were: rainfall (*w*) Apr-Sept = 37.1 (one year) and 73.6 (two-year); rainfall (*w*) Aug-Oct = 18.3; temperature (°C) Dec-Jan = -1.00 (one year) and -1.02 (two year); temperature (°C) Mar-Jun = 11.45.

Figure 3:


a
b
c
d
e
f
g
h
Body mass (kg)
Body mass (kg)
Body mass (kg)
Reproductive success
Rate of green-up
Rain (deviation from mean)
Temp °C (deviation from mean)
3.5
4.0
4.5
5.0
5.5
13
14
15
16
7.5
8.0
8.5
9.0
9.5
10.0
11.0
20.5
21.0
21.5
22.0
22.5
23.0
23.5
0.2
0.4
0.6
0.8
1.0
0.16
0.17
0.18
0.19
0.20
0.21
-4
-2
0
2
4
6
-3
-2
-1
0
1
2

- October total rainfall ($r^2 = -0.665$, df = 9, $P = 0.004$) and August - October effective rain ($r^2 = -0.947$, df = 9, $P < 0.001$, Supplement I).

Non-weather effects on body weight and reproduction

With the exception of the effect of fAPAR increase in spring on adult body weight, none of the non-weather factors tested were found to influence either reproductive success or body weight in any age-class ($P>0.05$ in all cases, Supplement D).

Weather effects on plant phenology

Mean maximum temperature in March – June correlated positively with the rate of increase in fAPAR in the spring (Pearson's correlation $r^2 = 0.861$ N = 9, $P < 0.001$, Fig. 3h).

Topography and rainfall effects on tree growth

The mean age of the trees sampled was 21 years (min=5 and max=55 years). Mean height above water was 2.16m and the median height above water was 0.5m. The linear mixed effects model that best explained ring-widths in tree cores from grey alder included rainfall from April-July and an interaction between rainfall and height above water level (Supplement J). The model indicated that rainfall and height category separately did not have significant effects (respectively, $F_{1,1258} = 0.74$, $P = 0.389$ and $F_{1,47} = 0.18$, $P = 0.893$) but that there was a significant positive interaction between the two variables ($F_{1,1258} = 22.21$, $P < 0.0001$; Fig 4; Supplement J). Running the same model separately on trees within each height category indicated that trees nearer the water grew significantly less (effect = -0.06 ± 0.02, $F_{1,594}$ = 9.23, P = 0.0025), and trees further from water grew significantly more in wetter years (effect = 0.09 ± 0.02, $F_{1,662}$ = 19.60, P < 0.0001; Fig 4; Supplement J).

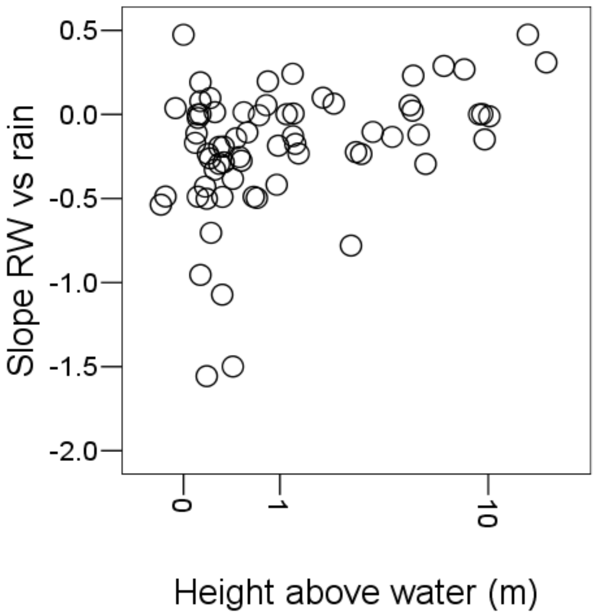


Figure 4: Interaction between height above water and rainfall on ring widths. Each point represents a single tree with the slope of the linear regression of rainfall on ring width (RW) represented on the y-axis and the height above water of the tree on the x-axis using a log scale. Linear regressions do not account for autocorrelation due to repeated measures and were used only to illustrate the relationship in this figure. A linear mixed model indicated that the relationship shown was real with trees on low ground tending to exhibit a negative relationship with rain and trees on higher ground tended to exhibit a positive relationship with rain.

Discussion

Our first prediction that beavers would follow similar patterns to ungulate herbivores was only partially met. As was expected, warmer spring weather was associated with a more rapid change in plant productivity and adult beaver did indeed tend to show reduced body weight after warm springs, though the effect was fairly weak in comparison to the effect of rainfall and not evident in any other age class. Additionally, direct measures of the rate of phenological development in plant growth were inversely related to adult body weight. However, contrary to predictions, high rainfall was not associated with higher body weight and reproduction. Instead rainfall was inversely related to body weight in all age-classes except two-year olds and also led to reduced numbers of offspring the following year. It is not clear why two-year old animals did not show the same relationship with rainfall as did other age-classes, but the sample size for this age-class was the lowest and so the effect of rain is more likely to have been masked by noise in the data.

Our second prediction that cold winters would extract a high thermoregulatory cost to beavers and therefore reduce their body weight and reproductive output appears to be partially met: Warm winters were associated with higher body weight in yearlings and two-year olds, but not significantly so in adults and winter temperature did not affect reproductive success. Though lodges and dens offer effective protection against low temperatures (Stephenson 1969; Dyke and MacArthur 1993), beavers remain active over winter and will experience high energetic costs when outside the lodge or den, particularly when swimming (Nolet and Rosell 1994). This cost is likely to be greatest in the younger smaller animals where the surface-to-volume ratio is greater (MacArthur and Dyke 1990). Consequently, the effect of winter temperature was not significant in the larger adults and did not influence their reproductive decision in January – February. Kits would not have experienced the winter prior to conception and so we would not expect an effect for this age-class.

The body weight of individual beavers have been found to correlate with their body weight when younger (Ruairidh Campbell and Frank Rosell *unpublished*). As a result, the effect of spring-summer rainfall on yearling beavers was found to be significant only if both current and previous years data were combined and, similarly, the effect of winter temperature on two-year olds was significant when temperatures from the previous two winters was combined. Climatic influences on early growth and development could therefore influence beavers later in life.

Care should be exercised when interpreting the result of studies on climate where a large number of climate variables have been analyzed and where other non-climatic factors have been ignored (Krebs and Berteaux 2006). In this study, we tested but did not find clear intra-specific effects that could also explain variation in body weight and reproduction and the climate effects we found were consistent over more than one beaver-variable.

Previous studies on ungulates that found negative effects of rain on body weight have argued that the effects were due to covariance with temperature (Sæther 1985; Stenheim *et al.* 2004). In this study, we found that rain was a much better predictor of beaver body weight and reproduction than was temperature, with no significant correlations between rain and temperature, suggesting that the negative effects of rainfall are not simply due to an interactions with temperature. To our knowledge, no other study on northern temperate herbivores have found such a strong negative relationship between life-history characteristics and rainfall as we revealed for beavers in Telemark This leads to the question of what the mechanism behind this negative effect of rainfall could be.

Effects of rain on foraging behaviour

One potential mechanism behind the negative effects of rain is that beavers may not detect predators so easily when in rain (Hilton *et al.* 1999) and are thus less inclined to risk exposure to predation by foraging on land. However, we have found no significant effect of rainfall on the proportion of time beavers spent on land (Supplement K), suggesting that predator avoidance is not the mechanism behind the effect of rain. Alternatively, beavers may suffer a thermodynamic cost to having wet fur, though since beavers are highly adapted to the aquatic environment, this hypothesis seems unlikely. Indeed, we have found no effect of rain on the proportion of their activity period that was spent in their lodge or bank-den (Supplement K) indicating that if there is a thermodynamic cost to rain, it is not great enough to force beavers to transport food items under shelter to be consumed.

Effects of rainfall on riparian vegetation growth

The general absence of evidence for negative effects of rainfall on ungulate herbivore life-histories, and the lack of a behavioural effect of rain on beavers suggest that theories gained from ungulate studies may not be wholly applicable to all herbivores. Beavers are distinguished from most ungulates by their semi-aquatic adaptations and habit of foraging in and near water. Water is less likely to be a limiting factor on the growth of plants near water compared with those growing further from water. Indeed, for near-water plants, excessive rainfall may actually inhibit plant-growth by water-logging riparian soil and reducing oxygen availability to roots (Kozlowski *et al.* 1991, p304; Johansson and Nilsson 2002). Our tree-core data showed that grey alder growing on ground at heights >0.5m above river levels was greater in wetter years, supporting the hypothesis of water as a limiting factor for plant growth away from water. In contrast, tree-cores from grey alder growing on low ground near rivers tended to exhibit reduced growth during wet years – a result corroborating Francis *et al.'s* (2005) finding that grey alder seedlings reduce, or cease, growth when their root systems are inundated. We therefore propose the working hypothesis that the mechanism underlying the negative effect of rainfall on body weight and reproduction of beavers in our study was that high rainfall depressed the productivity of many important food plants around rivers.

Implications for climate change

Jarema *et al.* (2009) modeled the climate envelope of North American beavers in their north-eastern range and found a greater abundance of beavers in areas with warmer temperatures and greater precipitation, in particular where both temperature and rainfall were less variable over the year. Jarema *et al.* (2009) predicted that beaver abundance will increase with human-mediated increases in precipitation and temperature. At first, this appears to be in direct opposition to our own findings. However, at the regional scale, it is not surprising that beaver abundance will be lower in dry cold regions where there is likely to be less suitable forage. Within biomes however, annual variation in rainfall and temperature could influence the annual growth of the established plants and through this affect the growth and reproduction of the beaver as we have described here. In the short term, increased rainfall and temperature in Northern Europe over the coming century, as forecast by the IPCC (2007), may have an adverse impact on the beaver, though warmer winters may benefit them. However, in the longer term, adaptive changes in the vegetation communities to novel climate regimes could negate these adverse impacts and the warmer wetter conditions may eventually benefit beavers.

Implications for territoriality

From our results, topography and drainage emerge as important to habitat quality for beavers. Beavers could mitigate the reduction in forage quality near rivers during wet years by foraging further from rivers and on higher ground. Since they routinely transport felled trees back to the safety of the river for consumption, this would incur higher energetic costs. Furthermore, though predation pressure is currently low in our study area, the ‘ghosts of predators-past’ (*sensu* Byers 1998) may make them unwilling to venture inland. Nonetheless, beaver territories containing low-lying swamp could be advantageous in dry years when trees are likely to be water-limited, but disadvantageous in wetter years. Conversely, well drained higher ground near water could be advantageous in wet years and disadvantageous in drier ones. Therefore, optimal habitat for beavers may be heterogeneous. A close parallel to this scenario has been found in the capybara *Hydrochoerus hydrochaeris*, a large semi-aquatic rodent that is similar to the beaver both in terms of ecology and phylogeny. Capybaras living in seasonally flooded tropical floodplain savanna need both low and high ground to survive because low ground provides the best quality grazing during the peak dry season but is flooded and overtaken by low quality forage species in the late wet season (Herrera and Macdonald 1989). Campbell *et al.* (2005) found that some beaver territories in our area may be larger than the minimum size needed for survival and reproduction, and argued that these extra large territories were maintained to avoid depletion of resources in the long-term. An alternative explanation for this pattern may be that these extra large territories are configured to cover patches of both high and low ground (*sensu* the Resource Dispersion Hypothesis, Macdonald 1983), as is the case for capybaras (Herrera and Macdonald 1989).

General implications

We have shown that anticipated changes in climate have the potential to influence animal populations in unexpected ways. The predicted relationship between cooler springs, slower rates of phenological advancement and greater body weight was evident in the beavers and lends further credence to the idea that this pattern is common across taxonomic groups. Similarly, the expected energetic cost of cold winter temperatures was also found in this study, particularly for the smaller younger age-classes. However, the strong adverse impact of high rainfall on the beaver was initially surprising and indicates that variation in precipitation may have a significant influence on herbivore populations through small-scale effects on plant growth arising from an interaction between rainfall and local topography. Many ungulates are much more mobile than beavers and therefore are more able to move around to take advantage of local changes in forage quality. If our results can be applied to other herbivores, then we have the testable prediction that ungulates would prefer foraging on higher, well drained, ground in wet years and lower, poorly drained, ground in dry years but we would not necessarily observe a clear relationship between rainfall and body weight or reproduction across an ungulate population. Moreover, we might expect to see a stronger influence of rainfall in herbivores that are more sedentary, due to either physical or social restrictions on mobility. Taking into account temperature−topography interactions improves models of red deer *Cervus elaphus* populations (Pettorelli *et al.* 2005). Similarly, failure to take into account moisture−topography interactions may be the reason why previous studies on northern ungulate herbivores have found such a large variation in the influence of rain on body weight and reproduction.

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Supplement A: Images of the study area

1. Gvarv River looking upstream, taken near its mouth into Lake Nordsjø. The mountain in the background is Lifjel.

2. Straumen River looking downstream, taken from Apalnes.

3. Sauar River looking upstream, taken near Gillaren.

4. Krokmann evju, a stream fed inlet (bayou) on Sauar River which forms approximately a third of one beaver territory.

Supplement B: Ageing and body weight correction in the Eurasian beaver

Methods

Beavers were assigned to an age class based on body weight. Smith & Jenkins (1997) reported that all age classes of *C. canadensis* gain body weight through spring, summer and autumn and, except for kits, will lose some body weight every winter. In our study site, the same pattern has been observed except that kits also appear to loose some body weight over winter. Thus, it is necessary to correct for the day of capture when analyzing effects on body weight and also to create body weight tables to age animals. In this study beavers are almost never trapped in winter and body weight is lost outside our sampling window. Therefore, we only consider weight gain in each age class. We conducted a linear regression analysis on day-of-capture (Day 1 = Jan 1st) versus body weight of animals that were initially trapped as kits, and thus were of known age. We split the data into 4 age classes: 0 year olds (kits), 1 year olds (yearlings), 2 year olds (subadults) and ≥3 year olds (adults). Kits are always significantly lower in weight than yearlings and therefore distinguishing between these age-classes is unambiguous. For example, the maximum recorded weight of a kit around day 200 (20th July, approximately the date of first emergence from the lodge) was 4kg whereas the minimum recorded weight of a yearling around the same day was 7.5kg and by day 250 (10th Sept), no kit has ever been found to weigh more than 7kg and no yearling has been found to weigh less than 11kg.

To distinguish between yearling, two-year and adult age-classes, weight-tables based on the 95% CIs of linear growth functions obtained from known-age animals in 1998-2006 that were first trapped as kits (for yearling age-class) or animals first trapped as kits or yearlings (two-year and adult age-classes) were used (Ruairidh Campbell and Frank Rosell *unpublished*). An animals whose weight was within the 95% CIs of >1 age-class on first being trapped was not assigned to an age-class until the minimum age was three. This most often occurred late in the year where animals fell between the two-year and adult age classes (N=27) but occasionally occurred for animals that fell between the yearling and two-year age-classes (N=3).

With the exception of kits, we used the resulting regression coefficients to correct for day of capture when analyzing effects on body weight. For kits, we used the following regression equation obtained from Wilsson's (1971) data on kit growth in captivity:

$$\text{Predicted body weight} = (D \times 0.034\text{kg}) + 0.525\text{kg}$$

Where the D is the number of days since the 15th May. Thus, kits are assumed to have been born on the 15th May with a body weight of 0.525kg and a daily body weight gain thereafter of 0.034kg. In all cases, body weights are presented as unstandardised residuals from the regression equations + the mean weight over all years within age class.

Results

All age classes exhibited a linear increase in body weight across spring to autumn (Table 1). Body weight gain was highest and least variable in yearlings. Adults showed the greatest variability, partly as a result of females being pregnant and thus heavier early in the season.

Table 1: Least squared linear regression equations of weight and day (day of capture, jan 1st = 1) for each age class excluding kits.

Age class	Linear regression equation	SE of slope	r^2	F	df	P
Yearling	3.445kg + (0.043kg × day)	0.004kg	0.787	132.887	37	<0.001
2 year old	11.660kg + (0.023kg × day)	0.004kg	0.453	32.243	40	<0.001
≥3 year old	18.302kg + (0.017kg × day)	0.005kg	0.164	11.995	62	0.001

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Supplement C: Means and sample sizes

Mean adjusted body weight (kg) with SD of beavers within each age class, reproduction (the mean number of kits born per breeding female) with SD and the total number of kits born in each year. No values for reproduction are given in 2008 as data from 2009 is required to provide an accurate estimate.

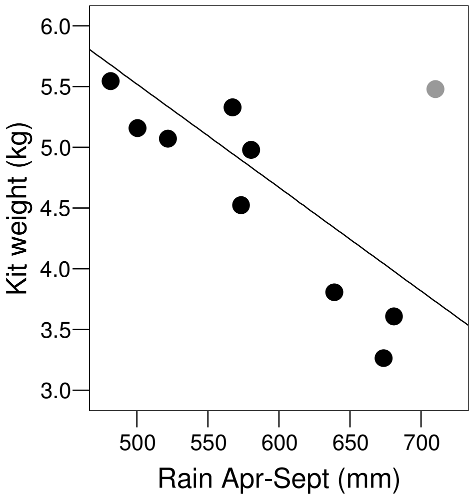
	kit			yearling			two-year old			adult			reproduction		
Year	Mean (kg)	N	SD	Mean (kg)	N	SD	Mean (kg)	N	SD	Mean (kg)	N	SD	Mean	N breeders	SD
1998	3.8	3	0.9	10.0	3	1.4	-	0	-	22.2	8	2.3	1.00	11	1.00
1999	5.5	9	0.9	10.0	11	1.9	14.9	1	-	22.7	46	2.4	0.65	20	0.88
2000	3.6	3	0.4	10.5	6	0.8	15.0	7	2.2	21.4	20	2.5	0.82	17	0.81
2001	3.3	1	-	8.8	6	1.7	15.9	7	1.1	21.9	24	2.0	0.19	16	0.40
2002	4.5	1	-	7.4	1	-	14.5	3	1.4	21.5	11	2.3	0.23	13	0.60
2003	-	0	-	8.2	3	0.1	14.4	1	-	21.2	5	1.9	0.64	11	0.67
2004	5.0	10	0.9	9.8	4	1.4	12.7	2	1.5	21.8	31	2.3	0.94	19	0.94
2005	5.2	3	0.8	10.6	8	1.2	16.8	1	-	22.3	26	2.0	0.36	22	0.66
2006	5.1	11	0.8	10.6	6	1.6	15.6	4	0.8	22.4	20	2.0	0.67	24	0.96
2007	5.5	4	1.0	11.0	7	0.6	16.0	7	1.6	21.9	38	2.2	0.43	21	0.87
2008	5.3	20	0.7	10.6	9	1.2	16.4	5	1.2	22.0	43	2.0	-	-	-

Supplement D: Table of statistical results

Factors tested against body weight and reproductive success of the Eurasian beavers in the Telemark study area. For adult weight, bivariate GLMs were used with sex as a random factor. For all other dependent variables, univariate linear regressions were used. All models were weighted by sample size (body weight variables) or two-year trapping effort (reproductive success). Statistically significant relationships are denoted with asterisks where '*' is significant at the 95% probability level, '**' at 99% and '***' at 99.9%.

