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Factors affecting fertility of red deer  
(*Cervus elaphus*) females in north-eastern Poland

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Czynniki kształtujące płodność samic jelenia  
(*Cervus elaphus*) w północno-wschodniej Polsce

Rozprawa doktorska w zakresie nauk biologicznych  
w dyscyplinie biologii

Praca wykonana w Instytucie Biologii Ssaków  
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## Streszczenie

Celem badań, przeprowadzonych w Puszczech Augustowskiej, Knyszyńskiej i Białowieskiej (północno-wschodnia Polska) w latach 2006-2011, było określenie parametrów rozrodczych samic jelenia szlachetnego (*Cervus elaphus*) oraz czynników kształtujących ich płodność. Parametry rozrodcze określono w oparciu o analizę narządów rozrodczych samic. Łącznie we wszystkich objętych badaniami kompleksach leśnych zebrano 541 prób. W porównaniu z innymi europejskimi populacjami, jelenie w badanych kompleksach leśnych występowały w niskich zagęszczeniach, łanie wykazywały duży potencjał rozrodczy, który był wyrażony wysokim poziomem płodności (85%), wczesnym przystępowaniem do rozrodu (1,5-letnie samice) oraz brakiem spadku płodności z wiekiem. W skali biogeograficznej wykazano, iż poziom płodności łań był ujemnie skorelowany z zagęszczeniem populacji. W północno-wschodniej Polsce prawdopodobieństwo płodności samic wzrastało z ich wiekiem i kondycją. Czynniki środowiskowe (niskie temperatury i obfite opady latem) mogły mieć pośredni, negatywny wpływ na płodność poprzez kondycję samic. Wśród płodów wykazano większy udział płodów męskich (1:0.68). Zależne od wieku różnice w kondycji fizycznej samic wykazywały tendencję, w której łanie w lepszej kondycji fizycznej miały większy udział płodów męskich, co potwierdzałoby hipotezę Triversa Willarda. Poziom śmiertelności cieląt w pierwszych 6 miesiącach życia był wysoki (41%) i wzrastał wraz z wiekiem samic. Oczekiwana długość życia nowo narodzonych samic wynosiła 4,3 roku. Wykazano zbliżony, niezależny od wieku, poziom śmiertelności samic. Młode samice (1-3-letnie) miały największy wkład w rozrodczość populacji (46%). W latach badań rozrodczość bilansowała ubytki powodowane przez śmiertelność, dlatego przewiduje się stabilizację badanej populacji jeleni. Uzyskane wyniki mogą mieć praktyczne zastosowanie w zarządzaniu populacjami jelenia i planowaniu wielkości odstrzałów łowieckich.

## Słowa kluczowe

jeleń szlachetny, *Cervus elaphus*, płodność, rozrodczość, samice, zagęszczenie populacji, kondycja, proporcja płci, GIS, meta-analiza

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Factors affecting fertility of red deer (*Cervus elaphus*) females in north-eastern Poland



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## ABSTRACT

Reproduction of mammalian females plays a key role in the population dynamics. Reproductive performance, however, depends on the broad set of extrinsic (weather conditions, food availability, predation, parasites) and intrinsic (population density, age of an individual, body condition, prior reproductive activity) factors. The highest significance is attributed to food availability, which is the main determinant of females' body condition and their readiness for reproduction. Forage supply, on the other hand, is strongly dependent on the habitat quality and weather conditions.

The main aims of this study, conducted in Augustów, Knyszyn and Białowieża Forests (north-eastern Poland) in 2006-2011, were to quantify the reproductive parameters of red deer (*Cervus elaphus*) females and to determine the factors affecting their fertility. Furthermore, I aimed at assessing the role of the reproductive input in the observed population dynamics under the existing mortality level. Finally, I conducted meta-analysis of the published data to compare some reproduction parameters of deer females from NE Poland with the available literature on other European populations.

Reproduction parameters, body condition and the age of red deer females were determined based on 541 samples (female reproductive tracks and jaws) collected in the surveyed woodlands of NE Poland. Fertility of females was assessed by macroscopic examination of ovaries and uteri, while their age was determined based on tooth cementum. Body condition was described by two indices: dressed body mass and percentage of mandible marrow fat. In addition, information on the lactation status of hinds was obtained. Red deer population density in the studied forests was estimated based on drive counts. Environmental factors, which expressed habitat productivity and weather conditions were calculated in GIS from the available data sets (Corine Land Cover 2006, MODIS, GSDMap). Finally, the association between reproductive parameters and intrinsic and extrinsic factors was established by incorporating of the statistical techniques including: regression models, correlations, analysis of variance (ANOVA), and generalized linear models (GLMs).

Compared to other European populations, red deer in NE Poland occurred at relatively low densities (3.6-6.8 ind./km<sup>2</sup>), and hinds exhibited high reproductive potential, which was reflected in the high fertility rate (85%), low age of the first reproduction (1.5-year-olds) and lack of reproductive senescence. A clear negative effect of the population density on

the hind fertility rate was evidenced at biogeographic scale. The strength of density-dependence in female fertility rates decreased with females' age.

At the population level in the studied woodlands, the body condition and the fertility rate of yearling females was significantly lower compared to older age classes ( $p < 0.001$ ). Pregnant females had significantly higher body mass and percentage of mandible marrow fat than non-pregnant hinds ( $p < 0.001$ ). At individual level, probability of hinds to be fertile was affected by their age and body condition. The positive effect of the body mass declined with the mother's age, while the opposite relationship was proved for the mandible fat content – its effect increased with the age of hinds. The probability of fertility in yearlings was positively associated with the body mass. The probability of fertility in adult females (2-19-year-olds) increased with the growing percentage of marrow fat, and the effect of this factor increased with the female's age. Environmental factors (low temperature and abundant precipitation in summer) could have a negative, indirect effect on fertility through the body condition of females. The foetus sex ratio was male-biased (1:0.68). Age-specific differences in the body condition of pregnant females showed a tendency that females in better body condition had more males among foetuses, which supported the Trivers-Willard hypothesis. The mortality rate of offspring in the first 6 months of lives was high (41%) and positively associated with the mother's age ( $p = 0.02$ ). This could have been the first sign of the reproductive senescence in mothers.

Life expectancy of females at birth was low (4.3 years), which was most probably caused by a high level of mortality enforced by wolf (*Canis lupus*) and lynx (*Lynx lynx*), other natural factors and hunting harvest. The mortality rate was stable across the female age classes. Younger age classes (1-3 years old females) had the highest contribution to reproduction (46%). On average, females were supposed to produce more male than female offspring during the course of their lives. The reproductive potential of females balanced the losses imposed by mortality factors. Hence, the population of red deer in NE Poland is supposed to be stable. Findings of this study are expected to have practical significance in the deer management and decision making regarding hunting bags.

## ABSTRAKT

Rozrodczość samic ssaków odgrywa znaczącą rolę w kształtowaniu dynamiki populacji. Wydajność rozrodu zależy jednak od wielu czynników, zarówno zewnętrznych (warunki pogodowe, drapieżnictwo, pasożyty) jak i wewnętrznych (zagęszczenie populacji, wiek osobnika, kondycja, wcześniejsza aktywność rozrodcza). Największe znaczenie przypisuje się dostępności bazy pokarmowej, którą uznaje się za czynnik decydujący o kondycji samic oraz ich gotowości do rozrodu. Z kolei ilość i jakość dostępnego pokarmu jest ściśle związana z produktywnością środowiska oraz warunkami pogodowymi.

Głównym celem badań, przeprowadzonych w Puszczech Augustowskiej, Knyszyńskiej i Białowieskiej (północno-wschodnia Polska) w latach 2006-2011, było określenie parametrów rozrodczych samic jelenia szlachetnego (*Cervus elaphus*) oraz czynników kształtujących ich płodność. Dodatkowym celem była ocena wpływu rozrodu na obserwowaną dynamikę populacji jeleni w warunkach istniejącego poziomu śmiertelności. Na ostatnim etapie opracowania przeprowadzono meta-analizę danych publikowanych w celu porównania parametrów rozrodczych samic jelenia z północno-wschodniej Polski z parametrami innych europejskich populacji tego gatunku.

Parametry rozrodcze, kondycja oraz wiek samic zostały określone na podstawie 541 prób (narządy rozrodcze oraz żuchwy samic) zebranych w badanych kompleksach leśnych. Płodność samic określono przez makroskopowe badanie macic i jajników, natomiast wiek łań oszacowano w oparciu o kostniwo zębów. Kondycja samic została opisana dwoma wskaźnikami: masą ciała oraz stopniem otłuszczenia szpiku kostnego żuchwy. Pozyskano też informacje o występowaniu lub braku laktacji wśród pozyskanych łań. Zagęszczenia populacji jeleni w badanych kompleksach leśnych oszacowano przy zastosowaniu metody pędzeń próbnych. Czynniki środowiskowe, które wyrażały produktywność badanych środowisk oraz warunki pogodowe zostały określone w oparciu o dostępne zbiory danych (Corine Land Cover 2006, MODIS, GSDMap) przy zastosowaniu narzędzi GIS. Zależności pomiędzy parametrami rozrodu samic oraz wewnętrznymi i zewnętrznymi czynnikami zostały ocenione poprzez zastosowanie narzędzi statystycznych takich jak: modele regresji, korelacji, analiza wariancji (ANOVA) oraz zgeneralizowane modele liniowe (GLMs).

W porównaniu z innymi europejskimi populacjami, jelenie w badanych kompleksach leśnych północno-wschodniej Polski występowały w niskich zagęszczeniach (3,6-6,8 osob./km<sup>2</sup>), łanie wykazywały duży potencjał rozrodczy, który był wyrażony

wysokim poziomem płodności (85%), wczesnym przystępowaniem do rozrodu (1,5-roczone samice) oraz brakiem spadku płodności z wiekiem. Wykazano, iż w skali biogeograficznej poziom płodności łań był ujemnie skorelowany z zagęszczeniem populacji. Siła zależności pomiędzy poziomem płodności a zagęszczeniem populacji malała wraz z wiekiem samic.

Na poziomie populacji, w badanych kompleksach leśnych, kondycja oraz poziom płodności półtorarocznych samic był istotnie niższy niż starszych łań ( $p < 0,001$ ). Ciężarne samice miały znacząco wyższą masę ciała oraz poziom otłuszczenia szpiku żuchwy w porównaniu z nieciążnymi samicami ( $p < 0,001$ ). Na poziomie osobniczym, prawdopodobieństwo płodności samic zależało od ich wieku i kondycji. Dodatni wpływ masy ciała zmniejszał się wraz z wiekiem matki, natomiast odwrotną zależność stwierdzono w przypadku zawartości szpiku kostnego w żuchwach – jego wpływ zwiększał się z wiekiem łań. Prawdopodobieństwo płodności młodocianych (1,5-rocznych) samic było dodatnio skorelowane z masą ciała matki. Prawdopodobieństwo płodności dorosłych samic (2-19-letnich) zwiększało się wraz ze wzrostem poziomu otłuszczenia szpiku żuchwy, wpływ tego czynnika wzrastał z wiekiem łań. Czynniki środowiskowe (niskie temperatury i obfite opady latem) mogły mieć pośredni, negatywny wpływ na płodność poprzez kondycję samic. Wśród płodów wykazano większy udział płodów męskich (1:0.68). Zależne od wieku różnice w kondycji samic wykazywały tendencję, w której łanie w lepszej kondycji miały większy udział płodów męskich, co potwierdzałoby hipotezę Triversa-Willarda. Poziom śmiertelności cieląt w pierwszych 6 miesiącach życia był wysoki (41%) i wzrastał wraz z wiekiem samic ( $p = 0.02$ ). Można wnioskować, iż spadek przeżywalności młodych mógł być pierwszym objawem pogarszającej się z wiekiem kondycji łań.

Oczekiwana długość życia nowo narodzonych samic była mała (4,3 roku). Najprawdopodobniej było to spowodowane wysokim poziomem śmiertelności związanym z drapieżnictwem wilka (*Canis lupus*) i rysia (*Lynx lynx*) oraz innymi czynnikami naturalnymi, jak również pozyskaniem łowieckim. Wykazano zbliżony, niezależny od wieku, poziom śmiertelności samic. Młodsze klasy wieku (1-3-letnie samice) miały największy wkład w rozrodczość populacji (46%). W latach badań rozrodczość samic bilansowała ubytki powodowane przez śmiertelność, dlatego przewiduje się stabilizację badanej populacji jeleni. Uzyskane wyniki mogą mieć praktyczne zastosowanie w zarządzaniu populacjami jelenia i planowaniu wielkości odstrzałów łowieckich.

## 1. INTRODUCTION

Mammals allocate the assimilated energy for many interacting and competing demands, including reproduction (Bronson 1985, Kozłowski 1992). Allocation of the acquired resources for reproduction (offspring) depends on the body size and life style of mammals (Brown and Sibly 2006, Sibly and Brown 2007, Charnov et al. 2007). The increasing body mass of mammals causes a decrease in the mass-specific productivity due to the growing costs of resource transportation within a larger body (Sibly and Brown 2009). On the other hand, productivity is also related to life history traits such as diet and mortality. When allowing for body mass, mammals having access to better, more predictable food resources exhibit higher rates of productivity, whereas lower mortality results in the reduced productivity (Sibly and Brown 2009). Efficient allocation of resources for reproduction requires an optimal reproductive strategy balancing the trade-off between the number of offspring and their size (Charnov 2001, Schroderus et al. 2012). Among the mammalian species, the reproduction strategy changes with the increasing body size from frequent and numerous litters to infrequent litters of a few large offspring (Western 1979, Stearns 1983). Based on the r/K selection theory (MacArthur and Wilson 1967, Pianka 1970) all mammals can be divided into two groups: r-selected species – quickly reproducing small animals (large, frequent litters), inhabiting as many niches as possible (rodents), and K-selected species – slowly reproducing large mammals (infrequent, single or a few large offspring), which strongly compete within the exploited niche (ungulates).

After the effect of body mass is factored out, mortality level affects many life history traits of mammals, including their reproductive strategies (Promislow and Harvey 1990, Bielby et al. 2007). According to Charnov's model of mammalian life-history evolution (slow-fast continuum concept), individuals exposed to high, environment-dependent mortality live "fast", grow rapidly, try to reproduce and produce many small offspring during a short period. Whereas, mammals following the "slow" strategy have longer life expectancy, slower grow and reach larger sizes before mating and produce single large offspring (Charnov 1993, Oli 2004, Dobson and Oli 2007).

Sibly and Brown (2009) proved that the main driving factor determining the reproductive strategy is the pre-weaning vulnerability to predation, regardless of whether an eutherian mammal allocates resources between a few large and many small offspring in the same litter or between one large litter and many small litters in the same season. Based



on this assumption, they divided eutherian terrestrial mammals into three general groups. (1) Even- and odd-toed ungulates living in open habitats produce a few large (often single) precocial offspring at infrequent intervals in order to decrease the predation probability of newborn offspring. Therefore, survival of unprotected, born-on-ground young, basically depends on their size. Larger, better developed offspring mature faster, thus they are more capable of escaping predators and of better coping with thermoregulation requirements. (2) Mammals, which protect newborns in burrows or nests, such as fissiped carnivores, lagomorphs, rodents and insectivores, produce – at frequent intervals – large litters with many altricial offspring, the survival of which is not size-dependent. (3) The last group is represented by primates, sloths, anteaters and bats, which carry their neonates until the weaning time. These mammals produce a few offspring. At birth, they are developed enough to cope with thermoregulation outside and to hold their mothers. The number of neonates is limited by the transportation capacities of mothers.

If one focuses on ungulates only, species and their reproduction strategies can still be divided along the slow-fast continuum even after the effects of maternal body mass and common ancestry are factored out (Saether and Gordon 1994). Diverse reproductive strategies are observed among ungulates, from species producing many small offsprings in a short period (roe deer *Capreolus capreolus*: Mateos-Quesada and Carranza 2000, wild boar *Sus scrofa*: Servanty et al. 2007) to species investing a long time in a single large offspring (European bison *Bison bonasus*: Krasińska and Krasiński 2013). These differences were attributed to ungulate diet and landscape characteristics. Omnivorous ungulates and browsers have larger litters and smaller neonates compared to grazers. Most of the browsers give birth in browse-type habitats, which provide anti-predator shelter to cryptic multiple neonates. Grazers, which are mostly social animals living in large groups in open habitats, produce large precocial neonates able to follow a herd shortly after birth (Seather and Gordon 1994).

Reproduction strategies can also vary within mammalian species, because individuals can adjust their strategy to local and temporal variation in predictability and availability of food resources. The best examples are mammals living in seasonal environments breeding usually only once a year and changing their strategies into continuous breeding in years with favourable environmental conditions (Pucek et al. 1993, Bronson 2009). Bronson (1985) compared reproduction strategies within three mammal species belonging to different taxa (rodent, hare and deer) along a latitudinal axis. Interestingly, all groups of mammals showed

a clear seasonal pattern of reproduction in the northern part of their range and continuous reproduction in the southern part. This change was explained by increased thermoregulatory costs at low temperatures and thus shortage of spare energy that could be allocated for reproduction.

The other aspect of female reproductive strategies in mammals concerns the timing of energy investment in reproduction. For both domesticated and wild mammals, the age of the first reproduction is strictly correlated with the critical body mass of females, which increases the probability of ovulation and conceiving (Langvatn et al. 1996). Therefore, young females face the trade-off between the growth (investment in the vegetative body) and early reproduction bearing thereby reproductive costs of early breeding. And thus, the probability of survival should affect the time of the first reproduction. Females from the populations with high mortality rates (low expectation of life at birth) are supposed to breed as early as possible (Harvey and Zammuto 1985) even though it can decrease their future survival by depleting the body resources and lowering the subsequent reproductive success and may lead to reproductive senescence at the end of life (Kozłowski and Wiegert 1986, Reiter and Leboeuf 1991, Kozłowski 1992, Bérubé et al. 1999). The influence of early reproduction on the female survival can depend on the female body size: early reproduction did not affect the survival of the largest females but it had the most profound negative effect on mediocre females (bighorn sheep *Ovis canadensis*: Festa-Bianchet 1988). Another study reported a negative relationship between early reproductive success and longevity, which was attributed to the variation in female quality (bighorn sheep: Bérubé et al. 1999).