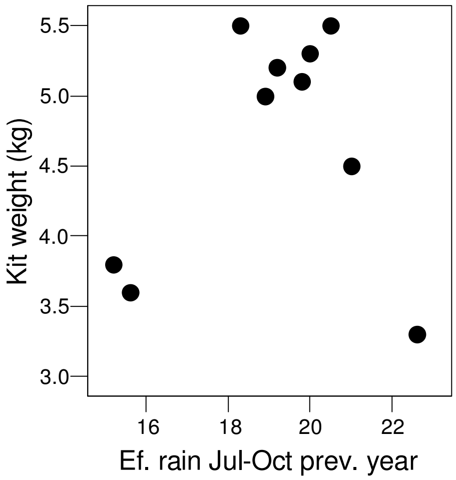
		Kit mass		Yearling mass		Two-year old mass		Adults mass		Reproductive success	
	Factor	Effect	P	Effect	P	Effect	P	Effect	P	Effect	P
Precipitation	Rain Apr-Sep	-	0.127	-	0.755	+	0.700	-	0.009 **	-	0.905
	Rain Apr-Jun	-	0.192	-	0.142	-	0.637	-	0.445	+	0.678
	Rain Jul-Sep	-	0.554	+	0.732	+	0.491	-	0.015 *	-	0.727
	Rain Aug-Oct prev. year	-	0.521	-	0.297	+	0.439	-	0.768	-	0.001 ***
	Rain Jul-Sep prev. year	+	0.331	-	0.383	+	0.675	-	0.581	-	0.036 *
	Rain Apr-Sep prev. year	+	0.181	-	0.296	-	0.952	+	0.860	-	0.111
	Rain Apr-Sep two years		·	-	0.247	+	0.600	-	0.038 *	-	0.175
	Snow depth Mar	+	0.154	-	0.439	+	0.730	+	0.071	-	0.538
Effective rainfall	Ef. rain Apr-Sep	-	0.002 **	-	0.477	-	0.629	-	0.005 **	+	0.335
	Ef. rain Apr-Jun	-	0.043 *	-	0.057	-	0.109	-	0.147	+	0.131
	Ef. rain Jul-Sep	-	0.039 *	+	0.777	+	0.823	-	0.014 *	+	0.807
	Ef. rain Aug-Oct prev. year	-	0.853	-	0.536	+	0.379	+	0.693	-	<0.001 ***
	Ef. rain Jul-Sep prev. year	+	0.049 *	-	0.362	+	0.546	+	0.161	-	0.019 *
	Ef. rain Apr-Sep prev. year	+	0.121	-	0.200	-	0.874	+	0.132	-	0.054
	Ef. rain Apr-Sep two years		·	-	0.020 *	-	0.657	-	0.460	-	0.167
Temperature	Temp Dec-Jan	+	0.630	+	0.009 **	+	0.090	+	0.572	-	0.378
	Temp Dec-Jan two years		·		·	+	0.001 **	+	0.381	-	0.256
	Temp Oct-Feb	-	0.764	+	0.030 *	+	0.397	-	0.172	-	0.801
	Temp Mar-Jun	+	0.412	+	0.295	-	0.944	-	0.039 *	-	0.577
	Temp Jul-Sep	+	0.582	-	0.344	+	0.895	+	0.132	-	0.347
	Degree days Mar-Jun	+	0.695	+	0.189	-	0.934	-	0.043 *	-	0.646
	Last frost	+	0.736	-	0.179	+	0.033 *	+	0.218	-	0.216
Non climatic	fAPAR inc. Mar-Jun	-	0.617	+	0.967	-	0.201	-	0.033 *		·
	fAPAR inc. Mar-Jun prev. year	-	0.423	-	0.229	+	0.653	-	0.237	-	0.582
	fAPAR July	-	0.661	+	0.706	+	0.367	-	0.796		·
	fAPAR July prev. year	+	0.747	+	0.842	+	0.994	-	0.778	+	0.611
	Repro. success	-	0.495	+	0.551	-	0.141	-	0.596		·
	Repro. success prev. year		·	+	0.712	+	0.498	+	0.072	-	0.437
	Litter size	+	0.496		·		·		·		·
	Litter size prev. year		·	+	0.175		·		·		·
	Kit sex ratio	+	0.471		·		·		·	-	0.985
	Kit sex ratio prev. year		·	-	0.462		·		·		·
	Group size	-	0.360	-	0.152	-	0.935	+	0.712	-	0.331
	Group size prev. year		·	-	0.065	-	0.376	-	0.343	-	0.480
	Adult female mass prev. year	-	0.242		·		·		·	-	0.922
	Kit mass prev. year	-	0.907		·		·		·	+	0.111

Supplement E: Beaver kit weight and rainfall



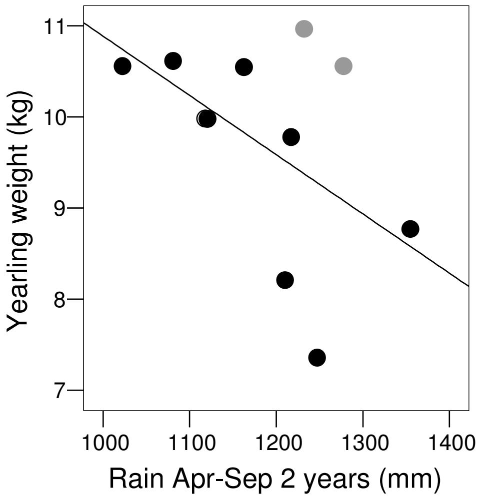
Relationship between rainfall in Apr – Sept and the adjusted body weight of beaver kits. The outlying grey data-point in the upper-right of the plot is 2007. The regression line is weighted by sample size and excludes the 2007 outlier.

Supplement F: Beaver kit weight and effective rainfall



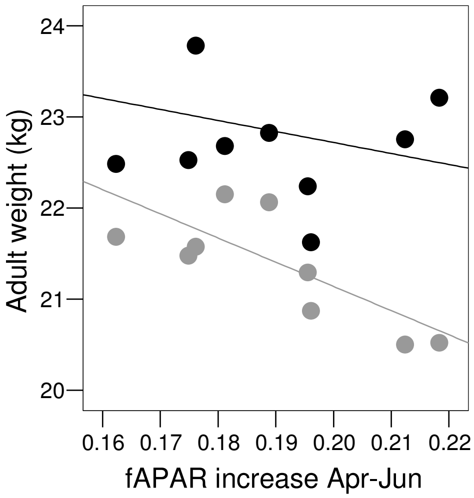
Relationship between effective rainfall in Jul – Oct pf the previous year and beaver kit body weight.

Supplement G: Yearling beaver weight and rain



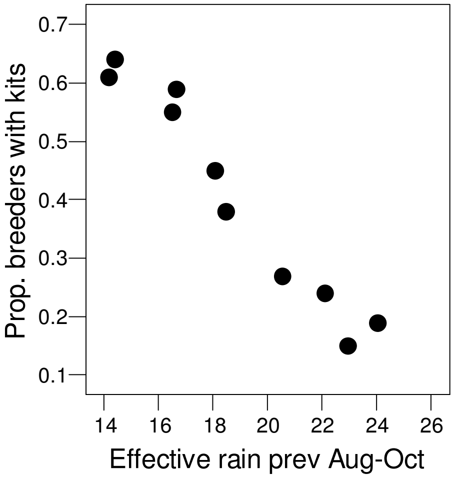
Relationship between rainfall in Apr – Sept plus Apr – Sept the preceding year and the body weight of yearling beavers. The two upper-right data-points in grey are 2007 and 2008 (i.e., 2006-2007 and 2007-2008 rainfall years).The regression line is weighted by sample size and excludes the 2006-2007 and 2007-2008 data-points.

Supplement H: Adult body weight and phenology



Relationship between the rate of phenological development (green-up) in spring, measured as fAPAR increase from Mar – Jun, and the date-adjusted mean annual weight of male (●) and female (●) adult beavers. Regression lines are from separate linear regressions for each sex, weighted by sample sizes.

Supplement I: Reproduction and rainfall



Relationship between rainfall in Aug – Oct and the number of litters born per family group (i.e., proportion of females that bred, max=1/family) the following year.

Supplement J: Interaction of rain and height on Grey alder growth.

Results from the best fitting (lowest BIC) mixed-effect model of transect ID, rainfall (Apr-Jul) and height category (<0.5m and >0.5m) above water (at tree base) on the growth of Grey alder, as measured by annual ring widths (all trees). The model was then run separately on each height category to confirm the different effects of rainfall with height.

Model	**Variable**	**Effect**	**SE**	**d.f. (n, d)**	**F**	***P***
All trees	Intercept	467.89	81.24	1, 1259	497.06	<0.0001
	Age	-4.26	0.45	1, 1259	176.59	<0.0001
	Transect	-	-	19, 47	3.50	0.0002
	Rain (Apr-Jul)	-0.16	0.04	1, 1259	0.66	0.4182
	Height Cat.	-57.78	25.08	1, 47	0.47	0.4960
	Rain*Height Cat.	0.12	0.03	1, 1259	20.48	<0.0001
Trees <0.5m above water	Intercept	185.70	32.16	1, 595	227.34	<0.0001
	Age	-3.11	0.60	1, 595	76.62	<0.0001
	Transect	-	-	11, 22	4.28	0.0018
	Rain (Apr-Jul)	-0.05	0.02	1, 595	8.47	0.0038
Trees >0.5m above water	Intercept	359.20	65.12	1, 663	263.02	<0.0001
	Age	-6.26	0.72	1, 663	150.00	<0.0001
	Transect	-	-	13,20	2.46	0.0342
	Rain (Apr-Jul)	0.09	0.02	1, 663	22.78	<0.0001

Supplement K: Effects of rainfall on the behavior of the Eurasian beaver

Materials and methods

The impacts of rain on beaver behavior were analyzed from behavioral observation of 17 animals. Twelve were observed in 2000 (eight adult males and four adult females from nine territories in Saua and Gvarv rivers) and five (three adult males and two two-year old males, from four territories in Saua and Sauar rivers) in 2007. In 2000, beavers were implanted with an Alterra TX30.3A1 intraperitoneal 30 MHz-radio transmitter (63g) equipped with a temperature sensor and movement sensor (Alterra-DLO) (Ranheim *et al.* 2004; Campbell *et al.* 2005). In 2007, beaver were fitted with either tail-mounted VHF radio-tags (142 MHz, Advanced Telemetry Systems) or tail-mounted proximity loggers with VHF transmitters (142MHz, SirTrack).

All beavers were tracked for a minimum of two complete Principal Activity Periods (PAP). A PAP started when the focal animal left the lodge in the evening and ended when it returned to the lodge the following morning and remained there for at least 20 minutes. Following Martin and Bateson (1999), the sampling rule followed was *focal sampling* and the recording rule followed was *continuous recording*, to a resolution of one minute (Martin *and* Bateson 1999, p84-88). When >1 behaviors occurred within the same minute, the time allocated to each was proportional to the number of behaviors witnessed within that minute. Radio-transmitters were used to maintain surveillance of the subject. All observations were conducted from a boat, binoculars were used throughout and a spotlight was used during dark periods, with no detectable influence on the subject (Herr and Rosell 2004). For this study, we are interested in the effect that rain might have on an animal's willingness to be exposed to the risk of predation while out of the water and also whether animals prefer to stay out of the rain. During observations, in addition to the behavior observed, focal animals were recorded as being on land or in water. Time spent in a lodge or bank-den was also recorded. During night-time observation sessions on the river, temperature and rainfall was recorded at regular intervals. Rainfall was recorded as a binary variable and the variable 'rain' expressed as the percentage of observations with rain each night.

Data analysis

To examine the effects of rainfall on the proportion of their PAP that animals spent on land and in a lodge, linear mixed-effects model were created using the *nlme* package in *R* 2.8.0 (R Development Core Team 2008). Random intercept model was used following Schielzeth and Forstmeier (2009). Fixed factors and covariates were Year, Month and Rain without interaction terms and Beaver was set as the random effect. For each behavior, several candidate models were compared, with and without a first-order autoregressive (AR1) correlation structure to account for repeated measures in animals, and with and without individual based weightings on variance structure. The model with the lowest Bayesian information criterion (BIC) value was selected.

Results

The best mixed-effect models contained an AR1 correlation structure within animal. For proportion of activity spent in a lodge or bank-den, a model with individual variance weightings was better than one without. Rainfall did not significantly influence the proportion of time animals spent on land ($F_{1,52} = 3.70$, $P = 0.060$, Fig 1: for every 1% increase in rain, beavers increased the time on land by 0.11% ±0.06 SE), or the proportion of time animals spent in their lodge or bank-den ($F_{1,52} = 1.17$, $P = 0.285$, Fig 2: for every 1% increase in rain, beavers increased the time in shelter by 0.03% ±0.03 SE).

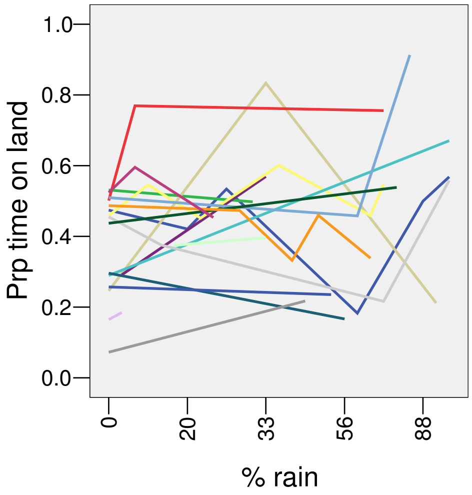


Figure 1: Plot of the percentage of the observation period with rain against the proportion of the observation period each animal spent on land. Each colored line represents an individual. Where the same percentage rain value reoccurs within an individual, the mean of time on land has been taken.

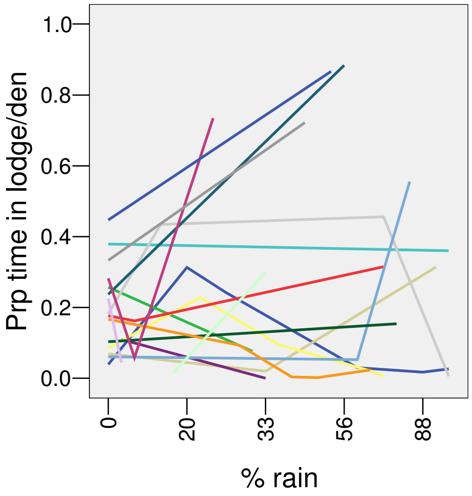


Figure 2: Plot of the percentage of the observation period with rain against the proportion of the observation period each animal spent in a lodge or bank den.

Discussion

One potential mechanism behind the negative effects of rain is that beavers may not detect predators so easily when in rain (Lima and Dill 1990; Hilton *et al.* 1999) and are therefore less inclined to risk exposure to predation by foraging on land. Indeed, beavers in Poland have been found to adjust their foraging patterns in response to the placement of predator odors (Rosell and Czech 2000). However, we found no significant effect of rainfall on the proportion of time beavers spent on land, suggesting that predator avoidance is not the mechanism behind the effect of rain. Predation risk is low in the study population since the wolves (*Canis lupus*), the main predator of beavers where the species' ranges overlap (Rosell *and* Czech 2000; Sidorovich *et al.* 2003; Andersone and Ozoliņš 2004), have not be found in the study area for around 100 years. While a reduction or almost complete extinction of fear of non- human predators has been recorded in populations where such predators have been absent (Berger 1998; Ward et al 1996), experiments on the Telemark beaver population have shown a significant reduction in time spent scent-marking in presence of both lynx and wolf scent (Rosell and Sanda 2006). Therefore perceived predation risk could also still influence their foraging decisions.

Alternatively, beavers may suffer a thermodynamic cost to having wet fur. The semi-aquatic mink *Mustela vison* does not appear to suffer reduced thermal efficiency of fur when wetted (Korhonen and Niemelä 2002) and since beavers are also highly adapted to the aquatic environment with a similarly dense underfur (12,000 cm^2 dorsal density and 23,000 cm^2 ventral density *cf.* 16,600 cm^2 mean density over the whole winter pelt in mink, Korhonen 1988; Rosell 2002), a lower surface to volume ration than mink, and an extensive counter-current blood vessel arrangement (Cutright and McKeen 1979) this hypothesis seems unlikely. Indeed, we did not find an effect of rain on the proportion of their activity period that was spent in their lodge or bank-den indicating that if there is a thermodynamic cost to rain, it was not great enough to force beavers to take food under shelter to be consumed.

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A life less ordinary: weather variability influences vital rates of the Eurasian beaver

Abstract

Ecologists are increasingly aware of the importance of environmental variability in natural systems. Organisms are subject to selection imposed by both the mean and range of environmental variation experienced by their ancestors, and further adapted through behavioural and life-history decisions. Changes in the variability of a critical environmental factor may therefore have consequences for the vital rates and population dynamics of a species. Anthropogenic climate change is affecting both the mean and the variability of weather and, in particular, the effect of changes in variability is poorly understood. Here we examine ≥90 year trends in different components of climate (mean and SD of precipitation and mean, seasonal amplitude and residual variance of temperature) and consider the effects of these components on survival and recruitment in a population of Eurasian beavers (N=242) over the last 13 years.

No trends in precipitation were detected but significant trends in the three components of temperature, outlined above, were observed, with mean and residual variance increasing and seasonal amplitude decreasing over time. Within correlative interactions, a higher survival rate was linked (in order of influence, based on Akaike weights) to lower precipitation standard deviation, higher mean precipitation and lower residual temperature variance. Greater recruitment was linked (in order of influence) to higher seasonal amplitude of temperature, lower mean precipitation and lower residual variance in temperature.

As a consequence, though both climate means and variance proved influential to population dynamics, overall components describing variance were more influential than those describing mean values. These findings provide an example of environmental variation being influential to the vital rates of a generalist, wide ranging and K-selected species with implications for population growth and the evolution of life-histories,

contrary to established precepts. To inform conservation strategies, future studies should address the issue of changing climate variability, in combination with mean trends, when modelling the impacts of climate-change on populations.

Introduction

The capacity for a species to make effective future predictions on which to base key life-history decisions (McNamara *et al.* 1995), such as when to reproduce, how much to invest in reproduction and the amount of resources to defend, is vital to fitness and survival. The degree of stochasticity in the environment can have a significant influence on optimal phenotype (Tuljapurkar *et al.* 2009). In fluctuating environments, decision-making processes are honed by evolutionary selection pressures according to the probability distribution of the environmental conditions experienced by the organism's ancestors (McNamara *et al.* 2001). As a consequence changes in the patterns of fluctuation in the environment can generate changes in the selective pressure on life-histories (Boyce *et al.* 2006; Ruzzante *et al.* 2008). Assessing future conditions accurately in fluctuating environments, however, has a higher potential for error compared with environments that are relatively predictable.

Changes in regional weather patterns are resulting from anthropogenic climate change and the variability in these conditions is predicted to increase significantly over the coming century (IPCC 2007). In particular, an increase in the frequency of extreme precipitation events has been predicted (Karl *et al.* 1995; Groisman *et al.* 1999; Easterling *et al.* 2000) while temperatures are predicted to show lower diurnal and intra-annual variation (i.e. seasonal amplitude), but more frequent heat waves (Karl *et al.* 1995; Easterling *et al.* 2000; Schär *et al.* 2004). There is mounting evidence that climate change is matching these predictions (e.g. Karl *et al.* 1995; Brunetti *et al.* 2000; Luterbacher *et al.* 2004; Schär *et al.* 2004).

Due to the complexity of patterns of climate change, where mean trends are set against a background of changes in frequency, amplitude and variation, it is imperative that we understand how the components that comprise climate impact on species. For example, there is increasing evidence that changes in climate averages (e.g. Hughes 2000; Walther *et al.* 2002; Parmesan & Yohe 2003) and in climate stability (e.g. McLaughlin *et al.* 2002; Boyce *et al.* 2006) are detrimental to biodiversity. At the population level, however, not all the impacts of increased environmental variability are negative (e.g. Drake 2005) and the effects of projected increases in weather variability remain poorly understood (Weltzin *et al*. 2003; Boyce *et al*. 2006).

Here we explore the effects of the different components of temperature and precipitation regimes on the mortality and recruitment of a temperate herbivore, the Eurasian beaver, *Castor fiber.* The beaver, a large rodent (> 20kg), is distributed across most of northern Eurasia between 35°N and 70°N (Halley & Rosell 2002; Műller-Schwarze & Sun 2003). Beavers are territorial, live in fresh water and forage predominantly on deciduous trees from which leaves, twigs and bark are consumed (Wilsson 1971; Haarberg & Rosell 2006) but will also take herbs, forbs and aquatic vegetation in summer (Jenkins 1979; Műller-Schwarze & Sun 2003). Beavers are monogamous and only the dominant adult pair breeds (Wilsson 1971). Copulation occurs around late January to early February (Wilsson 1971). Kits are born, after a 107-day gestation, around mid-May (Wilsson 1971; Parker & Rosell 2001) in litters of 1 – 5 (Campbell *et al.* 2005), are fully weaned at approximately two months of age and emerge from their lodge around mid-July (Wilsson 1971). Sexual maturity is usually attained at 1.5 – 2 years of age, whereupon offspring will disperse (Hartman 1997). If no suitable sites are available for settlement, however, offspring may remain philopatric for several more years, until a vacancy becomes available (Campbell *et al.* 2005). Eurasian beavers can live for as long as 20 years in the wild (Rosell & Pedersen 1999). Once paired, beavers tend to remain so until one is displaced or dies (Svendsen 1980; Műller-Schwarze & Sun 2003). The main natural predators of beavers are wolf, *Canis lupus*, and brown bear, *Ursus arctos* (Rosell & Czech 2000), though lynx, *Lynx lynx*, may also prey on beavers (Rosell and Sanda 2006). Smaller carnivores such as fox *Vulpes vulpes* (Kile *et al.* 1996) and possibly pine marten *Martes martes* (Rosell & Hovde 1998) and otter *Lutra lutra* (Tyurnin 1984) may also predate upon beaver kits and yearlings. Beavers can have a significant impact on their environment and on other wildlife due to their river damming and tree-felling activity (Rosell *et al.* 2005), giving the beaver the status of a keystone species (Paine 1995). Understanding how beaver populations may be influenced by anthropogenic climate change is thus important in the context of wider conservation because of the implications beaver activity has for wetland biodiversity and abundance in boreal ecosystems.

Here we examine climatic influences on beaver population dynamic parameters, emphasising how variability around long-term means interacts with beaver survival and recruitment rates. We hypothesise that a reliance upon typical seasonality and low variability in climate indices may be more influential in terms population success than trends in the mean of these values, and that age classes may be affected by interactive climate effects differently.

Material and methods

Study site

The study site was centred on three rivers, the Straumen (59°297' N, 09°153' E), the Gvarv (59°386' N, 09°179' E) and the Sauar (59°444' N, 09°307' E), in Telemark, southern Norway.Native bedrock is granite-gneiss with a thin layer of fluvial (Straumen and Gvarv) or marine (Straumen and Sauar) deposits in valley bottoms. The climate is cool-continental and lies on the boundary of the Dfb and Dfc classes in the Köppen–Geiger climate classification system (Kottek *et al.* 2006) with a mean annual temperature of 4.6 °C and a mean annual precipitation of 790 mm. Mean monthly 24 hour temperature dips below 0 °C for five months a year between November and March. All rivers exhibit reduced ice cover in winter due to the presence of lakes along their length, which reduce fluctuations in water temperature (Webb & Walling 1996), although all beaver families in the study area build winter food stores (caches) whether ice-cover occurs or not. All three rivers form part of the catchment of Lake Nordsjø. None of the studied beaver families built dams during the 13-year study period. Illegal culling is believed to be rare in the area (B Hovde and F Bergan pers. comm.) since few beaver families are in conflict with human land-use. A close relationship was maintained with local hunters, which allowed us to keep track of the majority of direct anthropogenic mortality in our population. Hunting pressure was low with 23 of a total of 268 animals (including floaters: animals that have dispersed from their natal territory but have not established a territory of their own) shot or kill-trapped during the course of the study. Predation pressure was also low as wolves have been substantially extirpated from the area for over 100 years, bears only occasionally pass through (Elgmork 1987) and lynx are present, but at low densities

(Rosell and Sanda 2006). Beavers have been in the study area since the 1920s (Olstad 1937).

Population monitoring

Between 1997 and 2009, inclusive, this study monitored beavers through an extensive live-trapping programme, using hand-nets from a motorboat, between March and November (Rosell & Hovde 2001). Captured individuals were immobilized in cloth sacks, sexed based on the colour of the anal gland secretion (Rosell & Sun 1999), tagged with a microchip (Avid or Trovan) and marked with unique colour-plastic (Dalton) and metal (National Band and Tag Co.) ear-tag combinations. Animals were assigned to an age-class (0 years = kit, 1 years = yearling, 2 years = subadult and ≥3 years = adult) based on body-weight (Rosell *et al.* in prep). Recaptures resulted from either the trapping or sighting of marked animals. Dominance status was determined by previous trapping and sighting history and incidences of lactation in females. That is, individuals dispersing into a territory were posited to have obtained the dominant breeding position, an assumption generally corroborated by data indicating the disappearance (usurpation) of the previous dominant individual of the same sex and, for females, lactation (signified by nipple length > 0.5cm) (Műller-Schwarze & Sun 2003, p82). In the majority of cases, where animals were already present in the territory at the beginning of the study, dominance status was explicit as other same-sex adult group members dispersed, or disappeared, and were not replaced by new animals. On two occasions, where more than one animal was a potential dominant individual, we resorted to the use of body weight to distinguish status, with dominance being inferred for the heaviest individual, following Smith *et al.* (1994). Unless there was evidence to the contrary, dominant individuals were presumed to maintain their status until they disappeared or died. Mean annual trapping effort (the number of nights in each year spent on the rivers trapping and sighting beavers) was 30 ± 15 SD.

Throughout the study we base our analyses on a demographic history file documenting the capture events of 242 individual beavers, each of which was caught between one and 11 times.

Climate data

Daily temperature and monthly precipitation figures were obtained from the Norwegian Meteorological Institutes *eKlima* online database (http://eklima.met.no/): Daily temperatures from Gvarv (Gvarv weather-station from 1919-1989, height 26m, 59°383' N, 09°183' E, Gvarv-Lindem 1989-1994, height 71m, 59°387' N, 09°202' E, Gvarv-Nes 1994 to 2009, height 93m, 59°383' N, 09°201' E) were available from 1919 to 2009; Monthly precipitation figures from Lifjell (height 354m, 59°455' N, 09°037' E) from 1896 to 2009. All beaver territories were within 18km of these weather stations.

The weather stations at Gvarv that we referred to were all within 1.4km of each other. Nevertheless, to make sure that historical relocation of weather stations in the study region had not influenced the continuity of temperature readings, we also obtained temperature records from 1954 to 2007 from Tveitsund in Telemark (height 455m, 59°027' N, 08°521' E, approximately 60km south-west of Gvarv). Temperature readings correlated consistently, and with high significance, with those from all weather stations at Gvarv, and there was no evidence that changes in the weather stations from which we utilise meteorological records affected temperature values (Supplement A).

We derive for each year indices that reflect effective climatic conditions (i.e. temperature and rainfall). A data-year was defined to start the 1st of March; to follow beaver life cycle patterns. Beaver population dynamics are known to be influenced critically by climatic conditions during the vegetation growing season (e.g. spring - autumn) (Jarema et al. 2009; Chapter 5). We thus evaluate each of the yearly climate indices described below using the climate data between the 1st April and the 30th of September.

Temperature

Temperature, as expected from the changing angle of incidence of the sun at the latitude of the study area, demonstrated clear evidence for seasonal variation (Figure 1). Given the sinusoidal nature of the variation of temperature within a year, we characterise yearly temperature with the terms:

- Mean (average) temperature for that year: μ_T.
- Amplitude of seasonal temperature changes: α_T.
- Residual variance around the daily predicted temperature values provided by these two previous indices. This residual variance can be interpreted as the yearly stochasticity in temperature. To derive a coherent scale across these terms we calculate the standard deviation in temperature, σ_T.

In our model, the temperature T on day *d* of year *y* is thus characterised as:

$$T_{d,y} = \mu_{T,y} + \alpha_{T,y} \cos(d\ c) + \varepsilon_y$$

Where: (i) ε_y represents the residual error associated with year y, and each ε_y value is obtained from a normal distribution with mean 0 and variance $\sigma^2_{T,y}$, (ii) c provides a constant ($2\pi/365$) such that the cycle concludes after one year.

Using a nonlinear regression procedure, based on least square (function '*nlinfit*' from Matlab, The MathWorks), for each year we then estimate $\mu_{T,y}$, and $\alpha_{T,y}$, for all temperature data available between 1919 and 2009. The sum of squared residuals over each year allows us to derive the yearly temperature variance, $\sigma^2_{T,y}$ and thus $\sigma_{T,y}$.

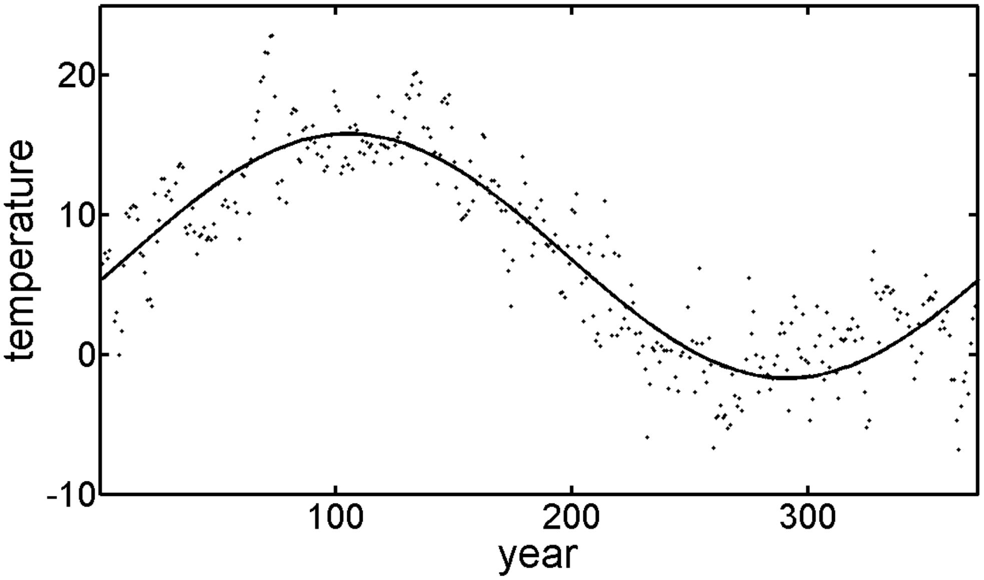

Figure 1

Daily temperature in Gvarv over one year from 1st March 2007. A clear seasonal trend within a year is present in the form of a sinusoidal underlying curve with period equal to a year. The solid line represents the yearly mean temperature, μ_T , plus the amplitude of changes, α_T in 2007. Some variation around these predictions (the solid line) remains and can be characterised by its variance, hence the definition of σ_T.

Rainfall

From inspection of daily rainfall records within a year, no significant within-year seasonal patterns were evident (Figure 2). This permitted rainfall within any given year to be characterised by mean rainfall, μ_R, and the standard deviation in rainfall, σ_R. These two indices were calculated for a period of 115 years from 1895 to 2009.

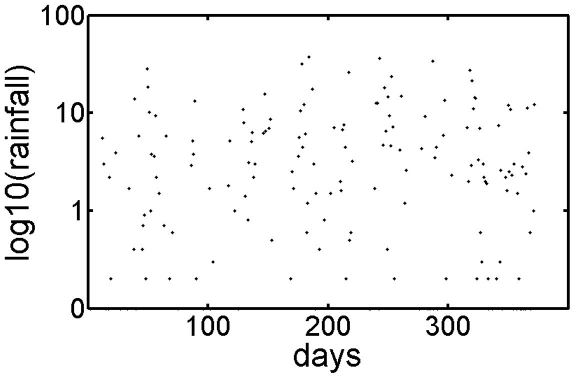

Figure 2

Daily rainfall over Lifjell over one year from 1st March 2007. No seasonal patterns were observed within a year.

Influence of climate indices on population dynamics

A Capture-Mark-Recapture framework, implemented in the program Mark (White and Burnham 1999, version 6.0), was used in our analyses to derive reliable estimates of survival and recruitment. All correlations were made with a significance value of alpha set at 0.05.

Informed by previous studies on North American beaver (*C. canadensis*: Payne 1984; McNew & Woolf 2005), we separated beaver survival rates by age-class. We recognise that losses to the population attributed to mortality could be due to dispersal out of the study area. Since dispersal is almost exclusively restricted to non-dominant individuals, the problem of distinguishing mortality and dispersal can be addressed by including dominance status in the model. We thus distinguish between: kit survival φ_k (two months ~ i.e. available to the trapping regime, to one year old), juvenile survival φ_y (between one and three years old), and adult (greater than three years), separated into dominant φ_{Da} or non-dominant φ_{Na}.

In all the model scenarios we present, capture probabilities were considered constant with age, but variable between years and between the three main study sites (reflecting differential sampling effort).

Survival rate

Survival rates were estimated for each of the three age class groups (kit, juvenile and adult) and dominance status within the adult class (thus four groups, g), using the 'Cormack-Jolly-Seber' (CJS) model (Jolly 1965, Lebreton *et al.* 1992). These rates were then used to construct a primary model, dependent upon year (*y*), $\{\varphi(y,g)\}$. This model was checked for goodness of fit using bootstrap methods (White 2002), allowing approximation of a corrected variance inflation factor ($\hat{c}$). In all models presented survival rates were modelled as a binomial distribution with a binary response (survived or not/died), and thus analysed with logistic regression.

Using a multi-model inference procedure (Burnham & Anderson 2002, 2004, Whittingham *et al.* 2006), we compared survival rate models constraining some iterations with climate indices (e.g. we investigate the linear relationship between the logit of survival estimate and climatic indices). In multi-model inference it is important that all variables are represented equally in the analysis (Burnham & Anderson 2002). Given that five climatic indices were available per year we were able to construct 32 models (i.e. one model with no climatic covariate, five models with one climatic covariate, 10 models with two, 10 models with three, five models with four and one model with five climatic covariates). We thus obtained a balanced set of candidate models that contained all climatic covariates equally.

For each model we derived the *QAICc* (*AIC* corrected for small sample size and adjusted for over-dispersion), which was then used to rank the support for each model (a lower value indicates a better supported model); as well as the Akaike weight for each model (Buckland *et al.* 1997, Burnham & Anderson 2002, 2004 and Whittingham *et al.* 2006). A different estimation of the parameter θ was derived from each model, linking the climatic component in the model with the logit of the survival.

We were then able to derive the relative influence of each climatic component as the sum of the Akaike weight of models containing this particular index (Burnham & Anderson 2004). Finally, we employed model averaging to derive estimates of the θ's and their associated confidence intervals. Model averaging accounts for uncertainty in model selection by calculating the mean value for a parameter of interest through averaging over all models in the candidate model set containing the parameter of interest, weighted by normalised AIC weights (Buckland *et al.* 1997, Burnham & Anderson 2002, 2004). To conform with recent theoretical developments (Burnham & Anderson 2002), confidence intervals were based on estimated unconditional variance, which accounts for two variance components: the conditional sampling variance, given a model, and the variation associated with model selection uncertainty.

Recruitment

The Pradel model (Pradel 1996) was used within the Capture-Mark-Recapture framework to estimate yearly recruitment parameters as well as survival rates. Ostensibly this recruitment parameter equates with apparent population fecundity, however the Pradel approach does not allow the specification of age classes, and thus we performed separate analyses for survival and recruitment. Recruitment estimates were derived from the number of recruits per individual per year; displaying a Poisson distribution, directing us to a *log* link function model.

Again a set of 32 models was constructed, where recruitment, *f,* was dependent (or not) upon the climate indices from the preceding year. Values for survival rates and capture probabilities were fixed to predetermined values, estimated using a CJS model with survival rates constant among age classes but dependent upon years and capture rates dependent on year and location.

Subsequent evaluation of the models was performed as detailed above, and this allowed us to determine the estimated influence of the coefficients of each climate component and their confidence intervals.

Results

Population characteristics

Examining recapture rates to provide an estimate of annual mortality indicated that mortality rates varied between years (Figure 3). Though recapture rates increased with trap effort (number of nights trapping over two years), this correlation was not quite significant (Pearson's correlation: r = 0.546, df = 9, p = 0.082). Trap effort did not correlate with population size (Spearman's correlation: rho = 0.002, df = 9, p = 0.995) and population size did not correlate with recapture rate (rho = -0.351, df = 9, p = 0.290).

Climate indices

Temperature

We determined values for mean temperature, μ_T , amplitude of seasonal changes, α_T, and the residual standard deviation in temperature,σ_T, between 1919 and 2009 (Figure 4).

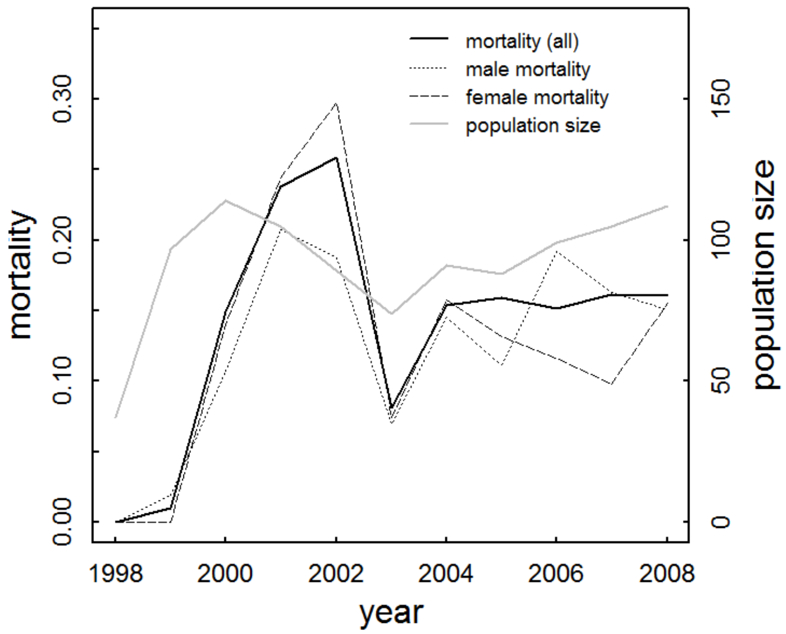

Figure 3: Mortality (proportion of animals not recaptured in following years, *x*+n) and total population size with year (*x*). Black solid lines represent the mortality both sexes combined, dashed black lines are females, dotted black lines are males and the grey line is the population size (minimum number of animals alive). Between 1998 and 1999 the study area expanded significantly while between 1999 and 2008 study area varied slightly as peripheral beaver territories were either added or dropped. Thus observed population changes may not accurately reflect true population densities.