In ungulates, the body weight of females was proved to have a strong effect on the age of the first breeding, heavier females conceived earlier than the lighter ones (red deer *Cervus elaphus*: Hamilton and Blaxter 1980, roe deer: Gaillard et al. 1996, moose *Alces alces*: Saether and Haagenrud 1985, white-tailed deer *Odocoileus virginianus*: Verme 1969). Therefore, in some populations exposed to unfavourable environmental conditions reproduction can be considerably delayed (red deer: Langvatn et al. 1996, Proaktor et al. 2008). In wild mammal populations, the reproductive senescence is often difficult to observe due to a high level of extrinsic mortality, still there is evidence of senescence even in short-lived species (wild meerkat *Suricata suricatta*: Sharp and Clutton-Brock 2009). The breeding investments in ungulates at any point are supposed to influence their future reproduction by affecting the body condition (Stearns 1992). Therefore, the reproductive pattern of ungulates follows a bell-shaped curve – an increase after reaching the puberty,

stabilization in prime-aged females and a decrease at the end of life (Rose 1991, Gaillard et al. 2000, Nussey et al. 2006).

Regardless of the strategy, reproduction of mammalian females is affected by a similar set of environmental factors, such as food availability, weather conditions, the day/night or annual rainfall cycles and social cues (Bronson 1985, 1989, Demas and Nelson 1998). Food availability (quantity and quality) is of the highest importance as it shapes the body expenditures on different demands, including reproduction (Clutton-Brock and Harvey 1978, Wauters and Lens 1995, Bergallo and Magnusson 1999). Only females in good condition can afford reproduction. Weather conditions, i.e. ambient temperature and/or precipitation, influence the reproduction directly by affecting the thermoregulatory costs and indirectly by having an impact on food resources (Grindal et al. 1992, Wade and Schneider 1992). Since many mammals live in a seasonally changing environment (varying food availability), they are seasonal breeders (Bronson 2009). Their reproduction success is dependent on proper timing of parturition, i.e. the most energy-demanding period (lactation) should be synchronized with the highest availability of high quality food (Langer 2003). In order to prepare the body metabolically for a breeding season, they use different predictors, i.e. day/night (house mouse *Mus musculus*: Nelson 1990) or annual rainfall cycles (Ogutu et al. 2008). Social cues, such as exposure of female to stress, can decrease reproduction by affecting the ovulation via hormone discretion (Tilbrook et al. 2000).

In ungulates, the reproductive performance depends on female's reproductive conditions (Guinness et al. 1978a). Fertility is of prime importance to female ungulates as it is closely related to pre-ovulation body condition determining the probability of ovulation and conceiving (Mitchell and Brown 1974). For example, the body weight was a good predictor of pregnancy probability in red deer (Albon et al. 1983), roe deer (Gaillard et al. 1992), and moose (Saether and Haagenrud 1983). The observed differences in fertility of ungulate females between age classes most often reflected age-specific variation in the body condition (Albon et al. 1986). The fertility – body condition relationship is affected by a set of interactive factors: habitat quality, population density, lactation, and weather conditions. Adverse environmental conditions, such as poor habitat quality, high population density, cold and rainy summer, negatively influenced the female body condition and caused a delayed recovery from lactation (red deer: Albon et al. 1983, Loundon et al. 1983, Langvatn et al. 1996, Coulson et al. 2000). Association between the population density and fertility is explained by intraspecific competition for the limited supply of high quality

food resources. Clutton-Brock et al. (1987) reported the age-specific impact of population density on red deer female fertility: fertility of the first breeders was more affected by the density compared to adult females. Moreover, fertility of females is suppressed by high cost of lactation. In red deer population on the Isle of Rhum (Scotland) in the nutritionally poor environment, all breeding hinds lost weight during lactation compared to yield hinds and, as a consequence, they reproduced every second year. However, the effect was most pronounced in young and old hinds (Mitchell et al. 1976, Guinness et al. 1978a, Clutton-Brock et al. 1983).

The other aspect related to reproductive performance of ungulate females is the effect of maternal body condition on the offspring sex ratio. According to Trivers and Willard's (1973) hypothesis, the breeding success of males in polygynous ungulates is more varied compared to that of female. Thus sons of mothers in good condition should have higher fitness than daughters of females in the same conditions. Therefore, females in good condition are expected to produce sons even though the overall cost of raising sons is higher than daughters. The sex of offspring may be determined after the conception, based on a different level of maternal glucose – a higher level is supposed to promote male embryos. However, the competitive 'maternal dominance' hypothesis was put forward, which assumes the determination of the offspring sex ratio before the conception – a higher level of follicular testosterone may affect the development of an ovum pre-programmed to receive a spermatozoon with the Y-chromosome (Grant and Chamley 2010). Nevertheless, both hypotheses are not contradictory, factors affecting the sex ratio of fetuses pre- or post-conceptually can operate synchronously and complement each other (Grant and Chamley 2010). The studies on the correlation between the maternal condition and the offspring sex ratio across different species and study sites showed an increasing proportion of male offsprings with the improving mothers' condition (Sheldon and West 2004). The power of the relationship was study-related. The strongest correlations were found for surveys, where maternal condition was measured pre-conceptionally for species with longer gestation periods and a distinct male-biased sexual dimorphism (Sheldon and West 2004). In the red deer population, the sex of the offspring was determined by the maternal condition and the position of mothers in the herd hierarchy as well as the population density and weather conditions (Clutton-Brock et al. 1984, Gomendio et al. 1990, Kruuk et al. 1999).

The red deer populations studied in this project inhabit large, seminatural woodlands in NE Poland and are exposed to high mortality from both natural factors (predation

by wolves *Canis lupus* and lynx *Lynx lynx*, severe winter conditions), and the hunting harvest. Therefore, they provided an opportunity to study reproduction of females in relatively natural conditions compared to other European populations of the species. In my study, I have tried to identify the presence of density-dependent and independent mechanisms and their potential influence on the condition and reproductive parameters of females, such as the fertility rate, the age of the first reproduction, the presence/absence of reproductive senescence, and the foetus sex ratio. Moreover, the calculated parameters made it possible to assess the expected dynamics of the surveyed populations, which can constitute a valuable source of information for red deer management.

## 2. AIMS OF THE STUDY

The main aims of the study, conducted in Augustów, Knyszyn and Białowieża Forests (north-eastern Poland) in 2006-2011, and based on the material from harvested animals, were as follows:

- (1) to quantify the reproductive parameters of red deer females,
- (2) to determine intrinsic and extrinsic factors affecting the fertility of females,
- (3) to assess the role of reproductive input in the observed population dynamics under the existing mortality level.

The objectives of the study required the following specific tasks to be accomplished:

- description of the population status, habitat, and weather variables,
- determination of females' fertility, age and the foetus sex ratio,
- measurement of female body condition indices – the body mass and the percentage of mandible marrow fat,
- construction of life tables – survivorship and fertility tables.

The following hypotheses have been tested based on the analysis of the collected data:

- fertility of females is positively correlated with their body condition, and negatively with the population density and unfavourable weather conditions,
- fertility of females increases in young hinds, stabilizes in prime-aged females, and declines in old hinds,
- the improving body condition of hinds causes a higher proportion of males among foetuses,
- survivorship of fawns in the first months of life is positively associated with the mother's age, due to the increasing experience of females,
- mortality of the studied red deer populations is balanced by females' reproductive potential.

Finally, some reproduction parameters of deer females from NE Poland were compared with the available literature on other European populations. Meta-analysis of data was performed to find biogeographic patterns of variation in red deer fertility.

### 3. METHODS AND MATERIAL

#### 3.1. Study area

The study area covered three large forests (Augustów, Knyszyn and Białowieża) latitudinally distributed in north-eastern Poland (total area – ca. 2900 km<sup>2</sup>; 22°50'-23°56'E, 52°35'-54°10'N, max distance: N-S –176 km and W-E – 73 km, Fig. 1).

*Augustów Forest* (AF; 1600 km<sup>2</sup>) straddles the border between Poland and Belarus. The Polish part of AF (where the presented study was conducted) covers 1160 km<sup>2</sup> (22°50'-23°33'E, 53°44'-54°10'N; Fig. 1, Photo 1). Most of the AF area is commercially managed by six State Forest districts (Augustów, Płaska, Szczebra, Głęboki Bród, Suwałki, and Pomorze). The rest of the area is protected by Wigry National Park (150 km<sup>2</sup>) and 13 nature reserves (37.5 km<sup>2</sup>). The eastern part of AF (60% of the area) is situated in the Niemen river basin (Czarna Hańcza river), the western part – in the Narew river basin (Rospuda and Blizna rivers). Around 5% of AF is covered by lakes (above 20 lakes in total).