A long-term trend of increasing yearly mean of temperature, μ_T, was detected ($b = 0.02$ with $F_{87} = 22.5$, $p < 0.001$, $R^2 = 0.20$) equivalent to a rise of 2°C since 1919 (Figure 4a). A significant decreasing long-term trend in yearly seasonal changes (seasonality) of temperature (amplitude), α_T, was also detected ($b = -0.02$ with $F_{87} = 6.6$, $p = 0.012$, $R^2 = 0.07$), equivalent to a 1.8°C reduction in the difference between winter and summer since 1919 (Figure 4b). Additionally there was a long-term trend in increasing yearly temperature residual standard deviation, σ_T ($b = 3\ 10^{-3}$ with $F_{87} = 9.35$, $p = 0.003$, $R^2 = 0.10$) (Figure 4c).

While a negative correlation was evident between mean temperature and the amplitude of seasonal changes ($b = -1.0$ with $F_{87} = 146.1$, $p < 0.001$, $R^2 = 0.63$) (Figure 4d), no such correlation was observed with regard to residual standard deviation (μ_T against σ_T, $F_{87} = 2.7$, $p = 0.11$ (Figure 4e) and α_T against σ_T, $F_{87} = 0.3$, $p = 0.58$ (Figure 4f)).

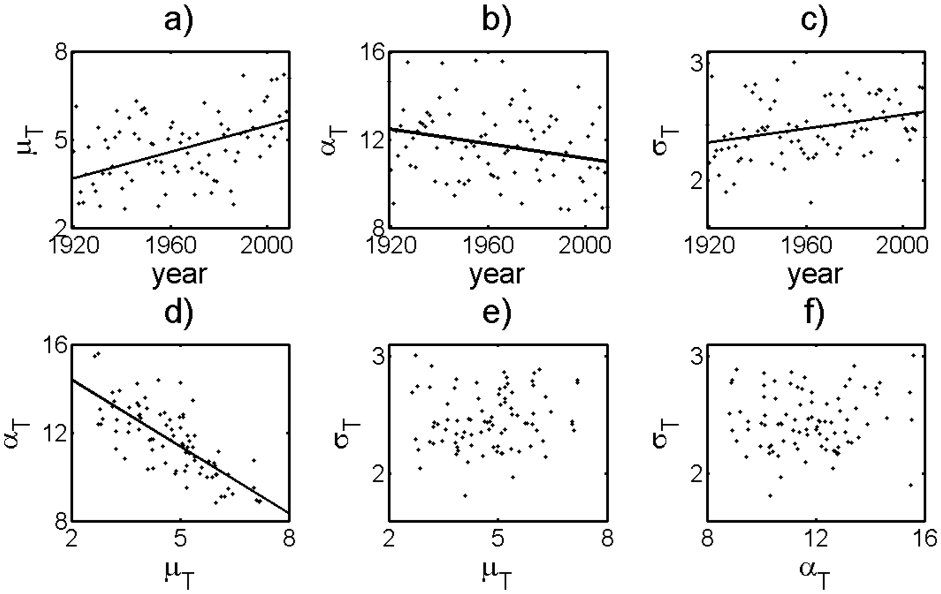

Figure 4: Mean (a), amplitude of seasonal changes (b) and residual standard deviation (c) in daily temperature between April and September for each year between 1919 and 2009. We observe long-term trends in these indices. The last three plots show the significant correlation between mean temperature and amplitude of change (d); and relationships between mean temperature and residual standard deviation (e); and amplitude of change and residual standard deviation (f).

Rainfall

We determined values of mean rainfall, μ_R, and standard deviation in rainfall, σ_R between 1895 and 2009 (Figure 5). No long-term trend in yearly mean or standard deviation of rainfall could be detected (for the μ_R: $F_{113} = 0.196$, $p = 0.66$, for σ_R: $F_{113} = 0.005$, $p = 0.94$). A strong positive correlation was, however, detected between the two indices ($b = 1.55$ with $F_{113} = 319$, $p < 0.001$) (Figure 5c).

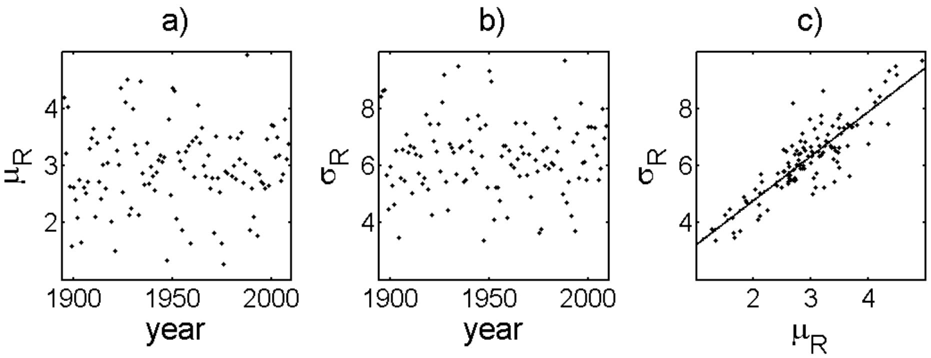

Figure 5: Mean (a) and standard deviation (b) in daily rainfall between April and September of each year between 1895 and 2009. Plot (c) shows the relationship between mean and standard deviation. We observe an influential positive correlation between the two indicess.

Influence of climate indices on population dynamics

Survival rates

Beaver survival proved to be correlated negatively with both the standard deviation in rainfall (see Figure 6), and in the standard deviation in temperature, and correlated positively with mean rainfall. All 32 models were compared and ranked according to their relative statistical support (see Table 1 for the top 5 models). Each model contained a different combination of covariates (the climate indices), and based on the support for each model, we established that indices linked with rainfall (σ_R, μ_R) were the most influential along with residual standard deviation in temperature (σ_T). Furthermore, based on 95% confidence intervals, the effects of these three covariates were biologically significant (i.e. confidence intervals do not include 0, see Table 2).

Table 1: Statistical summary of the five most supported models linking survival to climate indices. Based on Akaike weight, w_i, the most supported model, μ_R, σ_R, has twice the support of the second ranked model, σ_T. θ values represent the coefficient linking survival rate to each climate index within the logistic equation, with standard errors in parenthesis.

model	$QAIC_c$	$QAIC_c$	w_i	θ_{μ_T}	θ_{α_T}	θ_{σ_T}	θ_{μ_R}	θ_{σ_R}
μ_R, σ_R	915.25	0	0.21				2.243 (1.183)	-1.284 (0.564)
σ_T	916.92	1.66	0.09			-1.264 (0.814)		
$\sigma_T, \mu_R, \sigma_R$	917.46	2.20	0.07			0.223 (1.060)	2.434 (1.491)	-1.385 (0.738)
μ_T, μ_R, σ_R	917.46	2.21	0.07	0.050 (0.259)			2.284 (1.196)	-1.316 (0.584)
$\alpha_T, \mu_R, \sigma_R$	917.50	2.24	0.07		-0.008 (0.128)		2.236 (1.190)	-1.286 (0.565)

Table 2: Model averaging of the parameters linking survival rates to climate indices (within the logistic model). The relative influence of each parameter (based on Akaike weights) are presented along with the model-averaged estimated values of these parameters with confidence intervals, based on the estimated unconditional variances.

	Relative influence	θ	Lower 95 CI	Upper 95 CI
σ_R	0.65	-0.698	-1.110	-0.285
μ_R	0.60	1.120	0.297	1.944
σ_T	0.49	-0.452	-0.829	-0.075
α_T	0.27	-0.014	-0.045	0.016
μ_T	0.26	0.004	-0.055	0.063

Table 3: Statistical summary of the five most supported models linking recruitment to climate indices. Based on Akaike weight, w_i, the three most supported models all rank similarly. θ values represent the coefficient linking recruitment rate to each climate index within the log transformation with standard errors in parenthesis.

model	AIC$_c$	AIC$_c$	w_i	θ_{μ_T}	θ_{α_T}	θ_{σ_T}	θ_{μ_R}	θ_{σ_R}
α_T	2207.82	0	0.13		0.478 (0.068)			
α_T, μ_R	2207.93	0.11	0.12		0.419 (0.078)		-0.424 (0.305)	
$\alpha_T, \sigma_T, \mu_R, \sigma_R$	2208.25	0.43	0.10		0.336 (0.090)	-2.162 (1.169)	-2.632 (1.242)	0.902 (0.519)
α_T, σ_R	2208.65	0.82	0.08		0.453 (0.071)			-0.156 (0.142)
$\mu_T, \alpha_T, \sigma_T, \mu_R$	2208.84	1.02	0.07	0.482 (0.289)	0.554 (0.114)	-1.488 (0.980)	-0.763 (0.385)	

Table 4: Model averaging for the parameters linking recruitment to climate indices (with log transformation), giving the relative influence of each parameter (based on Akaike weights), the model averaged estimated values of each parameter, and associated confidence intervals, based on estimated unconditional variances.

	Importance	θ	Lower 95 CI	Upper 95 CI
α_T	0.998	0.462	0.402	0.522
μ_R	0.55	-0.624	-1.169	-0.079
σ_T	0.44	-0.574	-1.091	-0.057
σ_R	0.43	0.106	-0.118	0.330
μ_T	0.38	0.122	0.015	0.23

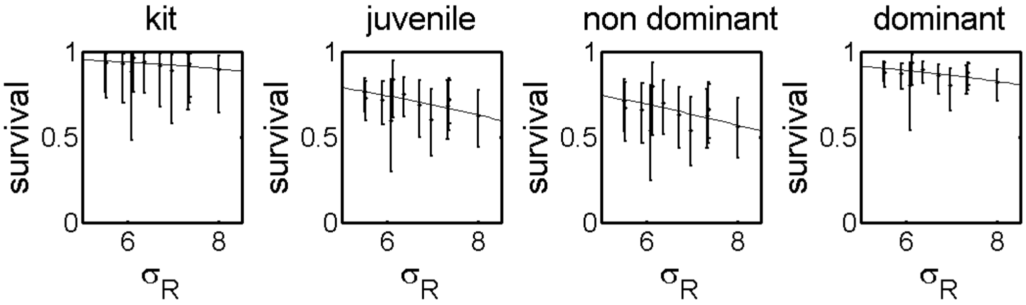

Figure 6: Survival rate estimates for kits (between two and 12 months old), juveniles (between 1 and 3 years old) and adults (3 years old or more) as a function of standard deviation in annual rainfall. Estimates of survival rates and their confidence intervals (error bars) are based on model averaging. Adult survival rate is separated into dominant and non-dominant classes. Juvenile and non-dominant adult survival rates are similar and both are lower than those of kits and the dominant adult class. The solid curves represent the model linking survival rates to standard deviation in rainfall. A coherent negative relationship is evident between survival rate and standard deviation in rainfall.

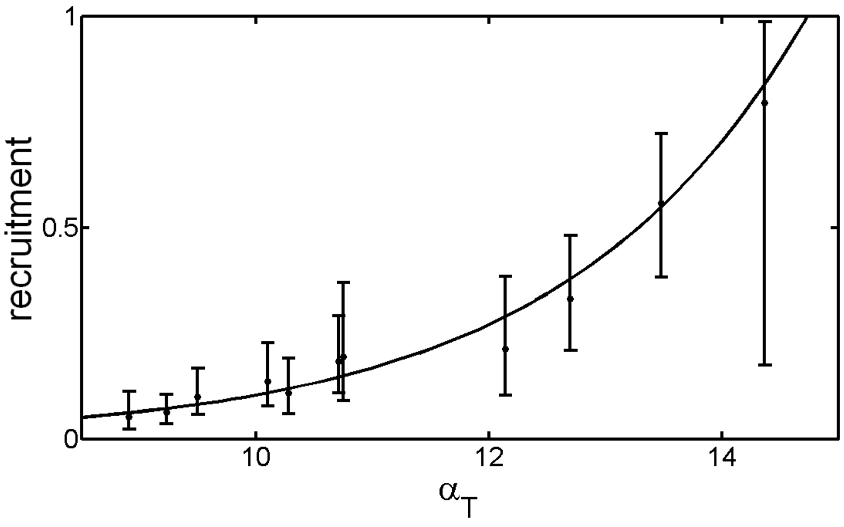

Figure 7: Recruitment estimates as a function of the amplitude of seasonal changes in air temperature. Estimates with 95% confidence intervals (error bars) are based on model averaging. We observe a positive relationship between recruitment and the amplitude of change in temperature. The solid curve represents the model linking recruitment to the amplitude of seasonal changes.

Recruitment rates

The recruitment of beavers into the population was correlated positively with the amplitude of seasonal temperature change (see Figure 7), and correlated negatively with mean rainfall and standard deviation in temperature.

Again, all 32 models were compared and ranked according to their statistical support (see Table 3 for the top 5 models) revealing that amplitude of seasonal temperature changes, α_T, mean rainfall, μ_R and residual standard deviation in temperature, σ_T were the most influential covariates predicting recruitment. As with survival, based on 95% confidence intervals, the effects of these 3 covariates were biologically significant (i.e. the confidence intervals do not include 0, see Table 4).

Discussion

There is a growing recognition among ecologists that an explicit consideration of environmental variance is essential to understand fully many of the important patterns and processes in nature (Ruel & Ayers 1999). Here we demonstrate that for beaver population dynamics that while mean values of precipitation and temperature influenced both survival and recruitment, the effect of climate variability, in the form of variance in precipitation and temperature and seasonal amplitude in temperature, was also highly significant in a variety of predictive relationships for age-class dependent survival and recruitment rate.

Effects on survival rate

Contrasting our mortality rates with those of other beaver population studies, our values tended to be relatively higher for juveniles and for non-dominant adults and lower for kits. While our Telemark mortality values were 0.14 - dominant adults and 0.36 - non-dominant adults, combined sub-adult and yearling 0.28, and kit 0.11, by contrast Figures from the Biesbosch population (Nolet & Baveco 1996) give adult mortality as 0.09, sub-adult mortality as 0.09, yearling mortality as 0.50 and kit mortality as 0.36; for the Elbe population (Heidecke 1984, in Nolet & Baveco 1986) adult mortality 0.08, sub-adult mortality as 0.12, yearling mortality as 0.19 and kit mortality 0.47

These comparisons indicate that a proportion of the losses in individuals we attribute to mortality, among juvenile and non-dominant adult beavers may actually be due to dispersal, while we may also be failing to include some kit mortality due to pre-lodge-emergence unavailability to our trapping protocol.

While we acknowledge this possibility, our measure of survival rate for kits and dominant adults is almost certainly a true reflection of reality since neither group are expected to disperse. It is thus plausible, and of interest in terms of demographic mechanisms, that years with low survival values for juvenile and non-dominant adults may indicate conditions that are particularly apposite for dispersal, which we detect in our mortality measures. Though some dispersers may become floaters, others will disperse in response to specific breeding vacancies that arise in the wider population, indicative of mortality of dominant adults outside our study area. Over the course of our study, floaters filled only 13 of 52 (25%) of vacant breeding positions, but detecting floaters reliably can be difficult and the true Figure may be greater.

Philopatry occurs frequently in our population, with some individuals remaining in their natal groups as non-dominant adults for several years (Campbell *et al.* 2005), which suggests that floating is a pre-dispersal strategy used only infrequently. The guiding principle for distinguishing between dispersal and survival in our population is that dispersal effects influence juveniles and sub-dominant adults differently from kits and dominant adults. Nevertheless, the fact that the slope of the negative relationships between variance in precipitation and survival was steeper for juveniles and non-dominant adults than other age classes indicates that some of the losses from the population of juveniles and non-dominant adults were due to dispersal into vacancies created by the increased mortality of dominant adults outside the study area.

The effect of residual variance of temperature and variance in precipitation on overall survival rates was negative while, in contrast to the results reported in chapter five of total rainfall on body weight and fecundity, the effect of mean precipitation was positive. The mean and the variance in precipitation exhibited a strong positive correlation, plausibly because precipitation data tend to be skewed towards zero (dry days) and therefore more wet days result in both higher total rainfall and higher variability in precipitation values. This correlation between the components of precipitation complicates the interpretation of the positive effect of mean precipitation on survival. A model containing mean precipitation as the sole explanatory variable more intuitively exhibited a negative effect on survival, consistent with previous findings of the effect of precipitation on body weight (chapter five). Plausibly the mechanisms underscoring the effects of precipitation on survival operate through effects on forage availability where high rainfall events lead to waterlogging and consequent lower growth of riparian vegetation, while more frequent moderately wet days (though minor contributors to total rainfall) provide moisture without waterlogging and thus promote riparian plant growth (see chapter five). In previous analyses (chapter five), the effect of temperature on beaver body weight in this study population has been established to be only marginally significant. The clear negative effect of residual temperature variance on survival rates underscores the importance of considering variance in environmental factors when examining biological systems.

Effects on recruitment

The study population was open to immigration and beavers often remained in their natal territory into adulthood. Thus recruitment was not necessarily the same as fecundity. For example, if an adult holding a breeding position were to die, a philopatric individual of the same sex residing in a territory outside the study area may move into this vacated position. Recruitment is therefore, in part, a response to mortality and thus factors affecting mortality will have an indirect influence on recruitment. This issue is the reverse of the mortality-dispersal issue considered above. Nevertheless, recruitment predominantly arises from within the study population (e.g. between 1997 and 2008, 143 beavers were recorded as born within the study area whereas only 22 moved into the study area during the same period) and therefore effects on recruitment are likely to reflect effects on fecundity and reproductive success.

The negative effect of mean precipitation on recruitment reconciles with an earlier analysis in chapter five, in which the mechanism for this relationship are discussed. The positive effect of seasonal amplitude in temperature may relate to cooler spring weather in years with higher amplitude, resulting in slower phenological development of forage plants and consequent lengthening of the period over which high quality early growth is available as forage (see chapter five). In previous analyses (chapter five), no effect of absolute temperature on beaver fecundity was observed in this study population. As with survival (above), the significant negative effect of residual variance in temperature on recruitment further underscores the importance of considering environmental variability in biological systems.