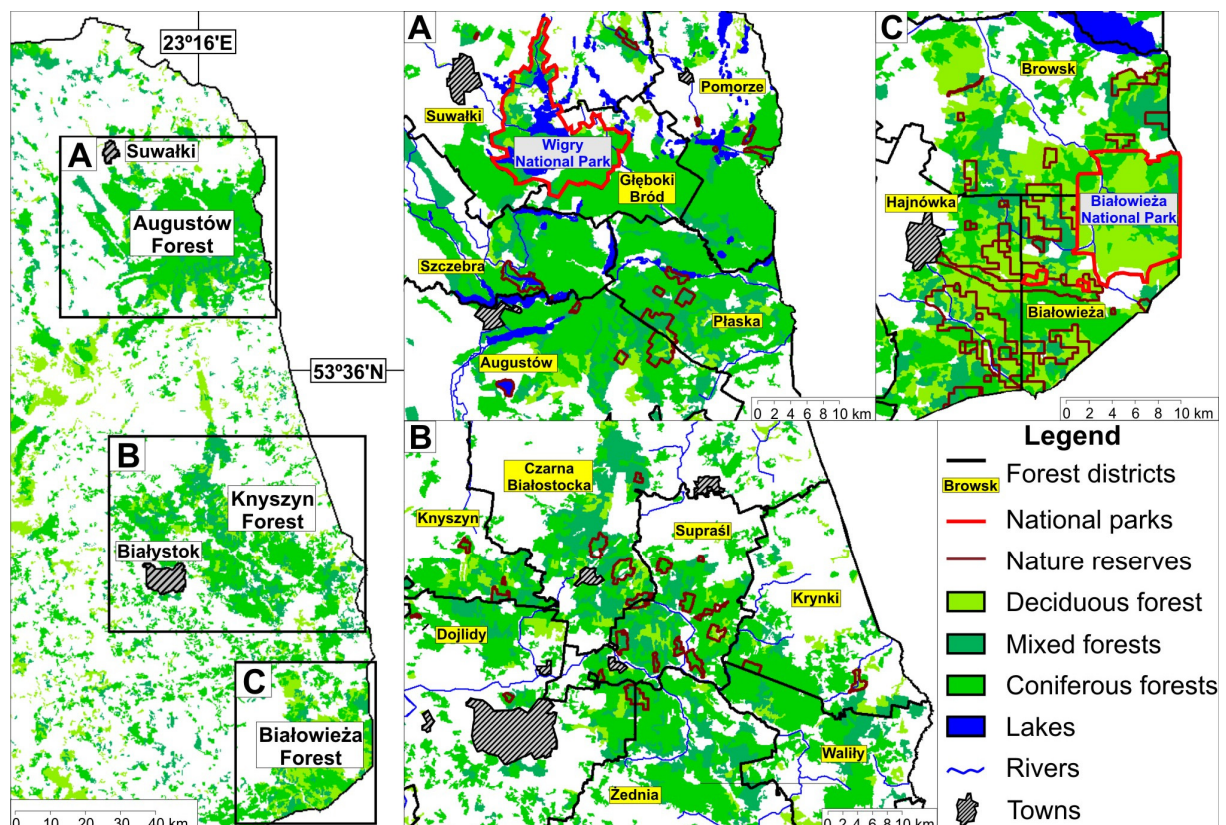


Fig. 1. Location of Augustów, Knyszyn and Białowieża Forests in north-eastern Poland.



Land relief of AF was shaped during the last glacial period (Vistulian) and the elevation ranges from 117 to 170 meters a.s.l. The north-eastern part is covered by sands and clays of the ground moraine and has the most diverse relief, many lakes and relatively rich soils. The central and southern part is flat and covered by sands (sandur) and poor podzolic soils. In this part, large areas are overlaid by peat soils (Sokołowski 2006).

Almost 85% of woodlands constitute coniferous forests where Scots pine (*Pinus sylvestris*; 77.4% of the area) and Norway spruce (*Picea abies*; 7.4%) dominate. Stands of silver and downy birch (*Betula verrucosa* and *B. pubescens*; 6.5%), black alder (*Alnus glutinosa*; 6.3%), and English oak (*Quercus robur*; 1.9%) occur with lower proportions. Forest associations exhibit a clear latitudinal gradient, which expresses the geological structure, soil quality and land relief – from relatively large proportions of spruce and deciduous trees on moraine hills in the northern part, to almost pure pine forests on the sandur plain in the central part, to bog forest associations with considerable contributions of birch and black alder in the lowest, southern part of AF. The average age of tree stands is 62 years (Sokołowski 2006).



Photo 1. Typical coniferous forest stand in Augustów Forest. Photo by Tomasz Borowik.



Four ungulate species occur in AF: red deer, moose, roe deer and wild boar. The most abundant are roe deer and red deer. In comparison with other large woodlands of north-eastern Poland, AF harbours a relatively large population of moose (Regional Directorate of State Forests in Białystok, unpublished data). Red deer, roe deer and wild boar are game species, while hunting on moose has been banned since 2001. Hunting on game ungulates (red deer, roe deer, wild boar) is organized over 17 hunting grounds (the area range: 34-106 km<sup>2</sup>), 10 of them are managed by 5 forest districts (Augustów, Płaska, Szczebra, Suwałki and Głębokki Bród), and 7 by hunting clubs. The hunting season for red deer, roe deer and wild boar generally covers autumn and early winter, excluding red deer and roe deer males which can be hunted during their rutting period: red deer – in late summer and autumn, roe deer – in late spring and summer. Wild boar males and juveniles are culled throughout the year except March (Wawrzyniak et al. 2010). Two large predators (wolf and lynx) occur, though the range of lynx is limited to the southern part of AF (Jędrzejewski et al. 2002, 2012).

The climate has many continental traits. Winter starts here early compared to other parts of lowland Poland and lasts around 114 days. Mean temperature of January is -6.7°C, while mean temperature of July – 16 °C. The total number of days with temperature below zero amounts to 70. Snow cover persists for 100 days. The vegetation season lasts 190 days. Mean annual temperature is 5.3°C. The annual precipitation is 590 mm (Grabowska-Bajkiewicz 1997).

**Knyszyn Forest** (KF; 1140 km<sup>2</sup>, 22°57'-23°52'E, 53°1'-53°29'N; Fig. 1, Photo 2) is located to the south of Augustów Forest. The KF is commercially managed by seven State Forest districts (Dojlidy, Czarna Białostocka, Knyszyn, Supraśl, Krynki, Waliły, and Żednia). The most precious fragments of habitats are protected by 21 nature reserves (total area 40 km<sup>2</sup>). The whole area is situated in the Narew river basin. The main river is Supraśl with tributaries: Sokołda, Czarna, and Płosa. The land relief – diverse and rich in geomorphologic forms – was created by the Middle Polish (Riss) glaciation. The elevation ranges from 118 to 210 m a.s.l. Numerous spring fens are an interesting feature of KF (Łoszewski 1984).

KF is mainly covered by coniferous forests (81% of the area), which in some places preserved primeval traits. The main tree species are Scots pine (70% of the total area), Norway spruce (11%), silver and downy birch (7%), and English oak (6%) (Sokołowski 2006). Black alder (4% of the total area) prevails in riparian and bog forests. The average age

of tree stands is 55 years. However, younger tree stands occur on the eastern edges of KF, where the afforestation program has been implemented.

The whole KF is inhabited by four ungulate species: moose, red deer, roe deer and wild boar. The European bison occur in the north-eastern part. Roe deer and red deer are most abundant. Wild boar occur at lower densities (Regional Directorate of State Forests in Białystok, unpublished data). Hunting of red deer, roe deer and wild boar is carried out beyond the borders of nature reserves in 27 hunting grounds (the area range: 28-88 km<sup>2</sup>) managed by one forest district (Supraśl) and 20 hunting clubs. The European bison is a protected species. In addition, the number of ungulates is limited by wolf and lynx predation (Jędrzejewski et al. 2012).

The climate of KF is transitional with strong continental traits. Winter lasts above 100 days, while summer – around 90 days. Mean annual temperature is 6.8°C. The lowest mean temperatures are recorded in January (-3.5°C), the highest – in July (18.5°C). The vegetation season (mean daily temperature above 5°C) is relatively short and lasts for around 200 days. Snow cover lasts for 80-90 days. Due to differences in the land elevation, the annual precipitation varies significantly between different parts of Knyszyn Forest (650-700 mm; Górniak and Jekaterynczuk-Rudczyk 1995).



Photo 2. Mixed-coniferous forest stand in Knyszyn Forest. Photo by Karol Zub.

**Białowieża Forest** (BF) is a transboundary (Poland-Belarus) woodland, which covers 1500 km<sup>2</sup>. The Polish (western) part of BF (635 km<sup>2</sup>; 23°31'-23°56'E, 52°35'-52°55'N; Fig. 1, Photo 3) is protected by Białowieża National Park (BNP; 105 km<sup>2</sup>) and nature reserves (118 km<sup>2</sup>), and commercially managed by three State Forest districts (Białowieża, Hajnówka and Browsk). BF is situated in the Narew and Bug river basins. The land relief was shaped by the Middle Polish (Riss) glaciation (Warta stage). The landscape is shaped by the ablation moraine plain interspersed with melt-out depressions filled with deep peat strata. The elevation ranges from 160 to 190 m a.s.l. The most common soils include brown (37% of the area) and lessive soils, whereas gleysol, muck and black soils are found in places affected by lotic or stagnant water (Kwiatkowski 1994).

BF is the last woodland on the North European Plain with large fragments of natural forests preserved. There are four main forest association classes: deciduous and mixed forests, coniferous forests, alder forests and riparian forests (Faliński 1986). The most abundant are oak-lime *Tilia cordata*-hornbeam *Carpinus betulus* stands (45% of the total area) and coniferous and mixed coniferous stands (37%). The deciduous and mixed deciduous bog forests cover 15% of the BF area. The forest is characterised by a high diversity of tree species, including the dominant Scots pine (27% of the total area), Norway spruce (25%), black alder (20%), English oak (12%), silver and downy birch (8%), while the other species, i.e. small-leaved lime, Norway maple (*Acer platanoides*), common ash (*Fraxinus excelsior*), aspen (*Populus tremula*), hornbeam and elms (*Ulmus* sp.) occur as admixtures (Sokołowski 2006). The average age of forest stands in the managed part of BF is 70 years, whereas in BNP – 130 years.



Photo 3. Typical deciduous forest stand in Białowieża Forest. Photo by Karol Zub.