Potential future impacts of climate on the study population

Though the frequency of heavy precipitation events in Norway is known to have increased generally over the past century (Groisman *et al.* 1999), we observed no significant changes in the mean or variability of precipitation our study area. Conversely, we observed significant changes in the components of annual temperature regime in accordance with the predictions of Karl *et al.* (1995) and Easterling *et al.* (2000); that is, increasing mean and residual variance but lower seasonal amplitude (see also Macdonald *et al.* 2010 who found absolute summer and winter conditions to be less influential than variability in equinoctial conditions in a population of European badgers). The negative correlation between mean temperature and seasonal amplitude of temperature change indicates that the changes in both mean and amplitude primarily arise from warmer winters and springs and not from warmer summers, since the latter would lead to an increase in seasonal amplitude. Obviously, the life-history strategy and behavioural tactics of animals are directed toward dealing with seasonal warmth in the summer, and seasonal cold in the winter; thus effects that countermand these norms are more pronounced when temperature variation occurs outside of typical seasonal patterns (see Macdonald *et al.* 2010)

While predictions based on these results should be circumspect, it is notable that the direction of change in components of temperature (in particular increasing residual variance and decreasing amplitude) follow the patterns which negatively impact on survival and recruitment for this beaver population (increasing residual variance was associated with lower survival and recruitment while decreasing amplitude was associated with lower recruitment). If temperatures in the study area continue to follow the trends evident over the past 90 years, the vital rates of the beavers in the study area may be impaired.

General implications

Our results further compliment Nouvellet *et al.*'s (submitted; see also Macdonald *et al.* 2010) work on badger *Meles meles* climate-population interactions by highlighting how climate variations, and changing seasonality of trends, and not just absolute (or phenological) changes in climate, can influence population vital rates. Like the badger (Macdonald *et al.* 2009), the beaver is a generalist forager (within its herbivorous remit) with a broad geographic range and on the slow side of the fast-slow life-history continuum (Promislow & Harvey 1990). Generality (Boyles & Storm 2007, but see Safi & Kert 2004), broad geographical distributions (Johnson 1998) and slow living (*sensu* Dalgleish 2009; Tuljapurkar *et al.* 2009) are all predicted to reduce population susceptibility to environmental variation. However, it appears that such species may remain vulnerable to perturbations affecting the parameters on which their prospect assessment algorithms are founded (see McDermott *et al.* 2008). Thus, environmental variation may still be influential to the vital rates of generalist, wide ranging and K-selected species with implications for population growth and the evolution of life-histories.

The population growth dynamics of herbivores tends to display a concave relationship with resource availability (Sibly & Hone 2002). Assuming that the primary influence of climate variability is through its effect on resources, Jensen's inequality (a mathematical property of non-linear functions, see Ruel & Ayres 1999 and Pásztor *et al.* 2000 for reviews) would propose that an increase in the variation of a resource, without necessitating any change in its mean value, would decrease population growth. Combining reduced vital rates with reduced population growth in a less predictable climate would thus increase the susceptibility of a population to extinction. Using a species-climate envelope model, Jarema *et al.* (2009) predicted that the abundance of North American beaver *C. canadensis* would increase with projected changes in climate. Though the model was otherwise comprehensive, the authors did not take into account the potential impact of climate variability. Our results here show that the prediction of an increase in abundance may be overly simplistic, with any increase in population density from an improved resource base being tempered by lower predictability in these resources. To inform conservation strategies appropriately it is thus imperative that future studies address the issue of changes in variability when modelling the impacts of climate-change on populations.

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Supplement A: Effect of weather station on temperature records

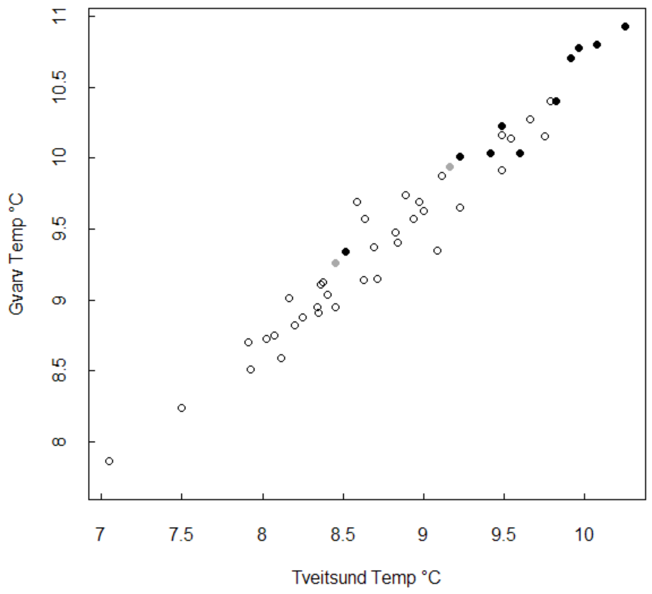
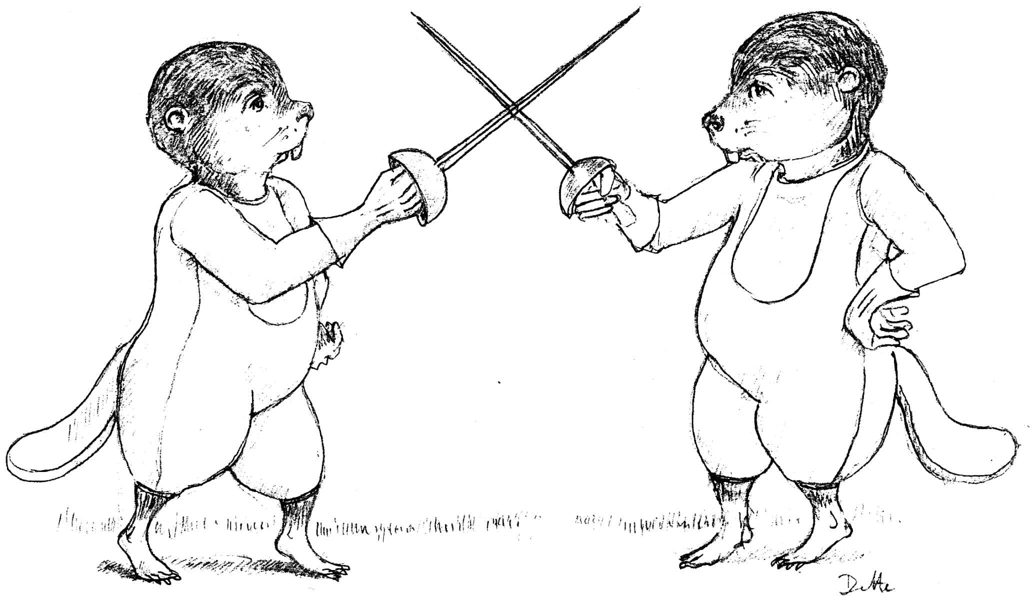


Figure 1. Gvarv (open circles), Gvarv-Lindem (filled grey circles) and Gvarv-Nes (filled black circles) weather station temperature readings (mean of mean monthly temperatures from Mar – Oct) all exhibited the same relationship with readings from Tveitsund weather station, also in Telemark, indicating that the changes in weathers stations at Gvarv did not affect the temperature data. This was confirmed with a GLM where the interaction between Tveitsund readings and station ID in Gvarv was not significant ($F_{1,44} = 0.002$. $P = 0.964$), demonstrating that the slope of the relationship was the same for all Gvarv stations.

Riparian resources: Territoriality in the Eurasian beaver



Introduction

A group territory is an area over which a group has exclusive or priority use and which it defends against conspecifics and sometimes other species (Powell 2000). Group territoriality involves territory-holding individuals allowing additional animals to share the space for which they have competed. Often, these additional occupants are the sexually mature offspring of the primary territory-holders (Emlen 1982, Lindström 1986). Sometimes, the individual advantages accruing to group members are obvious, including access to critical limited resources such as food, water or shelter (Davies and Houston 1984), reduced burden of predator vigilance (Pulliam *et al.* 1982) or an increase in the number of offspring raised (Doolan and Macdonald 1999; Russell *et al.* 2002). These benefits may offset the costs of territorial defence and reduced mating opportunities (Creel *et al.* 1997) or increased competition for limited resources such as food (Chapman and Chapman 2000), as well as other aspects of intra-group competition. Sometimes, however, social groups do not involve obvious cooperation, prompting the question of what selective pressures favour their formation (von Schantz 1984, Kruuk and Macdonald 1985, Carr and Macdonald 1986).

The configuration, size and defence of territories by social units results from a balance between these costs (energy expenditure and mortality risk) and benefits (access to resources). One school of thought attempts to interpret this balance in the context of the spatio-temporal patterns in the availability of limiting resources, such as food, water, and nesting/denning sites (Macdonald 1981; 1983, Bekoff and Wells 1982, Macdonald and Carr 1989, Doncaster and Macdonald 1992, Stamps 1994; Macdonald *et al.* 2004).

The 'Resource Dispersion Hypothesis' proposes that there are conditions of resource dispersion under which the smallest economically defensible territory required by a pair (or whatever is the minimum social unit) can, at minimal cost, also accommodate additional individuals (Macdonald 1983). This idea has been applied often to badgers (Kruuk 1978a; Kruuk and Macdonald 1985; Johnson *et al.* 2001; Macdonald *et al.* 2004; Kilshaw *et al.* 2009), and generalised more widely (Macdonald 1983, Macdonald *et al.* 2007; Johnson *et al.* 2001, 2002, Johnson and Macdonald 2003).

Eurasian beavers, *Castor fiber,* display many characteristics that make them an apposite model species with which to look at the implications of resource dispersion on their clearly defined social group territories. Beavers are semi-aquatic, live in philopatric family groups with robust dispersal processes, and have a ‘despotic’ monogamous mating system.

Beavers are central place foragers and rarely travel far from water with most foraging occurring within a few meters and generally not more than around 40m from the waters edge (Fryxell & Doucet 1991; Parker *et al.* 2001; Haarberg & Rosell 2006; Margaletić *et al.* 2007). They are most renowned for their ability to fell deciduous trees from which they consume the leaves, twigs and bark (cambium) for food while the woody stems may be used in the construction of lodges and dams (Wilsson 1971; Műller-Schwarze *et al.* 2003). In effect, however, they are ‘choosy generalist’ herbivores (Jenkins 1979) in that they can eat a wide variety of vegetation including aquatic plants, herbs, forbs and woody vegetation (both deciduous and coniferous) but within this herbivorous remit, they will forage selectively. When foraging on woody vegetation, small saplings (dbh <5cm) are generally preferred over larger trees (Haarberg *et al.* 2006; Margaletic *et al.* 2007). Tree are felled and transported back to the vicinity of water to be consumed, frequently at favoured sites on the river-bank known as feeding stations (Wilsson 1971, pers. obs.). Once felled, larger trees may need to be cut into smaller sections before they can be transported to water (Wilsson 1971, pers. obs.). Herbs and forbs are usually browsed *in situ* (pers. obs.), plausibly because their smaller size makes ingestion time so short that returning to water is not an energetically efficient strategy. As with other vertebrate herbivores, food selection appears to be mediated by nutrient content and digestibility of the available forage (Ganzhorn & Harthun 2000) with individuals attempting to maximize energy intake over time (Doucet & Fryxell 1993; Nolet *et al.* 1995). Beavers adjust foraging intensity and preference with distance from water, following a central-place-foraging strategy: foraging intensity declines while food selectivity and (within limits) size increases with increasing distance from the safety of water (Jenkins 1980; McGinley *et al.* 1985; Fryxell & Doucet 1991; Gallant *et al.* 2004; Haarberg & Rosell 2006; Raffel *et al.* 2009). They show seasonal changes in foraging preferences under some circumstances with shifts from deciduous woody vegetation in winter to herbs, forbs and aquatic vegetation during summer, and occasional consumption of conifers in spring (Jenkins 1979; Műller-Schwarze & Sun. 2003, p70), though preferences between sites and seasons vary (e.g. compare Nolet *et al.* 1994; Urban *et al.* 2008). In general, of the woody tree species available to the beaver in Europe, willow *Salix* spp. is favoured frequently (e.g., Fustec *et al.* 2001; Haarberg & Rosell 2006; O'Connel *et al.* 2008: Urban *et al.* 2008). Digestion of plant material is aided through hind-gut (ceacum) fermentation (Vecherskii *et al.* 2009) with material given additional digestion though the practice of caecotrophy (a type of coprophagy) (Wilsson 1971).

There are some parallels between beaver socio-ecology and that of another large semi-aquatic rodent, the capybara, *Hydrochoeris hydrochaeris*, which also partitions its activity between land and water. Macdonald *et al.* (2007) show how the group and territory sizes of capybaras can be interpreted within an RDH framework in the context of the areas and dispersions of dry land within fluctuating water levels. This prompts the question as to how resource dispersion affects the socio-spatial organisation of beavers. In particular, we note that beavers forage in patches of woody deciduous vegetation set within a matrix of non-deciduous vegetation and water.

In this short chapter, the purpose is to highlight, as a topic for further research, the impact of resource dispersion on beaver socio-spatial ecology, and to present some early indicative results to stimulate that research. This is a speculative exercise, and the analyses are fully acknowledged to be preliminary, but they do highlight questions for the future that have been thrown up by the research described in this thesis.

Materials and methods

Study site and population

The study site was centred on three rivers, the Saua (Nome municipality), the Gvarv and the Sauar (both Sauherad municipality), in Telemark, southern Norway (59°23′ N, 09°09′ E). Mean monthly temperature in this region dips below 0 °C for five months a year between November and March. All rivers include lakes along part of their length, moderating fluctuations in water temperature along the main riverine channels thus reducing freeze over in winter (though all beaver families in the study area build food stores whether ice-cover occurs or not). All three rivers form part of the Lake Nordsjø catchment. Beavers have been in the area since the 1920s (Olstad 1937).

Trapping program and sampling

Since 1998, beavers in the study areas have been monitored through an extensive live-trapping program using hand-nets from a motor boat between March and November (Spring-Autumn, Rosell and Hovde 2001). Individuals were tagged with a microchip (Avid or Trovan) on first capture and marked with unique colour-plastic (Dalton) and metal (National Band and Tag Co.) ear-tag combinations to aid repeated identification on recapture. Morphometric measures of weight (to the nearest 100g), body-length (cm) following the curvature of the spine from the nose-tip to the base of the tail (where fur gives way to scales), tail-length (cm) from the base to tip of tail and tail-width (cm) from edge to edge of the dorsal surface at the mid-point between base and tip, *inter alia*, were recorded upon each capture. Animals were sexed by examining the colour of the anal-gland secretion (Rosell and Sun 1999).

Establishing Territories

Territory sizes were established by combining data on the location of scent-mound and scent-sites with observational and telemetric data on the ranges over which social group members were active. – with groups defined by shared use of lodges and observations of non-agonistic interactions – and with reference to exclusivity and delineation between juxtaposed neighbouring groups.

These riverine-based territories, with associated riparian margins, remained stable over the interval 1998-2003, but then changed abruptly and significantly in the latter part of the study: 2004-2005 on the Gvarv river and from 2007 on the Straumen and Sauar rivers. This coincided with the disappearance (or mortality) of incumbent territory holders, resulting in the territories being divided by new arrivals. In two cases in 2007, fission of territories by philopatric group members while the original owners were still present creating three new exclusive groups in addition to the two original groups. In one group, this fission was accompanied by the reappearance of stick-displaying, an unusual behaviour associated with high levels of territorial stress (Thomsen *et al.* 2007).

Thus, for the purposes of analysis, we define “original” groups/territories, which are those that existed up until the change in territory borders plus any territory that remained unchanged over the entire course of the study. And we define ‘new’ groups as those territories that had changed, plus any territory that remained unchanged over the entire course of the study.

Resource dispersion: qualifying the feeding patch mosaic

We regarded territories as linear features buffered by riparian habitat. Based on studies of beaver foraging signs with distance from water (Parker *et al* 2001; Haarberg & Rosell 2006), we chose a 40m buffer within which to measure habitat (Fig. 1). All habitat within 40m of the riverbank was delineated based on similarity of habitat. For deciduous vegetation, similarity was based on dominant species composition, changes in canopy height and cover and changes in shrub-layer cover. It is likely that deciduous vegetation is a critical resource for beavers in the study area since >70% of observations of foraging activity involves deciduous vegetation (Campbell unpublished), while territory quality measures based solely on deciduous vegetation have been found to influence reproductive success (Chapter 4). Therefore, other (non-deciduous) habitat types are classified as ‘matrix’ habitat. Any habitat block that was <10m wide (from the river) was ignored, but habitat <10m deep (along the length of the river) was included as it may influence territory size. Defining habitat edges, particularly between deciduous and non-deciduous types, is uncomplicated in the study site since human land use (agriculture and forestry) along the river has created clearly defined habitat edges. Habitat maps were digitised into a GIS.

Using a Geographical Imaging System (GIS), we measured the proportion of all riparian land within 40m of the river that consisted of deciduous habitat (*pdec*), and the proportion of land within 40m of the river that was non-deciduous habitat (matrix habitat) but that was further than 40m from deciduous habitat (*mat40*).