Five native species of ungulates occur in BF: European bison, moose, red deer, roe deer, and wild boar. The most abundant are red deer and wild boar. Other species occur at lower densities (Forest Research Institute, unpublished data). The whole BF (except for the BPN) is divided into 9 hunting grounds (the area range: 25-93 km<sup>2</sup>), managed by 3 forest districts. Hunting is performed in the whole BF Forest, except for the National Park and nature reserves. Due to low roe deer densities, roe deer females and juveniles are not hunted. All game species are preyed by wolf (Jędrzejewski et al. 2000, 2002, 2012) and lynx (Okarma et al. 1997).

The climate of BF is transitional between Atlantic and continental types. The mean annual temperature is 6.8°C. The coldest month is January (on average -4.2°C), the warmest – July (on average 17.7°C). The annual precipitation is 633 mm. Snow cover persists for 92 days. The vegetation season lasts on average 205 days (Olszewski 1986).

### **3.2. Characteristics of the red deer population**

The first written records of red deer (Photo 4) in Białowieża and Augustów Forests date back to the 16th century, when there were numerous red deer populations in the forests of NE Poland (Hedemann 1939, Samojlik 2005, Sokołowski 2006). During the 17th-18th centuries, a continuous decrease in the number of red deer was reported. This led to extinction of the species in the most parts of NE Poland (including Augustów, Knyszyn and Białowieża Forest) at the end of the 18th century. The first reintroductions of red deer were performed in the second half of the 19th century and at the beginning of the 20th century. Karcov (1903) reported releases of red deer in BF, which were transported from Spała (central Poland), Germany, Bohemia, Russia and the Habsburg Empire. Most probably, there were no stable populations of red deer in AF and KF until the mid-20th century. The first red deer in AF were released in the early 1940s and came from Germany (Niedziałkowska et al. 2012). After World War II, almost 1000 individuals from woodlands of western and central Poland were translocated to the forests of north-eastern Poland (except for BF). Thereafter, deer populations in NE Poland have increased. In the 1990s, hunters carried out reduction of ungulates to prevent damages to forest plantations (Jędrzejewski et al. 2011). It resulted in a considerable decline in the number of red deer in the region. Since 2000, a slow recovery of the population size has been observed. Nowadays, the highest population density and proportion of red deer in the ungulate guild are observed in BF, moderate in KF, and the lowest in AF (Table 1). The annual hunting harvest in the study area ranged from 6% (BF)



to 11% (KF) of the winter (December-February) densities. Females constituted from 45% of hunting bags in KF to 68% in BF (Table 1).

Despite the fact that all populations of red deer in NE come from the past reintroductions from different parts of Europe, they belong to the same phylogenetic lineage (the western one) (Niedziałkowska et al. 2011).

Table 1. Mean red deer *Cervus elaphus* population density, percentage contribution in the ungulate guild and mean annual hunting harvest in the study area during 2008-2012.

Source: the Regional Directorate of State Forest in Białystok and Forest Research Institute.

Parameters	Augustów Forest	Knyszyn Forest	Białowieża Forest
Population density (N ind./100 km <sup>2</sup> )	364	561	684
Percentage in the ungulate guild (%)	34	39	47
Hunting harvest (N ind./100 km <sup>2</sup> )			
Total	34	60	41
Males	12	19	10
Females	17	27	28
Juveniles	5	14	3



Photo 4. Red deer *Cervus elaphus* hind in Białowieża Forest. Photo by Karol Zub.

### **3.3. Data collection**

#### ***3.3.1. Habitat productivity assessment and weather data acquisition***

Habitat productivity of the studied forests was determined by calculating the percentage of deciduous and mixed tree stands in the total forested area. Data on forest types were obtained from the Corine Land Cover 2006 database available on the website of the Inspectorate of Environmental Protection (<http://clc.gios.gov.pl/>). The area (in square meters) of each forest type was measured using the ArcGIS software by ESRI® (version 9.3.1). Information on the extent of supplementary winter feeding (expressed in tons of hay delivered) during the autumn-winter season of 2011 in the three woodlands was provided by the Regional Directorate of State Forests in Białystok.

For each forest and year (2006-2011), the mean summer (June-August) temperature was calculated from the MODIS data set (The Aqua MOD11 product – Land Surface Temperature and Emissivity; <http://modis.gsfc.nasa.gov/>; Wan 2008) by averaging eight-day temperature records provided at a spatial resolution of 1 km. Data on the total precipitation in summer (June-August) for each year (2006-2011) in Suwałki (AF) and Białystok (KF) were downloaded from WeatherOnline Ltd. – Meteorological Services website (<http://weatheronline.pl/>). This data source did not cover BF, therefore I calculated the total of summer precipitation in this area based on daily datasets (spatial resolution of 0.25 degree) provided by the Global Satellite Mapping of Precipitation (GSMaP) project (sponsored by JST-CREST, promoted by the JAXA Precipitation Measuring Mission Science Team, and distributed by the Earth Observation Research Center, Japan Aerospace Exploration Agency; Okamoto et al. 2005, Ushio et al. 2009).

#### ***3.3.2. Estimation of red deer population density***

Estimation of red deer population density was based on drive censuses organised in cooperation with the personnel of State Forestry districts and national parks, and members of the hunting clubs belonging to the Polish Hunting Association. In 2006-2011 (December-February), such inventories were carried out twice in AF (2008/2009, 2010/2011), once in KF (2010/2011) and five times in BF (2006/2007-2010/2011; Appendix 1: Table A1.1). In the study area, forest compartments or blocks of compartments were selected (mean size 1-2 km<sup>2</sup>, covering about 10% of the surveyed areas) to be surveyed.

On the assigned day, observers were distributed around three sides of the selected compartments or blocks of compartments at the intervals of 100-200 m to keep visual contact (Fig. 2; Photo 5). Observers remained stationary till the time when the line of the so called "beaters" placed along the fourth side (at intervals of 20-100 m) reached the opposite side of the surveyed compartments. Both observers and beaters noted ungulates passing through the line of observers (on their right hand side only) and leaving or entering the inventoried closed area (Pucek at al. 1975; Jędrzejewska et al. 1997; Borkowski et al. 2011). I calculated the red deer density in each of the surveyed compartments by dividing the number of observed individuals by the compartment area. Mean red deer density of the surveyed hunting grounds, forest districts, national parks or whole forests was obtained by averaging the deer densities in appropriate compartments (Appendix 1: Table A1.1).

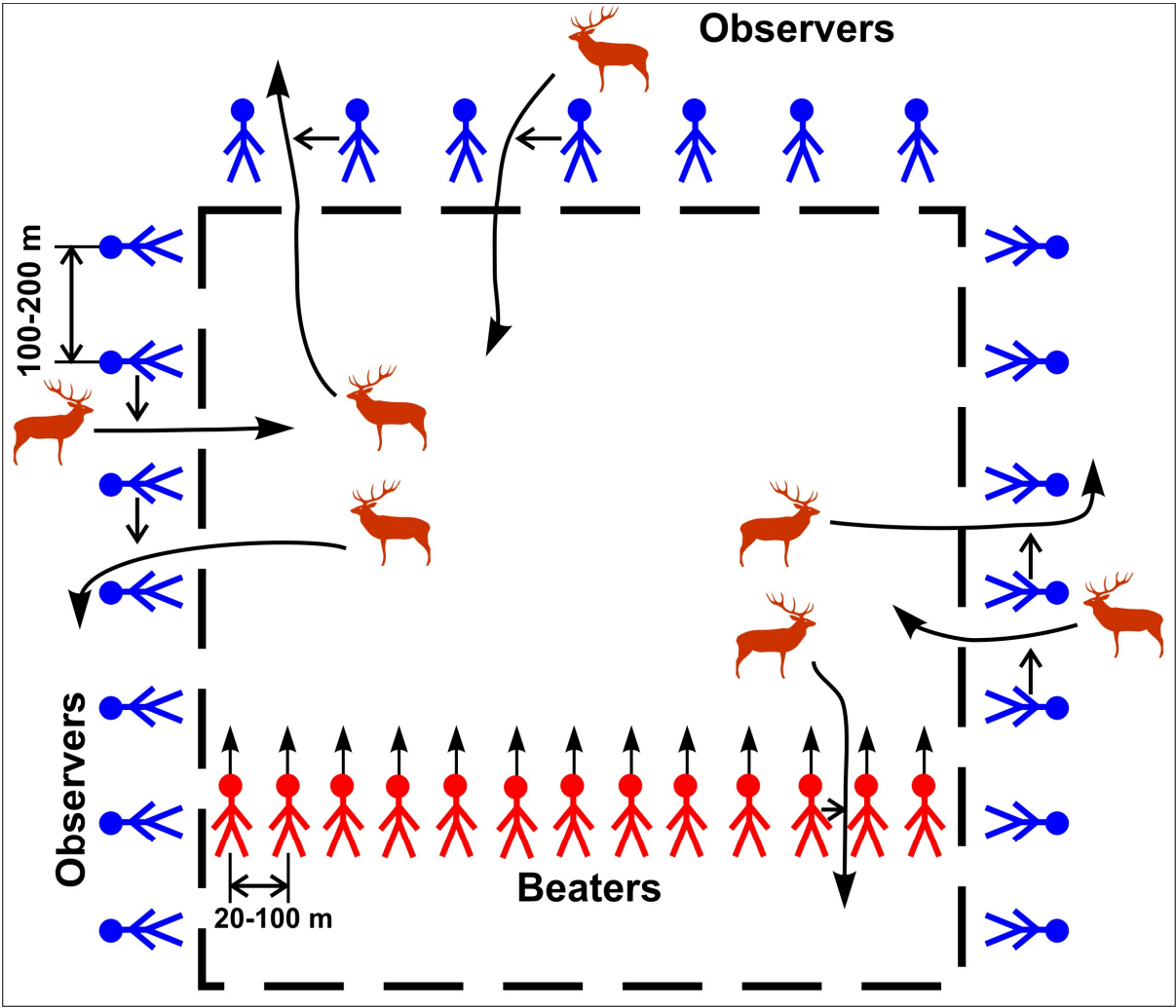


Fig. 2. Scheme of drive census of ungulates in one of the surveyed forest compartments.





Photo 5. Beaters distributed along the compartment line shortly before moving inward – Białowieża National Park, January 2010. Photo by Tomasz Kamiński.

### ***3.3.3. Collection of red deer samples***

During the hunting seasons (1st October – 15th January) of 2006/2007 to 2010/2011, I asked hunters to collect reproductive tracts and jaws of red deer females culled in Augustów, Knyszyn, and Białowieża Forests. Before the first hunting season all involved hunters obtained video tutorials presenting the proper way of extracting the reproductive tract demonstrated by a veterinary physician. They also received labelled plastic bags to store the extracted materials. Hunters put female reproductive tracts together with their jaws into bags and filled the labels with the information on the location (the hunting ground number and forest compartment number when available), date as well as lactation status and dressed body mass (after evisceration) of an animal. All samples were stored by hunters in freezers at -10°C and then transported to the lab of the Mammal Research Institute PAS in Białowieża for further analysis.



In total, I collected 541 samples: 243 in AF, 81 in KF, and 217 in BF (Fig. 3). The material covered five autumn-winter seasons: 2006/2007 – 33 samples, 2007/2008 – 101, 2008/2009 – 96, 2009/2010 – 139, and 2010/2011 – 172. Most samples (338) were complete i.e. they included a reproduction tract, a jaw and all the information on the attached labels. The overall median date of culling was the 18th of October.

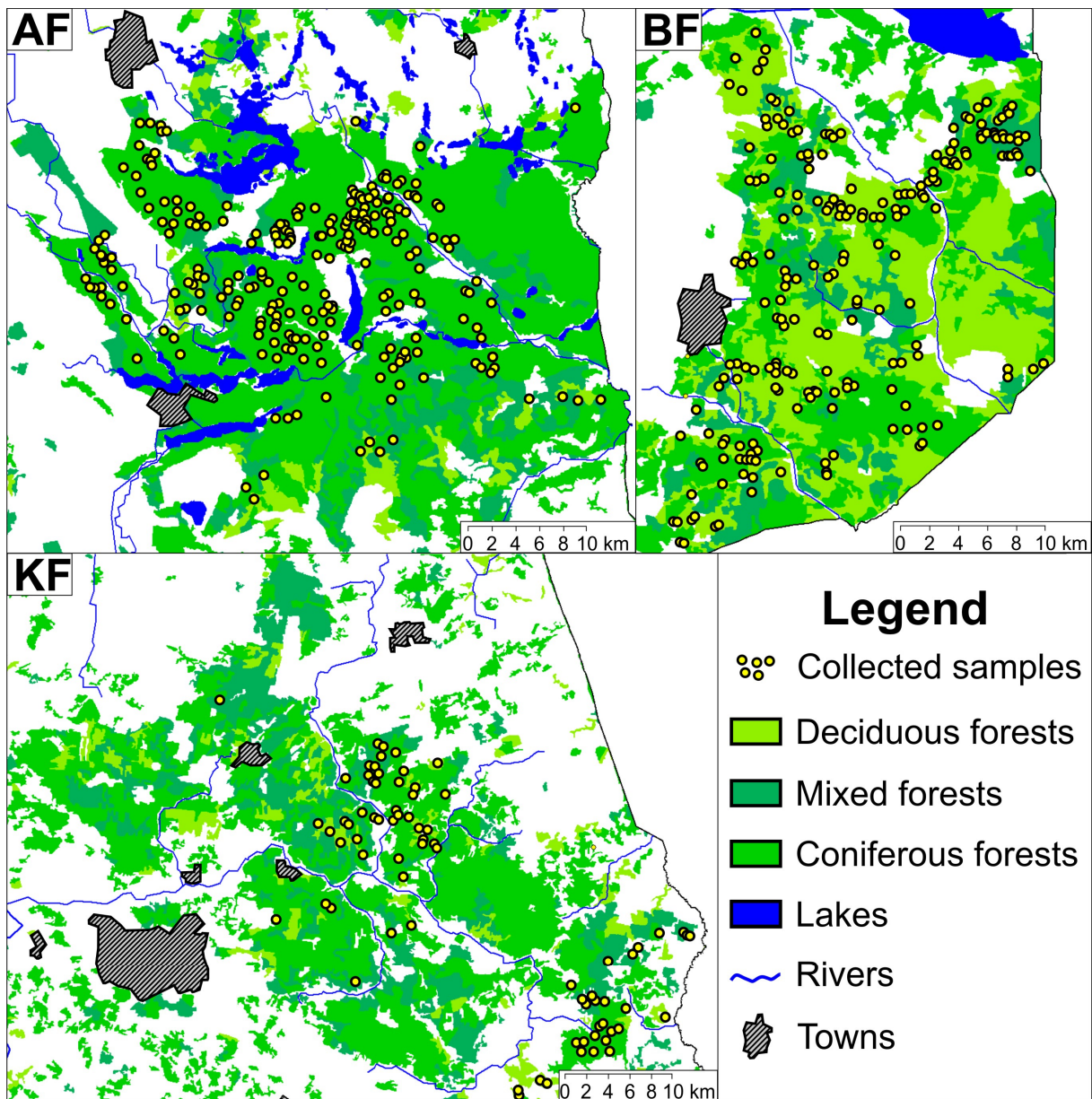


Fig. 3. Spatial distribution of red deer female samples collected in Augustów (AF), Białowieża (BF) and Knyszyn (KF) Forests in 2006-2011.

#### ***3.3.4. Determination of the body condition and the age of hinds***

I applied two indices of the female body condition: (1) body mass, and (2) percentage of mandible marrow fat. After culling, eviscerated carcasses were weighed with an accuracy of 1 kg and body mass was noted. In total, I received 395 records of the hind body mass.

To calculate the percentage of fat in mandible marrow, I extracted the entire marrow from the obtained jaws (N = 450), weighed it with an accuracy of 0.1 g, and dried at 70°C until reaching a dry weight, and then weighed it again. The percentage of fat in the marrow for each sample was calculated as  $\text{dry marrow weight/fresh marrow weight} \times 100$  (Okarma 1989).

Female age was determined by applying tooth cementum aging method. The growth of mammalian tooth cementum has a cyclic nature, thus annual "rings" (dark from winter and light from spring and summer) are observed at the tooth cross-section (Fig. 4). Hence, counting these rings enables assessment of animal age. In case of ungulates (including red deer), all analyses are performed on primary incisors (I1) (Matson 1981). I extracted the incisors (N = 473) from jaws with pliers and cleaned them from the remaining gum tissues. Such prepared teeth were sent to Matson's Laboratory LLC (Milltown, USA), which offers professional age determination services. Age of sampled females was assessed with an accuracy of 1 year.

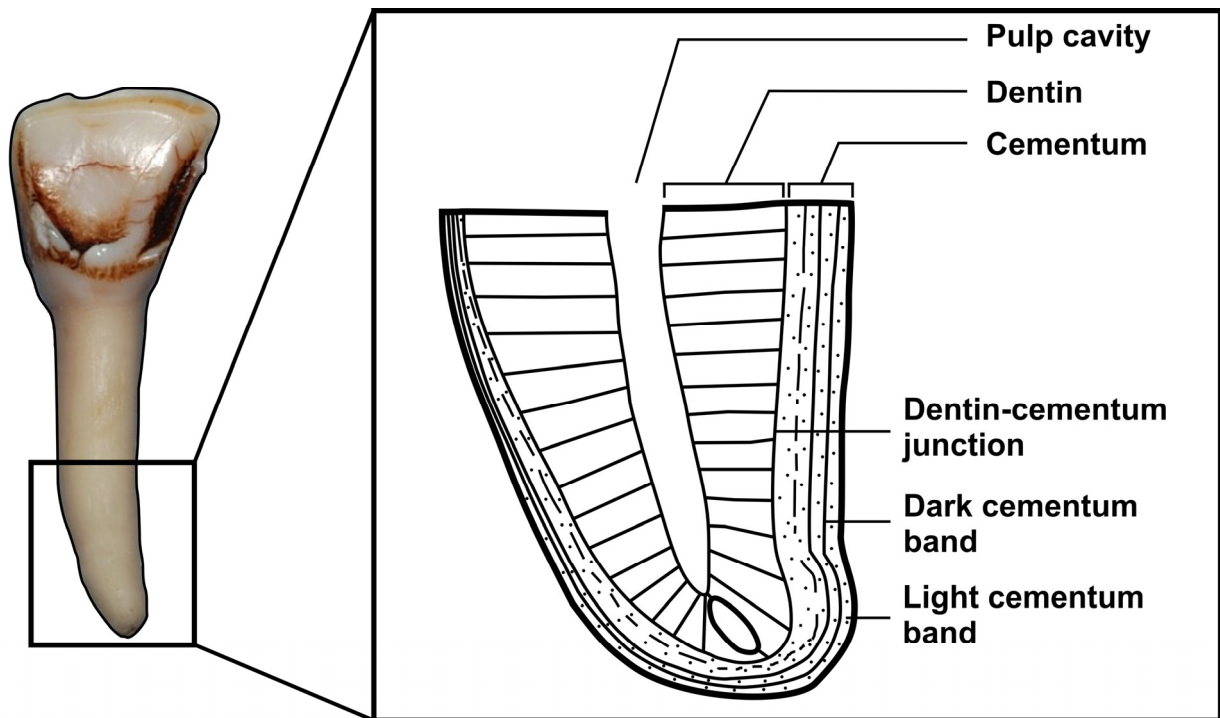


Fig. 4. Cross-section of the primary incisor (I1) of a 2.5-year-old red deer female, with the presentation of annual rings of dark and light cementum used for age determination by the cementum aging method.