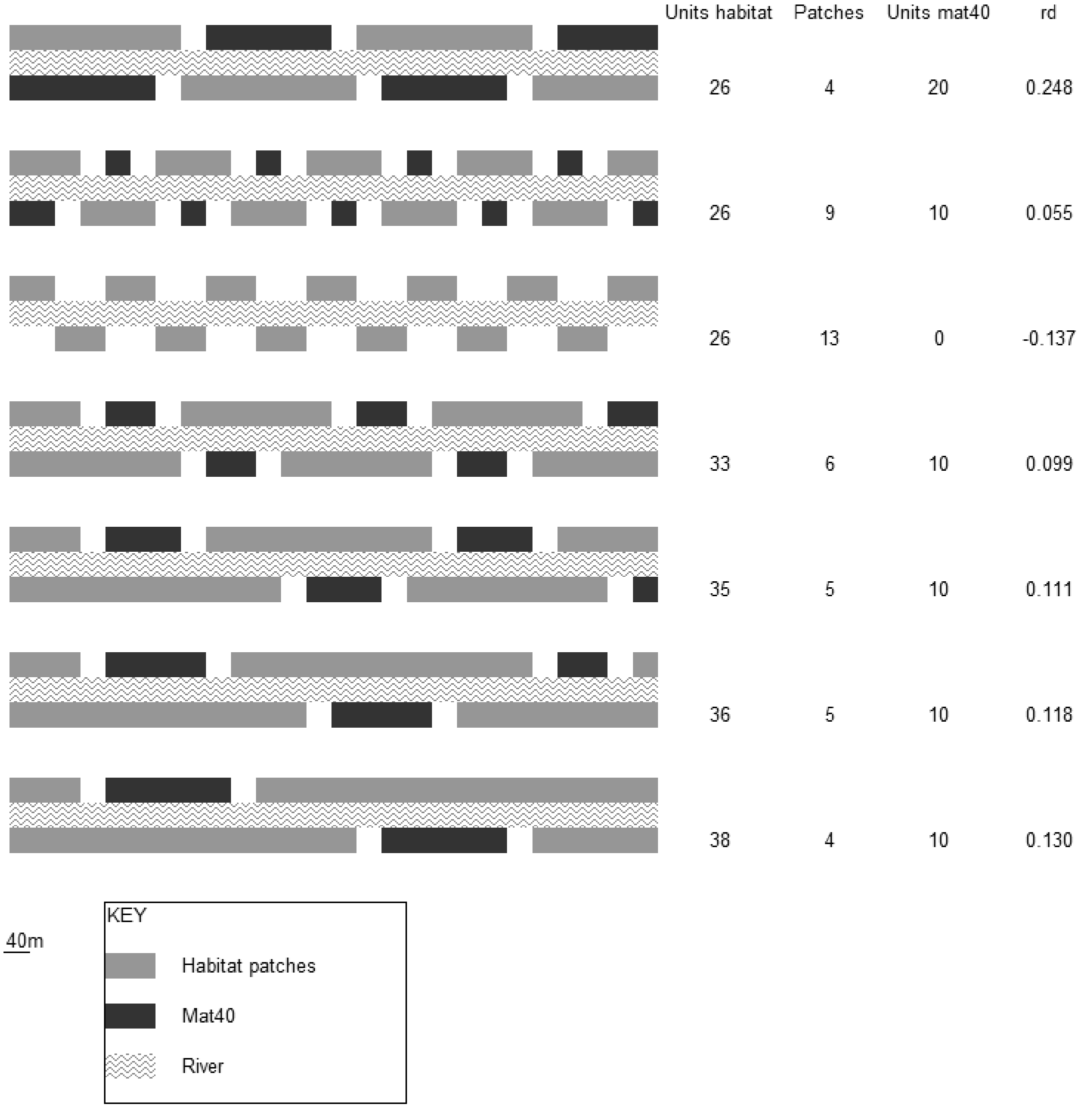
Exploratory correlations showed that over all territories (old and new) *pdec* was inversely correlated with *mat40* (r = -0.391, df=29, P = 0.029), i.e. territories with proportionally more deciduous habitat tended to have proportionally less *mat40.* Any relationship of *mat40* and territory size could therefore simply be due to the amount of deciduous habitat and not its dispersion. It was therefore necessary to correct for this correlation to arrive at a measure of resource dispersion that was independent of the total amount of deciduous habitat: A regression of *mat40* as response variable on *pdec* as predictor, yielded residuals which were taken as a measure of resource dispersion (*rd*). Thus *rd* represents deviation from the expected proportion of matrix habitat further than 40m from deciduous habitat given the abundance of the deciduous habitat. Higher values indicate that there is more matrix habitat that is further away from deciduous habitat for a given proportion of deciduous habitat, i.e. resources are more dispersed (Fig. 1).

Patch quality

Patch quality (*q*) was assessed as the mean percentage of shrub-layer cover in the deciduous habitat (*pdec*). In addition, since an earlier analysis found that Grey alder (*Alnus incana*) growing within 0.5m of mean river level grew less well in wet years, the amount of low and high ground could be an important factoring determining territory quality (chapter 5) we included a measure of the ratio of low to high ground. The ratios of low to high ground were determined from a GIS using the nearest 5m contour to river level. This measure is coarse compared to the scale of the effect of topography on Grey alder growth, but serves to distinguish between territories that predominantly consist of low-lying versus high ground, i.e. 'hilliosity'. The stream gradients on each study river were low (<1m over the entire lengths of the sections of the three river within the study area) and therefore the location of the territory on the river will not influence this measure of hilliosity strongly. The rivers were at different altitudes with respect to the 5m contours however and therefore, river was included as a factor in all analyses using the ratio of low to high ground. Our prediction from hilliosity is that territories with a mix of high and low ground would be of higher quality (chapter 5). Therefore our predicted relationship with hilliosity is quadratic.

Social group parameters

Since groups are built up though retention of offspring past minimum age of dispersal (2 years), they will be influenced by the reproductive history of the group (Campbell *et al.* 2005). In effect, group sizes in the population are entirely due to the propensity of offspring to stay. The longer offspring are likely to stay in the natal territory, the greater likelihood that groups will build. Thus group size was defined as the mean age of offspring in the last year they were seen in the territory (with the assumption that they had dispersed) or the age at which they dispersed, if we had been able to track their dispersal. Offspring that disappeared prior to dispersal age were excluded from this measure as they may have suffered mortality. For offspring that were still resident in their natal territories at the end of the study period, their age at that point was used. The measure was highly correlated with mean annual number of offspring of dispersing age resident in the territory ($r = 0.705$, $df = 19$, $P < 0.001$). Any variation between these two measures of group size is likely due to the reproductive output of the breeding female: productive females will have more offspring that may stay and therefore, a measure of group size that simply consist of the mean number of philopatric animals in a group per year will be confounded by any effects of habitat on fecundity.



Units habitat	Patches	Units mat40	rd
26	4	20	0.248
26	9	10	0.055
26	13	0	-0.137
33	6	10	0.099
35	5	10	0.111
36	5	10	0.118
38	4	10	0.130

Figure 1: Illustration of the effect of the configuration of habitat patches on the measure of resource dispersion (*rd*). Higher values of rd indicate that resources are more dispersed and can be regarded on the ground as a situation where a foraging animal will have further to travel between successive patches. In the top three examples, the total amount of suitable habitat remains the same but as the number of patches of suitable habitat (habitat patches) increases, the amount of matrix habitat >40m from suitable habitat (*mat40*) decreases and thus *rd* declines. In the bottom four examples, the amount of *mat40* remains the same but as the amount of suitable habitat increases, the size of the blocks of *mat40* also increases and thus *rd* increases.

Statistical analyses

All analyses were conducted in R (version 2.10.0, R development core team 2009).

To examine the effects of variables on territory size, we used linear regression. Comparing differences between old and new territory configurations and between territories that contracted and those that did not, we used a Welch two-sample t-test. To examine the effects of variables on group size, we constructed a GLM which included all possible variables (territory size, *pdec*, *q*, *rd*, and the full quadratic term for hillosity). We then used a single-term deletion process whereby at each stage the term whose deletion reduced AIC the most was removed and the process repeated until removal of any term did not result in a reduction of the AIC.

Results

The study area was found to contain 20 territories in the old configuration and 23 in the new configuration of which habitat data was available for 17 (old) and 18 (new) (Table 1; Fig. 2). Thus over the course of the study, nine new territories were created while six were lost. Of those lost, three disappeared, to be engulfed by neighbouring groups, while the remaining three were divided into more than one new territory. In addition, five territories shifted either expanded or contracted in response to the disappearance or change in ownership of neighbours. Four territories showed no change in borders over the course of the study.

Including groups without habitat data, mean territory length (km of riverbank on both sides of the river) was 4.3 ± 1.6 km among original groups and 3.4 ± 1.4 km among new groups. Of groups with habitat data, each territory, on average, contained 51 ± 17 % pdec (see table 1).

Table 1: History, size, habitat, offspring propensity to stay and change in ownership associated with change in configuration of the territories used in the analyses.

River	Territory	Created / changed	Size (km)	Decidious area (ha)	*pdec*	*mat40*	*rd*	High deciduous area (ha)	Mean age at dispersal	New owners
Gvarv	Evjutunet	<1999	2.04	2.40	0.33	0.07	-0.28	0.44	3.00	0
	Gvarvbrua	<1999	7.15	10.01	0.37	0.16	-0.11	3.51	3.67	0
	Gvarvbrua (lower)	2005	1.70	3.30	0.49	0.08	-0.03	1.67	3.00	1
	Gvarvbrua (middle)	2005	3.42	4.06	0.31	0.20	-0.15	1.05	2.00	1
	Haugen	<1999	4.65	7.36	0.48	0.06	-0.06	2.00	4.50	0
	Nordsjø 1	<1999	3.36	5.62	0.44	0.39	0.08	0.14	4.78	0
	Nordsjø 1	2005	3.94	5.65	0.38	0.29	-0.05	0.14	2.33	0
	Nordsjø 2	<1999	5.21	11.48	0.62	0.02	-0.02	0.64	4.00	0
Sauar	Patmos 0	<2002	5.61	12.46	0.60	0.07	0.14	4.32	3.00	0
	Patmos 1	<2002	4.16	12.38	0.77	0.00	0.14	3.28	3.50	0
	Patmos 2	<2002	3.00	7.71	0.70	0.01	0.04	3.28	3.25	0
	Patmos 2a	2007	2.37	6.55	0.73	0.02	0.08	2.76	-	0
	Patmos 3a	2004	3.91	9.36	0.75	0.13	0.17	2.28	3.33	0
	Patmos 3a	2007	3.77	9.11	0.77	0.08	0.15	2.12	-	0
	Patmos 5	<2002	4.53	8.60	0.50	0.21	0.04	4.59	3.50	0
Straumen	Lunde 1	<1998	3.00	2.41	0.24	0.53	-0.05	1.38	3.00	0
	Lunde 1	2007	3.92	3.39	0.25	0.39	-0.11	1.93	-	0
	Lunde 2a	<1998	2.73	2.17	0.28	0.04	-0.22	1.02	4.00	0
	Lunde 2b	<1998	3.75	7.37	0.52	0.00	0.01	1.70	4.60	0
	Lunde 2b	2007	3.73	6.84	0.63	0.04	0.13	1.72	-	0
	Lunde 2c	2007	1.58	1.43	0.21	0.00	-0.30	0.42	-	1
	Lunde 3a	<1998	2.05	2.15	0.27	0.00	-0.26	0.70	3.33	0
	Lunde 4	<1998	6.87	13.70	0.57	0.11	0.06	2.89	3.71	0
	Lunde 4a	2007	4.36	10.40	0.66	0.04	0.13	2.34	-	1
	Lunde 4b	2007	4.65	8.80	0.60	0.15	0.07	4.10	-	1
	Lunde 5	<1998	6.11	13.06	0.56	0.10	0.02	7.67	4.89	0
	Lunde 5a	2007	2.28	5.29	0.59	0.00	-0.07	2.88	-	1
	Lunde 5b	2007	2.76	6.70	0.62	0.16	0.14	4.45	-	0
	Lunde 5c	2007	2.16	4.75	0.56	0.16	0.11	3.06	3.00	1
	Lunde 6	<1998	4.55	9.40	0.55	0.30	0.15	5.91	4.60	0
	Lunde 6	2007	3.93	7.07	0.49	0.31	0.10	4.19	-	0

Figure 2 (following pages): Map of a) Gvarv, b) Straumen and c) Sauar showing habitat within 40m of riverbank and outlines of territories. Green shows deciduous habitat. Grey shows matrix habitat. Dark shades of each represent low ground and light shades high ground. Territories do not overlap except at borders. Overlaping polygons therefore represent territories at different times.

Figure 2: a)

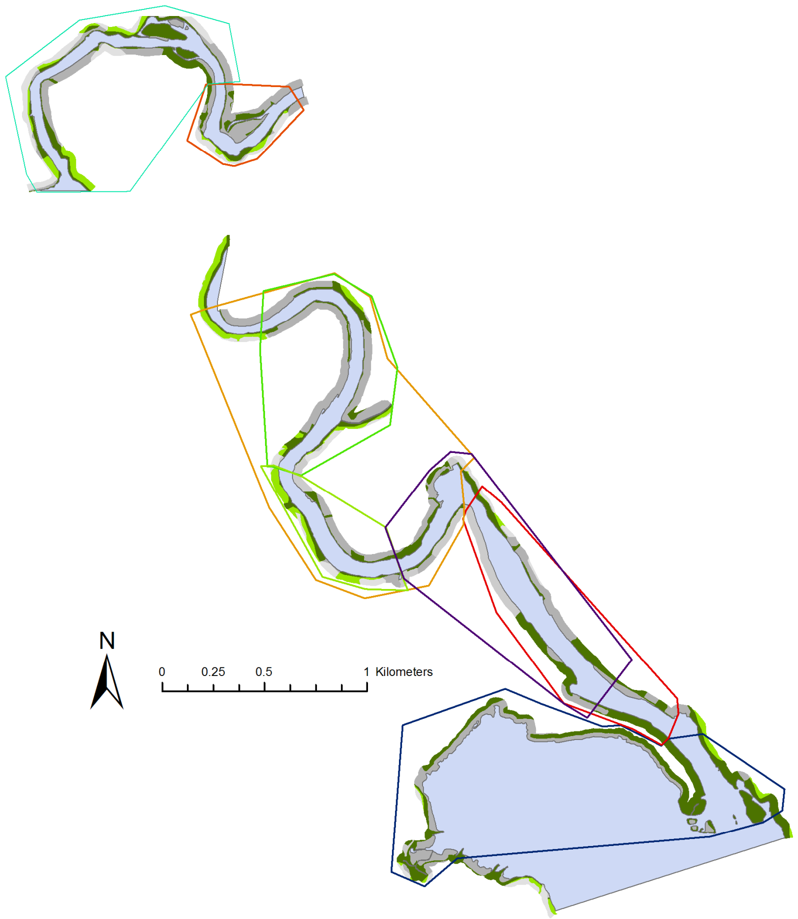


Figure 2: b)

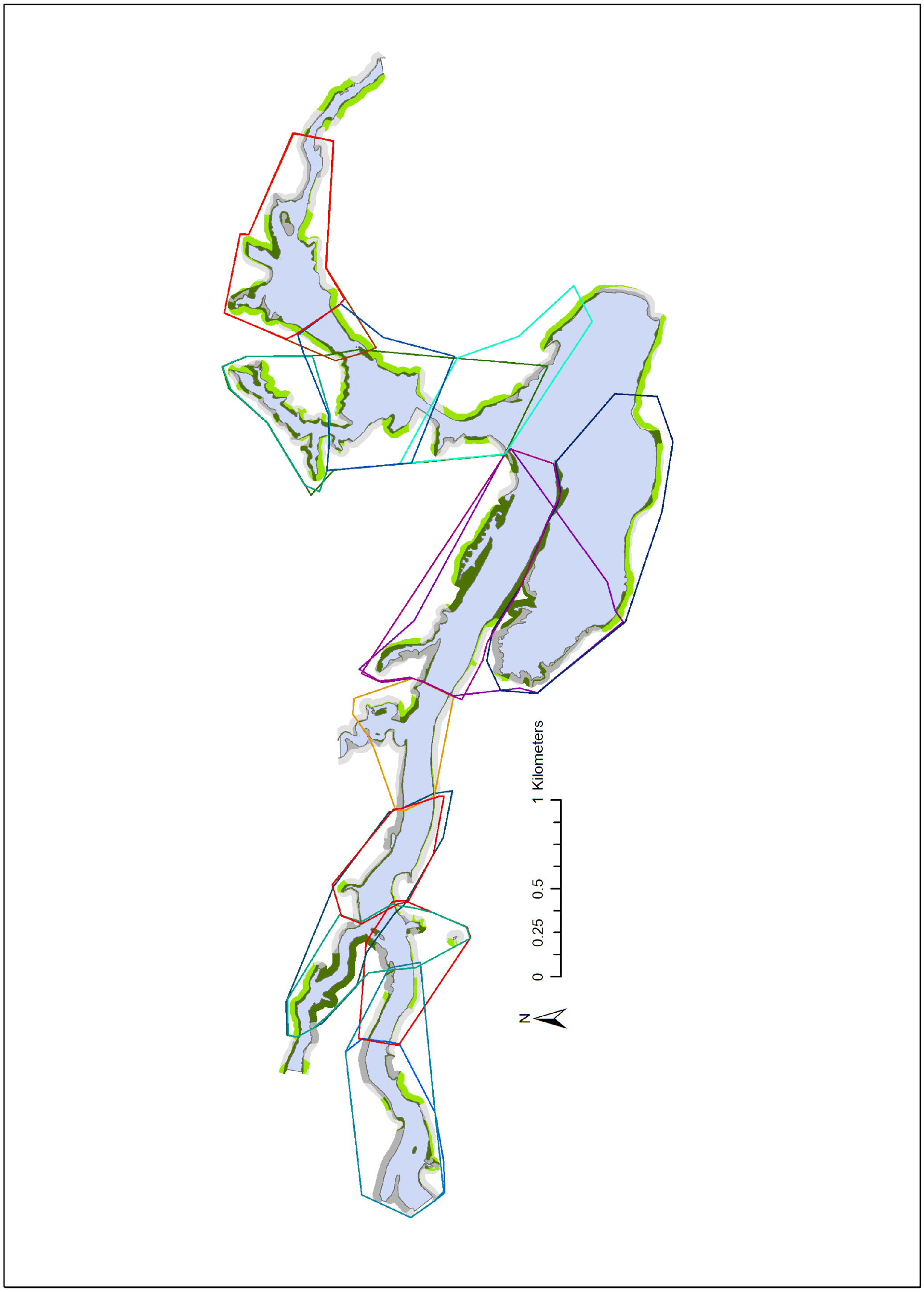
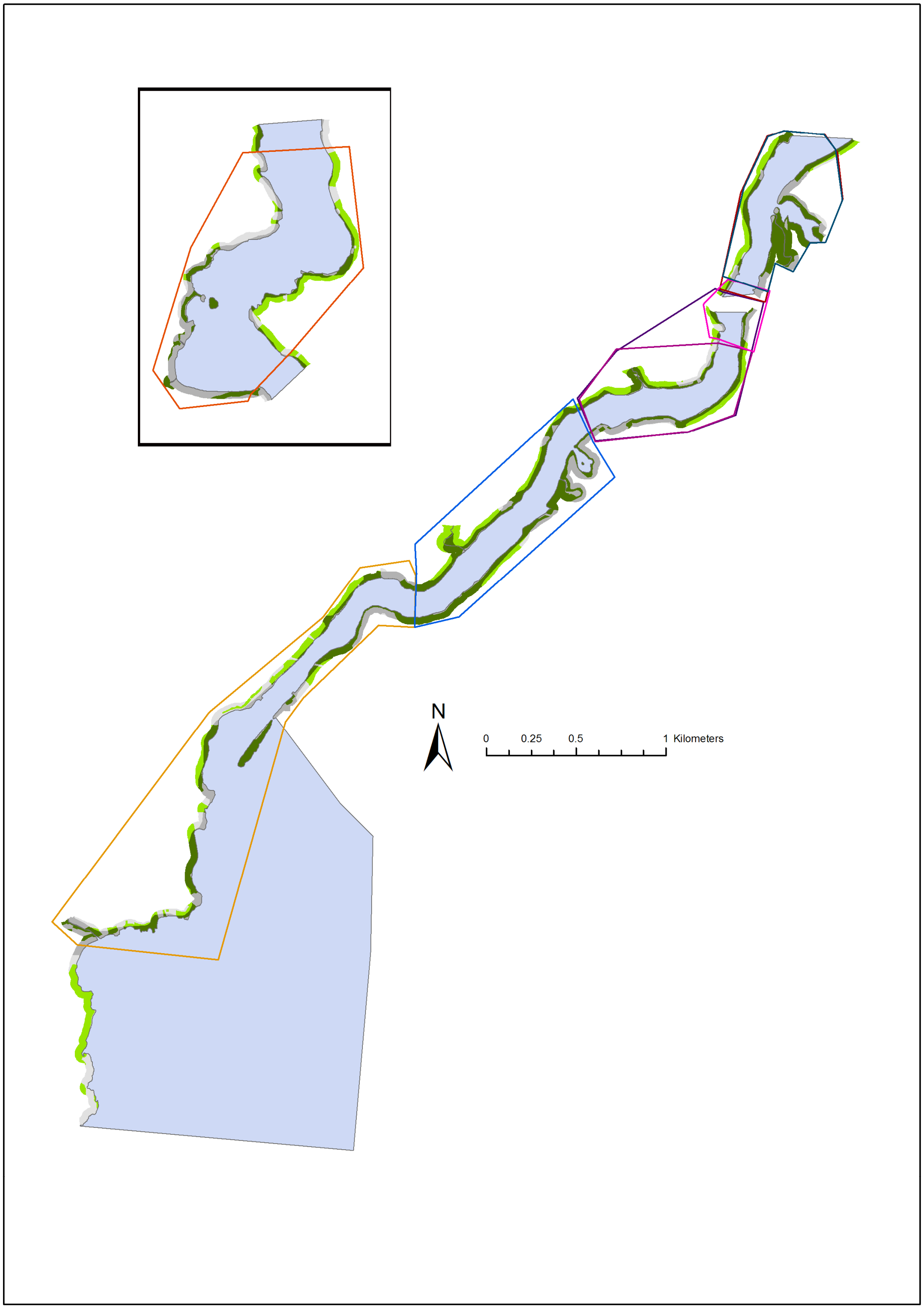


Figure 2: c)



Resource configuration and territory size

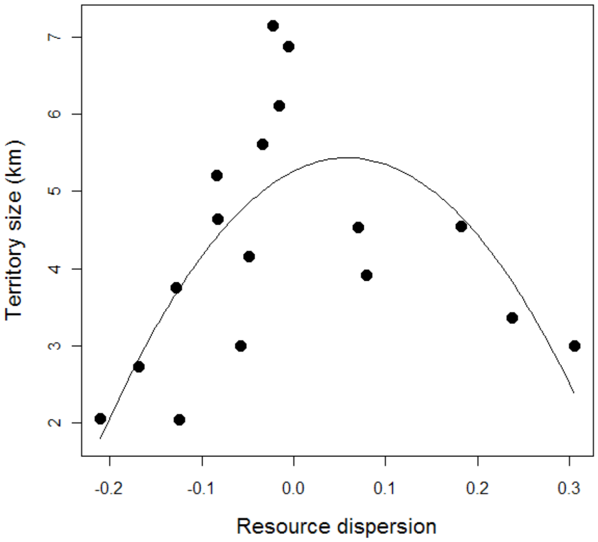
There was a tendency for the natural log (ln) of territory size to increase with *pdec* in the original groups, but this relationship was no more than indicative (r^2 = 0.139, df = 15, P = 0.078), and was less marked in the sample of new groups (r^2 = 0.049, df = 16, P = 0.190). Territory sizes in the old groups showed a significant quadratic relationship with resource dispersion (*rd*) (r^2 = 0.427, df = 14, P = 0.008) with the smallest and the largest territories exhibiting the lowest *rd* (Fig. 3a). In contrast, territory size in the new group showed a significant positive relationship with *rd* (r^2 = 0.2606, df = 16, P = 0.034 , Fig. 3b). Territory size in both groups was not related in a quadratic fashion to hilliosity (old: r^2 = -0.141, df = 14, P = 0.990, and new: r^2 = -0.069, df = 15, P = 0.643).

Territories that reduced in size between their original and new group status were, prior to the change, significantly larger than territories that remained stable (Welch t-test, t = -3.46, df = 15, P = 0.004), had significantly greater *pdec* (t = -2.37, df = 14, P = 0.032), but were not significantly different in terms of resource dispersion (t = -0.323, df = 12, P = 0.753). Territories in the new configuration were not significantly smaller (t = -1.923, df = 30, P = 0.064), did not have lower *pdec* (t = 0.333, df = 33, P = 0.741) and did not have different resource dispersion (t = -0.020, df = 30, P = 0.984) than for the old configuration.

Habitat quality and group size

Mean age at dispersal was 3.8 ± 0.6, and 3.0 ± 0.5 for territories in old and new configurations respectively. Variables retained in the model of group size were River, territory size *pdec*, and *q* (Table 2). Size of territory and *pdec* both showed positive effects on group size, though not significant at the 95% probability threshold. Habitat quality (*q*) on the other hand was significantly inversely related to group size (Fig. 4).

a): old group



b): new group

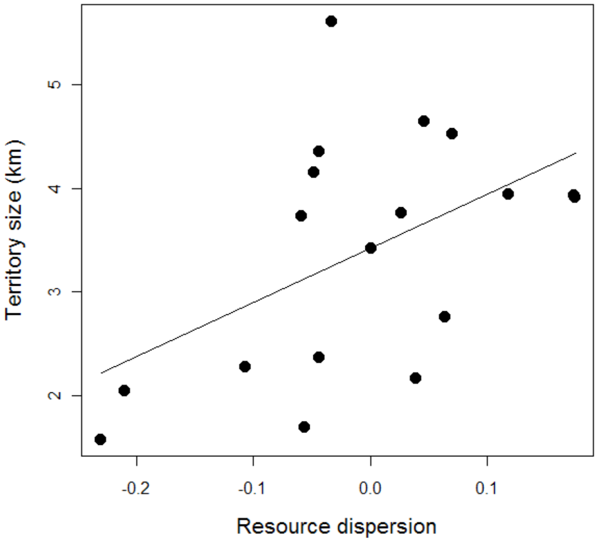


Figure 3: Relationship of territory size with resource dispersion in a) the old territory configuration and b) the new territory configuration.

Table 2: Summary of parameter values and statistics for the best fit GLM that explains propensity to stay (mean age at dispersal).

	Estmate	SE	df	F	P
intercept	4.408	1.191			
River			2,17	2.502	0.118
Tsize	0.120	0.092	1,16	3.784	0.072
pdec	2.115	1.208	1,15	3.269	0.092
q	-0.056	0.023	1,14	5.826	0.030

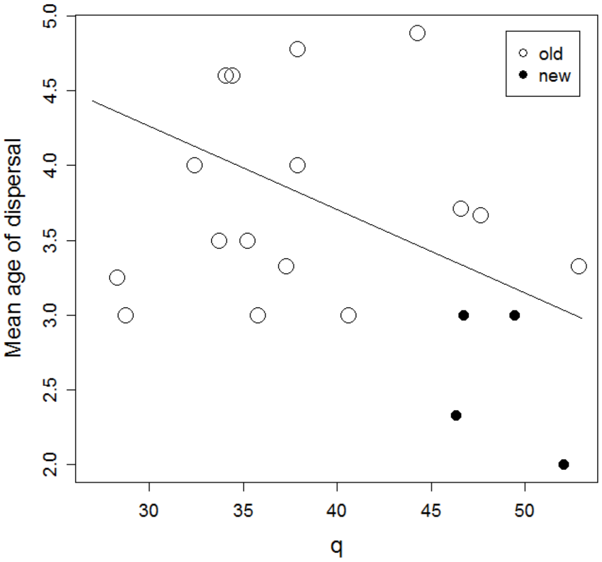


Figure 4: Influence of mean patch quality (*q*) on group size (the mean age of dispersal by offspring). Fewer data were available from new territories due to their being insufficient time for offspring to mature and disperse.

Discussion

All territories had a similar proportion of a key habitat, deciduous woodland, irrespective of their size. Territory sizes increased with resource dispersion under the new configuration. In contrast, however, territories in the old groups showed a quadratic relationship with territory sizes initially increasing with resource dispersion and then declining as resource dispersion increased further (Fig. 2a). Moreover, the largest territories exhibited moderately low resource dispersion. Mean age of dispersal was inversely related to habitat quality, though it was positively related to resource availability in that larger territories and those with a higher proportion of deciduous habitat showed a weak (no significant) trend to later dispersal.

Territoriality

Campbell *et al.* (2005) in finding that larger territories also had proportionately more resources (deciduous habitat) argued that these larger higher quality territories were maintained due to settlement pattern, with early arrivals claiming bigger and better territories and defending these successfully against subsequent claimants. This pattern was accordance with a value asymmetry for territory owners and intruders (Maynard Smith 1976; Tobias 1997). Assuming that an economic configuration for territories is to encompass sufficient resource patches, with more dispersed patches resulting in larger territories (*sensu* RDH, Macdonald 1983), our findings of a few larger territories also showing low resource dispersion is in agreement with Campbell *et al.* (2005). Knapton and Krebs (1974) reported in song sparrows (*Melospiza melodia*) in linear habitat that removal of individuals resulted in a reconfiguration of territories, with new owners obtaining smaller territories within the area of the original larger territories. Here was see a similar situation: death of some territory holders in combination with fission of two other territories from within has allowed a repacking of territories so that the new configuration is more economical (*sensu* the RDH, Macdonald 1983). It is notable that the largest territories with the most resources (proportionately and therefore absolutely) were the ones most likely to contract. This contraction indicates that beaver territory borders are more flexible than Campbell *et al.*'s (2005) suggested.

The quadratic relationship of size with resource dispersion in the old configuration was largely due to two territories, Nordsjø 1 and Lunde 1 (see table 1). These results would suggest that these territories were of low quality and it is notable that both territories expanded during the reconfiguration. Nevertheless, though Lunde 1 exhibited very low reproductive success over the course of the study with only one kit detected in nine years (c.f. area mean of 0.9±0.8 kits / year, Campbell *et al.* 2005), Nordsjø 1 exhibited very high reproductive output with eight kits detected in five years. This indicates that other factors are important in dictating demographic parameters in beaver territories. Nordsjø 1 was also the only territory in the study area to build canals, which would have allowed group members access to resources further inland than the habitat surveys covered.

Offspring retention

The relationship of age of dispersal and mean percentage shrub layer cover is unexpected. However, as is common in studies which attempt to equate habitat quality with use and population density, we are potentially faced here with an inversion in causality. It is reasonable to argue that habitat quality is lower in territories where offspring stay longer is because increased philopatry results in greater depletion of resources (Brown 1982). This result may therefore indicate a cost of nepotism. The positive effect of territory size and proportion of deciduous habitat, though below significance, does indicate however that territories which are both large and contain a high proportion of suitable foraging habitat will be more likely to retain offspring. In chapter 4, I found that territory quality measured as area of each habitat multiplied by its mean percentage shrub layer cover, and summed over all patches within the territory (a measure which equates to the total resource availability, and not the proportionate availability), had a positive effect on fecundity. Thus larger and richer territories show both greater production and slightly greater retention of offspring. In this context, we can argue that beaver territories were not 'uneconomical' under the old configuration. Instead, these results show that the value asymmetry in territorial conflict (Maynard Smith 1976; Tobias 1997) results in a disparity in the cost of obtaining a territory versus the cost of maintaining one.

Conclusions

In summary, these results indicate that resource dispersion can play a significant role in dictating the size of beaver territories. Our findings also indicate however that under certain conditions, social factors such as settlement history can lead to a breakdown of 'economic' models of territoriality, though in a wider sense, the resulting territory configuration is not uneconomic. Thus, not all beaver territories are equal. Resource dispersion and mean patch quality does not appear to play a role in philopatry in the beaver, similar to some predictions of RDH. Total availability of resources may influence delayed dispersal, but ultimately, our results show that such philopatry can cost nepotistic parents through resource depletion.

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Discussion

Summary of findings

In chapter 2, I established that juvenile beavers that were structurally smaller than same-age peers managed to narrow the gap in size by trading-off gain in body condition against a higher rate of size increase. Two questions remain from this analysis: Firstly, why size was more important than body condition and secondly, whether the loss in body condition had survival consequences. In chapter 3, I answered these two questions by establishing that structurally bigger beavers tended to obtain dominant breeding positions while low body condition was associated with lower survival. I was also able to establish that being very large and having a high weight for their size also lead to reduced survival probability, that is, stabilising selection was operating on structural size and bulk. Beavers therefore provide an interesting model for natural selection, in-so-far that selection on body size for reproduction and for survival do not match. In chapter 4, I established that after an initial increase in fecundity until the age of 4 – 6 years, female beavers showed reproductive senescence. Though the age of the father did not influence reproductive success, in both sexes the pattern of changes in body-condition with age matched the pattern of reproduction, with both body condition and fecundity initially increasing and then senescing. I also found that mothers in high quality territories showed higher fecundity, and a later peak in fecundity, while rainfall had a negative influence on fecundity for all ages equally. There was a trade-off between offspring quantity and quality for younger mothers (<7 years) but not for older mothers. Litter size did not change with age and I did not find a trade-off in fecundity from one year to the next. In chapter 5, my findings reiterated that rainfall affected fecundity negatively across the population, and furthermore that rainfall had a negative influence on body weight in all age-classes except subadults. I examined growth-rings in Grey alder trees and established that in areas close to water level (<0.5m), high rainfall suppressed tree growth; plausibly as a result of root waterlogging; thus resolving a potential mechanism for the counterintuitive negative effect of rainfall on beaver body weight and fecundity. I also found that cold winters reduced the body weight in young (<2 year old) beavers and a rapid spring green-up (phenological changes in plant growth) associated with a warmer spring temperature reduced adult body weight slightly. In chapter 6 I established that the variability of weather had an effect at least as important as that of absolute weather on survival and recruitment (a corollary of fecundity). In particular, I found that survival of the beavers in the study area was positively influenced by low variability in both daily rainfall and daily air temperature, though the effect of mean rainfall appeared to be positive, possibly as a result of covariance within the model. Recruitment was positively influenced by high seasonal amplitude in air temperature, low mean rainfall and low variability in daily air temperature. Finally, in chapter 7, I established that abrupt changes in the configuration of beaver territories in the study area, due to mortality of incumbent owners and fission from within the territory had resulted in a repacking of territories: Prior to the changes, not all territories conformed to 'economic' configurations relating to resource availability and distribution. It was notable that several territories were large than two were small relative to other territries with simlar resources. After repacking, where larger territories contracted more than smaller ones, territories tended to conform to a model of resource distribution whereby larger territories contained more dispersed resources. I furthermore established that the quality of habitat was lower in territories where offspring were more inclined to philopatry, indvating that nepotism carries a cost in beaver families.

Growth rates

In any species where competitive ability is related to skeletal size, investment in structural growth may be favoured over the accumulation of energy reserve tissues. Where lower reserves equate to lower survival probability, one might infer that individuals would choose to invest in energy reserves in order to enhance their prospects for survive. The biological imperative of reproduction, however, can lead to risk-taking strategies in order obtain that crucial opportunity to procreate and beavers are an exemplar of such: larger animals are more likely to obtain breeding positions and so juveniles invest in size growth even though the resulting lower body condition increases mortality risk. In addition, it appears possible to be over-large, with the largest and bulkiest individuals suffering higher mortality. There is then stabilising selection on size and bulk through their impacts on survival, but directional selection towards larger size through the probability of obtaining the imperative breeding opportunity. This fundamental disparity between survival and the likelihood of reproduction provides an interesting insight into natural selection: selection acting against these large animals may offset evolution towards larger size, such that those individuals who go on to form the greater portion of the reproductive population are a second tier of the “largest of the medium-size” individuals, while the largest, in a “charge of the large brigade” fail to survive. The best strategy for a beaver under these circumstances is to be average, but not mediocre.

The implication for our life-history paradigm research is that, since variation in size is reduced by increased investment in size-growth by smaller beavers, the impacts of specific external factors [on the beaver] should be investigated using body weight, or condition, and not body length. Compensation in size was not prefect however, and therefore poor body-conditions during development that reduced body size not only increased mortality risk as the individual attempted to gain size, but also handicapped the individuals later, in adulthood, by reducing the chance that they would obtain a breeding position. Since it was size and not weight that was compensated, the wider implication of this result is that when testing for the affects of compensatory growth, size *per se*, and not just weight (e.g. Solberg *et al.* 2004), is crucial. For example, in polygynous species, a body of evidence dictates that we would predict that females would exhibit weight compensation but males would exhibit size compensation since body condition may affect fecundity in females and larger size may influence the ability of the male to protect females from other males (Clutton-Brock *et al.* 1978; Jarman 1983; Festa-Bianchet 1998; McElligott *et al.* 2001). Evidence of cohort effects, or correlation between time intervals, on body-weight and size have been used by some studies as evidence militating against compensatory growth (e.g. Keech *et al.* 1999; Solberg *et al.* 2008). Conversely, we observe from the beaver that compensatory growth can be imperfect and so cohort effects may still occur despite growth compensation.

Reproduction

Reproductive senescence in the beaver may be more widespread than has been previously reported (Henry and Bookhout 1969; Payne 1984). Longitudinal studies, such as the one presented here, are free from the assumptions that can confound studies of reproductive senescence in cross-sectional studies. For example, cross-sectional studies are subject to a tautology where the signal of senescence can be masked by unequal mortality in high and low quality mothers where only high quality mothers, who may also have higher fecundity, survive to old age.

Many of the predictions of the mechanisms of reproductive senescence are similar. Thus empirical tests of the operative mechanisms are difficult in correlative studies on wild populations. For example, both the maternal experience hypothesis and the disposable soma hypothesis predict an initial increase in fecundity with age while both the antagonistic genetic pleiotropy hypothesis and the disposable soma hypothesis predict a decline in fecundity later in life. Nevertheless, with assiduous analysis, disentangling this evidence is still feasible. The maternal experience hypothesis alone predicts that both body condition and fecundity increase with age initially in the beaver. Furthermore, territory quality influences the resources available to mothers over their entire reproductive lives so that mothers in different territories will have had different nutritional histories. In contrast, ephemeral effects, such as rainfall, will affect all mothers more or less equally. Therefore only the disposable soma hypothesis predicts that the effect of territory quality should interact with the mother's age while rainfall does not. Conversely, the antagonistic genetic pleiotropy hypothesis predicts that senescence has the potential to occur in all animals irrespective of territory quality and reproductive history. Therefore, the finding that mothers in low quality territories senesced earlier than those in high quality territories refutes the antagonistic genetic pleiotropy hypothesis. The maternal experience hypothesis predicts an improvement in the reproductive capacity of the mother with age and the disposable soma hypothesis predicts an increase in reproductive investment with age. Both hypotheses therefore predict that fecundity will increase with age. Thus, the finding that only younger mothers showed a trade-off between offspring quantity and quality then lends support to either hypothesis: older mothers, despite not showing a tendency to increase litter size with age, are more able to, or investing more in larger litters. That there could be a current-future offspring trade-off in fecundity in operation also warrants evaluation, since I determined that senescence occurred earlier for mothers in low quality territories, i.e., the greater reproductive investment by these mothers caused a more rapid accumulation of damage and therefore earlier senescence. Proximally, no such trade-off was evident, allowing us to refute this possibility, since reproductive success in the previous year did not influence fecundity.

The life-history implications of these findings (for the beaver) are that securing a high quality territory is imperative. For males, securing a young mate is also a prudent strategy. In conclusion, antagonistic genetic pleiotropy is not required to explain senescence. although several or all of these mechanisms could operate in tandem to cause senescence, Occam's razor dictates however that we discard the antagonistic genetic pleiotropy hypothesis.