### ***3.3.5. Ascertainment of fertility and sex of foetuses***

Fertility of red deer females was assessed by examining the uteri and ovaries from shot hinds (N = 541). I assumed that most of the hinds conceived at the first ovulation of the season (the end of September – beginning of October). Fertile females were those hinds which had current corpora lutea in ovaries, with or without embryos in an uterus. Infertile females were those without current corpora lutea and embryos. As all females culled since the early November onward and classified as fertile had all the signs of pregnancy (corpora lutea and embryo or foetus), I assumed that all of the sampled fertile hinds were pregnant.

The presence of lactation in shot females was used as an indicator of reproductive activity of hinds in the previous year and as an index of fawn survival in the first months of lives. After the culling, hunters examined the udder for the presence of lactation and wrote down the observations on an attached label. In total, I obtained 323 records of lactating females, 151 from AF, 45 from KF, and 127 from BF.

Sex of foetuses was determined by visual inspection, immediately after extraction of foetuses from uteri. Only foetuses larger than 2 cm could have been determined for sex (N = 156).

### 3.4. Statistical analysis

To model which factors affect the red deer female fertility, I described the following set of parameters for each sampled individual: the presence of pregnancy and lactation, the body mass, the age, and the percentage of mandible marrow fat. In addition, at the level of forest district or hunting ground (when more detailed data were available), I calculated a percentage of deciduous and mixed forests, the amount of supplementary winter feeding, the population density, the mean summer temperature, and the total summer precipitation.

Due to a small number of sampled hinds in older age categories, the comparison of the body condition indices and the percentage of pregnant, lactating and pregnant-lactating females belonging to different age categories required creating 8 classes for the pooled data: 1 year old, 2 years old, 3 years old, 4 years old, 5-6 years old, 7-8 years old, 9-11 years old, and 12-19 years old. Similar analyses conducted separately for the three surveyed woodlands required data grouping into 5 classes: 1 year old, 2-3 years old, 4-6 years old, 7-11 years old, and 12-19 years old. Since the body condition indices followed a normal distribution, I tested differences in the body condition between age classes with one-way ANOVA, whereas pairwise comparisons between age classes were performed with the post-hoc Tukey HSD test allowing a multiple comparison of the means. The same tests were used to compare differences in the body condition of hinds in the same age classes among the studied forests.

To reveal factors affecting the percentage of mandible marrow fat, I ran a multiple regression model. I checked for multicollinearity between potential explanatory variables by applying both simple regression models and Pearson's correlation coefficients. Only non-correlated ( $r < |0.5|$ ), most relevant covariates were included in the final models. From the whole set of possible predictor variables I applied the following ones: body mass, age, population density, the total summer precipitation, and mean summer temperature. The Akaike Information Criterion (AIC) with the second-order correction for a small sample size ( $AIC_c$ ; Burnham and Anderson 2002) was used for model ranking. The model with the lowest  $AIC_c$  was selected as the best model. I checked the normality and homoscedasticity in the distribution of the final model residuals by inspecting the quantile-quantile distribution plot and model residuals against plots of fitted values (estimated responses). To illustrate

the individual effect of each significant explanatory variable on the percentage of mandible marrow fat, I calculated regression models by substituting formulas with coefficients provided by the model and mean values of corresponding independent variables.

The differences in the proportion of pregnant, lactating and pregnant-lactating females between all age classes were tested with Pearson's Chi-squared tests. For testing of pairwise comparisons, Fisher's exact test was applied. The same procedure was used to compare differences in the proportion of pregnant, lactating and pregnant-lactating females in the same age classes among different forests. The differences in the body condition indices between pregnant and non-pregnant females for the pooled data and separately for the three age classes (1 year old, 2-3 years old, 4-19 years old) were tested with one-way ANOVA. I could not compare the body condition indices of lactating pregnant and lactating non-pregnant females due to a small sample size of the latter group of hinds.

In order to analyse which factors affected female fertility, I fitted generalized linear models (GLM) for binomial data (Zuur et al. 2009). I set pregnancy as a dependent binomial variable: "1" was attributed to pregnant females and "0" to non-pregnant ones. After checking collinearity between potential explanatory variables, I used the following: body mass, age, percentage of mandible marrow fat, population density, mean summer temperature, and the total summer precipitation. In total, I ran three models, the first one included all females, the second one – subadult females (1 year old) and the third one – adult females ( $\geq 2$  years old). In the case of the first and the third model, I used the main effects of the population density, mean summer temperature, and the total summer precipitation as well as interactive effects of age and body condition indices (body mass and percentage of mandible marrow fat). The second model had all explanatory variables included as the main additive effects.

For each of the above mentioned models, I obtained the whole set of models with different numbers and combinations of explanatory variables, which I ranked with the Akaike Information Criterion (AIC) with the second-order correction for a small sample size ( $AIC_c$ ). Since I did not find the single best model in the set of analysed models, I used model averaging on the selected confidence set of models:  $\Delta AIC_c \leq 5$  for the first model,  $\Delta AIC_c \leq 4$  for the second and the third one. This method provided the averaged coefficients and 95% confidence intervals. In order to calculate the relative importance for each of the explanatory variables in the selected confidence set of models, I summed up Akaike weights for all models containing a given predictor variable (Burnham and Anderson 2002). Then I rescaled

the obtained sums to 0-1 scale, where 1 was the total sum of weights in the confidence set of models and was attributed to variables present in all models. Therefore, the importance of a variable depended on the value: the higher the value, the higher the significance of the factor. I used the likelihood ratio-based  $R^2$  as a measure of explained variation (Nagelkerke 1991).

For graphical presentation of an individual effect of each significant explanatory variable on probability of female to be fertile, I corrected the values of a given variable by the effects of other variables. Corrections of the variable values were performed according to the following procedure: (1) I applied multiple regression models in order to indicate the strength of the relationship between the explanatory variables; (2) each predictor variable was set as a dependent variable; (3) residuals and a mean value of dependent variable was calculated for every model; (4) row values were corrected for each variable by adding appropriate residuals to the derived mean.

The deviation of the sex ratio of foetuses from the 1:1 ratio was tested with Fisher's exact test. Differences in the foetus sex ratio between the age classes of their mothers (1 year old, 2-3 years old, 4-6 years old, and 7-19 years old) were checked with Pearson's Chi-squared test. Pairwise comparisons between individual age classes were tested with Fisher's exact test. Differences in the body condition indices between red deer females carrying male and female foetuses from different age classes were examined with one-way ANOVA.

To assess the life expectancy and the net reproduction rate of red deer population in the study area, I designed static life (survivorship) and fertility tables (Krebs and Horperg 1972). The number of females in the "0" age category was estimated based on the fertility rate of females and the proportion of females among foetuses, whereas the number of 0.5-year calves – based on the number of offspring which suckled hinds in the autumn-winter season (lactation data). For females older than 1.5 year, the frequencies were calculated by summing up the females in each age category. To deal with a problem of meaningless mortality rates (some of the frequencies of lower age categories exceeded those of higher categories) I smoothed the frequencies by fitting an exponential function to the data (Begon 1986). Then, I used the smoothed frequencies as a basis in the calculations of the survivorship and fertility tables. Additionally, during the assessment of net reproduction rates, for appropriate female age categories, I used data on the female fertility rate and the foetus sex ratio.

The strength of the relationship between the age of a given mother and the percentage of calves which survived until the age of 0.5 year was tested by a simple regression model. The percentage of calves which survived until the age of 0.5 year was calculated by dividing the expected number of offspring in each age category by a corresponding number of fawns which survived to reach the age of 0.5 year.

All statistical analyses were performed with the R program (version 2.13.2; R Development Core Team 2012).

## 4. RESULTS

### 4.1. Habitat productivity and red deer population density

The mean percentage area of deciduous and mixed tree stands in hunting grounds ( $N = 33$ ) in the whole study area equalled 45% ( $SE \pm 4.8\%$ , range 4.6-92.5%). Values calculated separately for the studied forests were as follows: AF – 16%, KF – 40%, BF – 78% (Fig. 5). The amount of supplementary winter feeding varied between forest districts from 0.07 to 0.99  $\text{ton}/\text{km}^2$ . The most intensive supplementary feeding was carried out in AF – 0.78  $\text{ton}/\text{km}^2$ , moderate in KF – 0.31  $\text{ton}/\text{km}^2$  and the least in BF – 0.12  $\text{ton}/\text{km}^2$  (Fig. 5). Red deer population density varied between forest districts and national parks from 2.57 to 7.59  $\text{ind.}/\text{km}^2$ . The highest mean density was found in BF (6.35  $\text{ind.}/\text{km}^2$ ), moderate in KF (5.69  $\text{ind.}/\text{km}^2$ ), and the lowest in AF (3.64  $\text{ind.}/\text{km}^2$ ) (Fig. 5, Appendix 1: Table A1).