Effects of weather

Before beginning a discussion of the impacts of weather on beavers, I will consider briefly the use of some the different variables in the analyses. In chapter 5, body weight was used as an indicator of the impact of the environment on the population, while in chapter 6, survival rates were employed. Both body weight and survival rates, as indicators of environmental impacts on a population, have their strengths and weaknesses: Using body weight makes the assumption that low body weight has fitness consequences – though there is evidence presented in chapter 3 that this assumption is reasonable. Using survival as the indicator runs the risk; in open populations, that dispersal out of the population will confound any true measure of mortality – though as I show in chapters 3 and 6, distinguishing and comparing age-classes with different expected probabilities of dispersal can aid in reducing this dilemma.

The negative impact on herbivores of rapid phenological development due warm spring temperatures is well established by studies of northern temperate ungulates (e.g. Wilmshurst *et al.*1995; Langvatn *et al.* 1996; Mysterud *et al.* 2001). Our finding that warm spring temperatures similarly influence body weights of adult beavers (though the effect was weak), indicates that this effect can be generalised across herbivores. That cold winter temperatures reduced the body weight of juvenile beavers was also as expected (Wunder 1975; Karasov 1986): the implication being that the mortality risk from increased investment in size growth over weight gain in juvenile beavers (chapter 2) is greater in colder winters. That higher rainfall during the growing season reduced, instead of increased, body weight of all age classes (except subadults) and also reduced fecundity in subsequent years was more surprising and required further analysis to arrive at a viable mechanism. Tree growth rings fortunately provide historic records of vegetation growth. Analysing cores from the food tree species used most commonly (though not most favoured) showed that trees growing near water level grew less in wet years. We hypothesis that reduced growth of forage plants near water in wet years underscores the negative effect of rainfall. Beaver could forage further away from water in wet years, but this strategy would carry an increased risk of predation (whether real or apparent, Byers 1998; Hilton *et al.* 1999) and thus in wet year beavers may continue to feed on lower quality forage nearer to water. It seems that the best territories could contain a mix of high- and low-lying land near water facilitating the most optimal foraging – i.e. these territories would allow foraging on high land in wet years and low land in dry years. The wider implication of this result is that the availability of low and high ground may also correspond with the influence of rainfall variation for other herbivore populations. Environmental variability transpires as an important factor in life-history and demography (Drake *et al.* 2005; Boyce *et al.* 2006; Tuljapurkar *et al.* 2009; Dalgleish *et al.* 2010; Macdonald *et al.* In press; Nouvellet *et al.* submitted).

Compared with the effects of changes in mean weather values, the mechanisms responsible for the effects of weather variability are more difficult to conceptualise. Plausibly the mechanism underscoring the negative effect of rainfall variability on survival operate through effects on forage availability where high rainfall events lead to waterlogging and consequent lower growth of riparian vegetation, while more frequent moderately wet days characteristic of low rainfall variability provide moisture without waterlogging and thus promote riparian plant growth (chapter 5 & 6). The positive effect of seasonal amplitude in temperature may relate to cooler spring weather in years with higher amplitude, with the consequences for the rate of phenological development discussed earlier. The cause of the negative effect of daily temperature variability on both survival rate and recruitment is, on the other hand, particularly difficult to conceive. For example, the effect may be due to variation in forage quality. Jensen's inequality in isolation seems unlikely since there is no evidence that the effect of weather on the beaver is anything other than linear (chapter 5).

Conclusions

Attempts to understand the ontogeny and maintenance of life history traits are still in their infancy (Roff 1992) and there is, as yet, no comprehensive and parsimonious theory of life history evolution. This may be due, in part, to life history strategies resulting from a complex synthesis of interacting factors that include age at maturity, body size, the schedule of fertility with age, senescence rate and lifespan (Roff 1992). The matrix in which this synthesis- unfolds consists of environmental variables (climate and habitat) and inter-specific interactions that characterise the specie's niche and, to which, through its evolutionary history, it has adapted (Stearns 1992). Throughout this thesis, I have been forced to recourse to specific aspects of the biology of the beaver in order to explain the observed patterns in the relationships I found. The greatest limitation then to the resolution of a generalised life-history theorem is therefore that niche parameters are defined by different characteristics between species.

Trade-offs are fundamental to life-history concepts, where the species niche is characterised by optimal resolutions to constituent parameters (Roff 1992; Stearns 1992; Charnov 1993). Three of the chapters in this thesis (chapters 2 – 4) dealt specifically with trade-offs and their consequences. From examining growth trade-offs in the beaver, I found that, in iteroparous species with determinate growth, the foremost life history decision may be whether to grow faster and thus be more competitive but risk greater mortality probability, or to grow more slowly, with enhanced survival prospects (conservation of soma) but at the risk of impaired reproductive opportunity, indeed perhaps never reproducing. The optimal resolution will also hinge on the strategy adopted by other individuals in the population, however, in this focal beaver population the optimal resolution appeared to be to grow fast, but not 'too fast'. Trade-offs also operate in reproductive decisions in the beaver: I found a trade-off between reproductive effort and somatic maintenance that dictated the trajectory of reproduction over the lifetime of the animal and its investment in number and quality of offspring, thus highlighting the more general point that trade-offs are irrefutably at the core of their life history decisions.

Trade-offs can indeed be found operating through the rest of the chapters in this thesis: A trade-off in the development and maintenance of the digestive system versus other somatic tissue results in digestive constraints (Hume 1989), the consequence of which is that individuals do less well in years where the quality of forage is low (chapter 5). This situation is exacerbated because beavers face a trade-off in foraging versus predation risk (Byers 1998), the resolution of which is that beavers are unwilling to forage further inland when riverside vegetation is poor (chapter 5). A trade-off in adaptation to varied environmental conditions (phenotypic plasticity) versus adaptation to more limited environmental conditions (canalisation) (Van Tienderen 1991), may lead to suboptimal decision making when the environmental conditions are variable (chapter 6). Finally, a trade-off between resource acquisition and defence, and its interaction with the dispersion of resources and settlement pattern dictates the size of beaver territories (chapter 7). Thus trade-offs are the most generally applicable concept we have to explain the variation in life-histories and, in their role as dictators of selection pressures on life-histories, are a significant factor in evolutionary ecology and population dynamics.

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Appendix 1

Ageing and body weight correction in the Eurasian beaver

Excerpt from Rosell, F., Campbell-Palmer, R. nd Campbell RD (in prep). Handling, marking and sample collection from Eurasian beavers (*Castor fiber*) without chemical immobilisation.

Introduction and Methods

Beavers can be assigned to an age class based on body weight. Smith & Jenkins (1997) reported that all age classes of *C. canadensis* gain body weight through spring, summer and autumn and, except for kits, will lose some body weight every winter. In our study site, the same pattern has been observed except that kits also appear to loose some body weight over winter (Campbell et al. submitted). Thus, capture data can confound both studies that use body weight as a predictor variable and those that classify age by weight. Therefore we use our trapping data from 1998 – 2006 to create body weight tables to age our animals. It is likely however that annual trends in growth rate will differ from other populations and accordingly, the accuracy of age classifications should be assessed if these tables are applied to other populations. In our study beavers are almost never trapped in winter (Dec – Feb) and body weight is lost outside our sampling window. Therefore, we only consider weight gain in each age class from spring to autumn. We split the data into 4 age classes: 0 year olds (kits), 1 year olds (yearlings), 2 year olds (subadults) and ≥3 year olds (adults). Kits are always significantly lower in weight than yearlings and therefore distinguishing between these age-classes is unambiguous. For example, the maximum recorded weight of a kit around day 200 (20th July, just after the time when kits first begin emerging from the lodge) was 4kg whereas the minimum recorded weight of a yearling around the same day was 7.5kg and by day 250 (10th Sept), no kit has ever been found to weigh more than 7kg and no yearling has been found to weigh less than 11kg (Fig. 1). To obtain growth tables, we conducted a linear regression analysis on day-of-capture (Day 1 = Jan 1st) versus body weights of all records of all animals. Due to size-dependent growth, growth rates are usually not linear across the lifetime of an animal (Kaufmann 1981) and the same hold true for the beaver (Campbell et al. submitted). However, because we are only considering growth separately within each age class from spring to autumn, growth rates over these shorter periods approximate a linear relationship with time (see Campbell et al. submitted) and therefore using linear regression is valid. Some individuals were measured more than once. To avoid autocorrelation, the traditional approach would have been to take the mean body weight and mean year-day for each individual within an age-class. However, this would bias the data towards the middle of the year with a consequent loss of information early and late in the year. To avoid this, we adopted a simplified model-averaging approach that involved splitting the data, analysing each set separately and then combining the estimates from each set. To split the data for model averaging, we created three datasets. All datasets contained all records of individuals that were only measured once within an age-class, plus one record from an individual with multiple records. Records were chosen for the first of the three datasets by selecting a record from each individual at random. For the second dataset, the record following the one used in the first dataset (or the first record if the previously used record was last) was selected. This was repeated for the third dataset except for individuals that had only two records within an age-class, where either of the records was selected at random. No kit was measured more than twice. Only five adult individuals and none from other age-classes had more than three records and therefore we stopped at three datasets. We then took the means of the linear regression lines and their

Table 1: Growth tables by date for the Telemark beavers. Figures in parentheses are upper and lower 95% CIs. All values were obtained from the mean predictions of three separate models.

Year-day	Date	Kit body weight (kg)	Yearling body weight (kg)	Subadult body weight (kg)	Adult body weight (kg)
70	11-Mar		6.8 (3.8 - 9.7)	13.5 (10.1 - 17.0)	18.2 (13.9 - 22.4)
80	21-Mar		7.2 (4.2 - 10.1)	13.7 (10.3 - 17.2)	18.3 (14.2 - 22.5)
90	31-Mar		7.6 (4.7 - 10.4)	14.0 (10.5 - 17.4)	18.5 (14.4 - 22.7)
100	10-Apr		8.0 (5.1 - 10.8)	14.2 (10.7 - 17.6)	18.7 (14.6 - 22.8)
110	20-Apr		8.4 (5.5 - 11.2)	14.4 (11.0 - 17.8)	18.9 (14.8 – 23.0)
120	30-Apr		8.8 (5.9 - 11.6)	14.6 (11.2 - 18.0)	19.1 (15.0 - 23.1)
130	10-May		9.2 (6.4 - 12.0)	14.8 (11.4 - 18.2)	19.2 (15.2 - 23.3)
140	20-May		9.6 (6.8 - 12.4)	15.0 (11.6 - 18.4)	19.4 (15.4 - 23.5)
150	30-May		10.0 (7.2 - 12.8)	15.2 (11.8 - 18.6)	19.6 (15.6 - 23.7)
160	09-Jun		10.4 (7.6 - 13.2)	15.4 (12.1 - 18.8)	19.8 (15.7 - 23.8)
170	19-Jun		10.8 (8.0 - 13.6)	15.6 (12.3 - 19.0)	20.0 (15.9 – 24.0)
180	29-Jun	2.9 (0.8 - 4.9)	11.2 (8.4 - 14.0)	15.9 (12.5 - 19.2)	20.2 (16.1 - 24.2)
190	09-Jul	3.1 (1.1 - 5.2)	11.6 (8.8 - 14.4)	16.1 (12.7 - 19.5)	20.3 (16.2 - 24.4)
200	19-Jul	3.4 (1.4 - 5.5)	12.0 (9.2 - 14.8)	16.3 (12.9 - 19.7)	20.5 (16.4 - 24.6)
210	29-Jul	3.7 (1.6 - 5.7)	12.4 (9.6 - 15.2)	16.5 (13.1 - 19.9)	20.7 (16.5 - 24.8)
220	08-Aug	4.0 (1.9 - 6.0)	12.8 (10.0 - 15.7)	16.7 (13.3 - 20.1)	20.9 (16.7 - 25.1)
230	18-Aug	4.2 (2.2 - 6.3)	13.2 (10.3 - 16.1)	16.9 (13.5 - 20.3)	21.1 (16.8 - 25.3)
240	28-Aug	4.5 (2.5 - 6.5)	13.6 (10.7 - 16.5)	17.1 (13.7 - 20.6)	21.2 (17.0 - 25.5)
250	07-Sep	4.8 (2.7 - 6.8)	14.0 (11.1 - 17.0)	17.3 (13.9 - 20.8)	21.4 (17.1 - 25.7)
260	17-Sep	5.1 (3.0 - 7.1)	14.4 (11.5 - 17.4)	17.5 (14.1 - 21.0)	21.6 (17.2 – 26.0)
270	27-Sep	5.3 (3.3 - 7.4)	14.8 (11.8 - 17.8)	17.8 (14.3 - 21.2)	21.8 (17.4 - 26.2)
280	07-Oct	5.6 (3.5 - 7.7)		18.0 (14.4 - 21.5)	22.0 (17.5 - 26.4)
290	17-Oct	5.9 (3.8 - 8.0)		18.2 (14.6 - 21.7)	22.1 (17.6 - 26.7)
300	27-Oct	6.2 (4.0 - 8.3)		18.4 (14.8 - 22.0)	22.3 (17.7 - 26.9)
310	06-Nov	6.4 (4.3 - 8.6)		18.6 (15.0 - 22.2)	22.5 (17.8 - 27.2)
320	16-Nov	6.7 (4.5 - 8.9)		18.8 (15.2 - 22.4)	22.7 (17.9 - 27.7)

95% CIs over the three datasets to arrive at our predicted body weights and their 95% CIs. Thus, the information from the repeated measures was retained without biases from a few frequently measured individuals and without underestimating the confidence intervals around the predictions. Growth tables for kits, yearlings and subadults were obtained from data on animals that were initially trapped as kits, and thus were of known age. Using these tables, we then distinguished animals that were yearlings when first trapped from animals that may have been older. We then added these animals first trapped as yearlings to the dataset of animals first trapped as kits to obtain growth tables for subadults and adults. Females that were in a dominant breeding position were excluded from the analysis of adult body weight since pregnancy is likely to influence body weight and its relationship with year-day. The 95% CIs of the linear regression are then used to assign a newly trapped animal to an age-class. An animals whose weight is within the 95% CIs of >1 age-class on first being trapped cannot be assigned to an age-class until the minimum age is three. In our population, this most often occurs late in the year where animals fall between the two-year and adult age classes (N=27) but occasionally occurs for animals that fell between the yearling and two-year age-classes (N=3).

To assess whether body weight was influenced by sex and therefore separate growth tables for each sex would be required, we analysed the effects of sex on body weight and its relationship with year-day in each age-class using a linear mixed model (LMM) with a Gaussian error structure with an identity link function, using the function *lmer* in the R package *lme4* (v. 0.999375-32 in R 2.9.2; Bates and Maechler 2009; R Development Core Team 2009). We began with the explanatory variables of sex and year-day and a sex × year-day interaction and we included random intercepts for individual ID. We then reduced this full model to its minimum adequate model (MAM) using single-term deletion, starting with the interaction term. Terms were discarded if they did not improve

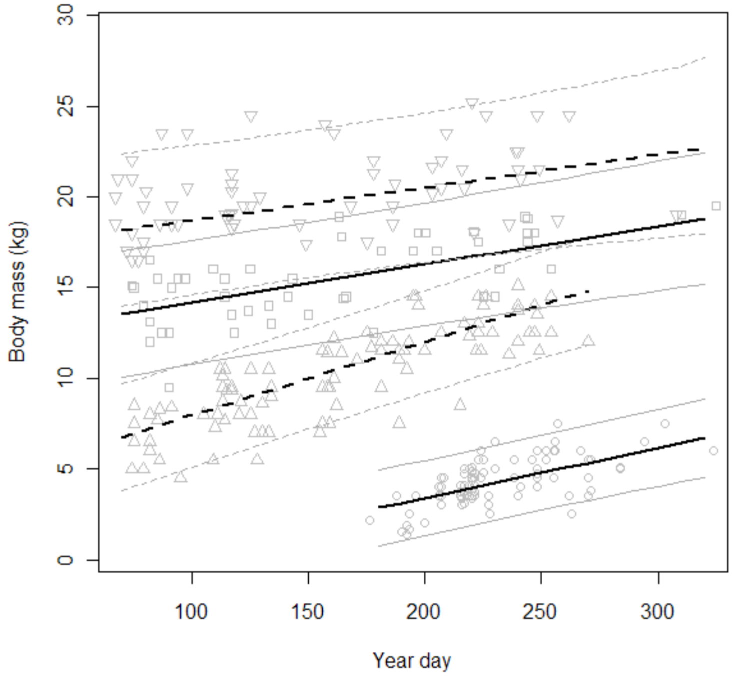

Figure 1: Relationships between body weight and year-day in the beaver. Symbols are circles = kits, triangles = yearlings, squares = subadults and inverted triangles = adults. Regression lines (black) and the 95% CIs of the predictions (grey) are from averages of three models and are solid for kits and subadults and dashed for yearlings and adults.

the explanatory power of the model. Explanatory power was assessed using Akaike's information criterion (AIC, Burnham and Anderson 2002) and standard likelihood-ratio tests. Following the principle of model parsimony, a model term was considered to be extraneous firstly if its removal resulted in a model with a lower AIC and secondly, in situations where the AIC of the more parsimonious model was higher, if the likelihood-ratio test between the two models indicated that the higher AIC was not significantly different ($p > 0.05$) from the earlier model. We estimated 95% CIs from a Markov Chain Monte Carlo (MCMC) sample (n = 10,000) from the posterior distribution of each parameter estimate and calculated *p*-values of parameters in the LMM directly from the

Table 2: Growth rates (kg day^{-1}) in each age-class within years obtained from the averaged regression models and a linear mixed model (LMM) with random intercepts for individual ID. Effects of sex were dropped from the models and so values are for both sexes combined. 95% CIs and *p*-values were obtained from Markov Chain Monte Carlo (MCMC) samples (n = 10,000) of the posterior distribution of the parameter estimates.

		Average regression estimate	LMM estimate	MCMC lower	MCMC upper	MCMC *p*
Kits	Intercept	-2.096	-2.458	-4.155	-0.659	0.010
	Year-day	0.028	0.029	0.021	0.036	<0.001
Yearlings	Intercept	3.922	3.684	2.440	4.962	<0.001
	Year-day	0.040	0.042	0.035	0.050	<0.001
Subadults	Intercept	12.061	12.042	10.746	13.263	<0.001
	Year-day	0.021	0.021	0.015	0.030	<0.001
Adults	Intercept	16.888	18.163	17.181	19.411	<0.001
	Year-day	0.018	0.012	0.006	0.018	<0.001

MCMC 95% CIs instead of from the z distribution using the R package *languageR* (v.0.955 in R 2.9.2; Baayen 2009).

Results and Discussion

From the averaged regressions, all age classes exhibited a linear increase in body weight across spring to autumn (Table 1, Fig. 1). Yearling can be difficult to distinguish from subadults late in the year while subadult and adult animals can be difficult to distinguish by body weight through-out the year (Fig. 1). After excluding dominant adult females, which may be pregnant, the sex × year-day interaction and then the sex were dropped from the MAM LMM in every age-class, indicating that sex did not influence body weight or the rate of increase in body weight over the year in any age-class. Year-day was retained in all MAMs. In agreement with the averaged regression models, the MAM LMMs found that body weight in all age-classes increased within each year (Table 2). The averaged regression model predicts lower intercept and a steeper slope of year-day for adults than the LMM indicating that using our growth tables may result in a higher risk of subadult animals trapped early in the year being unclassified.

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