The amount of supplementary feeding was negatively correlated with the percentage of deciduous and mixed tree stands ( $N = 24$ ,  $p < 0.001$ ) (Fig. 6). The amount of hay provided by managers in winter decreased with the increasing share of deciduous and mixed tree stands (more productive forests).

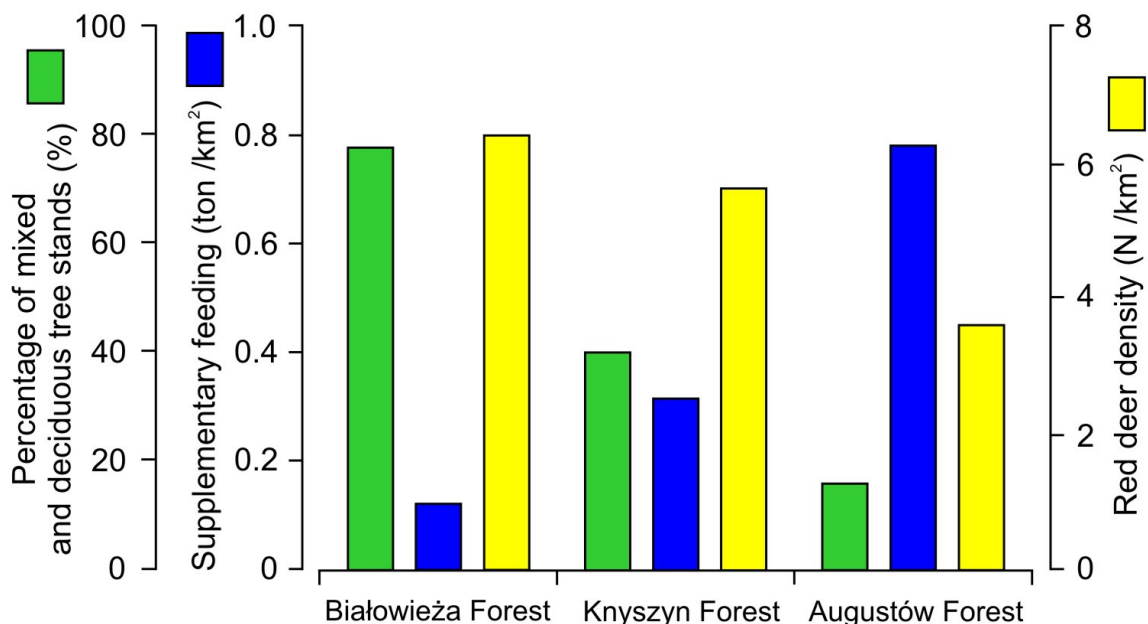


Fig. 5. Percentage area of mixed and deciduous tree stands (2011), the amount of hay provided by managers as supplementary winter feeding for ungulates (2011), and mean population density of red deer in Augustów, Knyszyn, and Białowieża Forests (2006-2011).



The percentage area of deciduous and mixed forest tree stands positively affected the red deer population density ( $N = 32$ ,  $p = 0.02$ ) (Fig. 7). The highest densities (above 6 ind./km<sup>2</sup>) were found in hunting grounds where deciduous and mixed tree stands covered more than 50% of the area. Although the amount of hay provided by managers as supplementary winter feeding was higher in less productive (coniferous) forests, it did not significantly increase the deer population density.

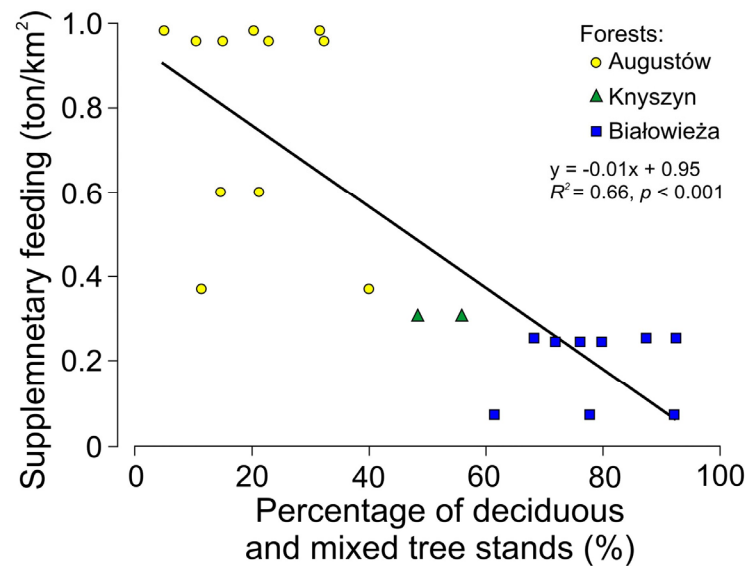


Fig. 6. The relationship between the amount of hay provided during winter as fodder for ungulates in forest districts and the percentage of deciduous and mixed tree stands in hunting grounds. Data for 2006-2011.

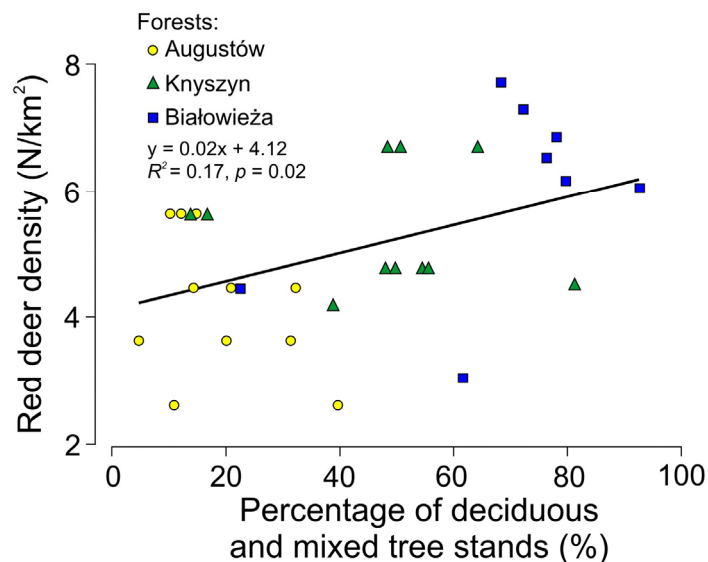


Fig. 7. Relationship between the percentage area of deciduous and mixed forest stands in hunting grounds and the red deer population density in forest districts (Augustów and Knyszyn Forests) and hunting grounds (Białowieża Forest). Data for 2006-2011.

## 4.2. Body condition of hinds

Neither body mass of females nor their mandible marrow fat declined in the course of the autumn-winter season (body mass:  $N = 383$ ,  $p = 0.923$ ; mandible marrow fat:  $N = 414$ ,  $p = 0.396$ ; Fig. 8). Therefore, data from all hinds were pooled and analysed regardless of the sampling time.

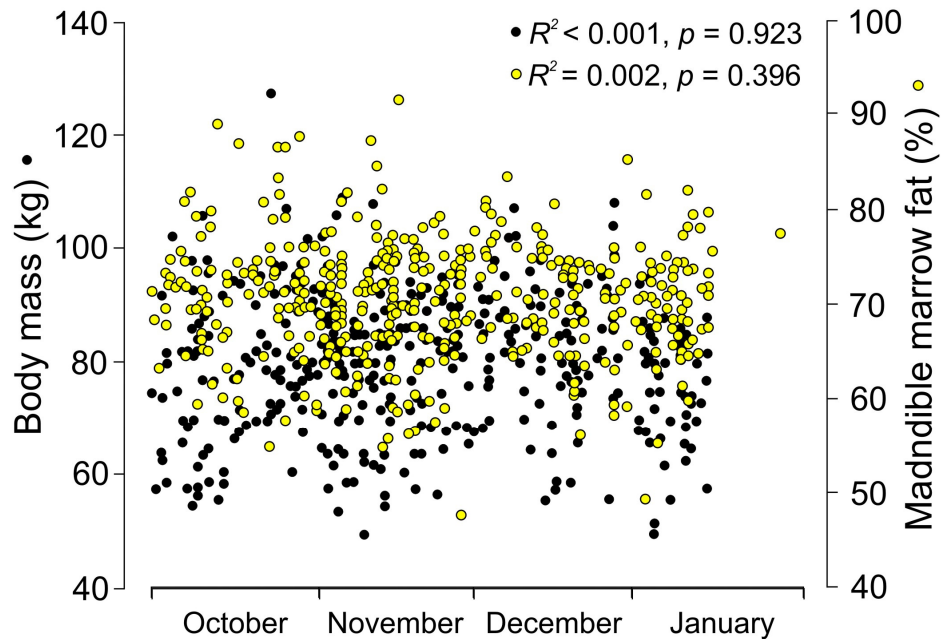


Fig. 8. Indices of body condition of female red deer in relation to the date of sampling, 2006-2011.

I did not detect any effect of the population density on the female body mass ( $N = 395$ ,  $p = 0.846$ ) (Fig. 9), while the percentage of mandible marrow fat decreased with the increasing red deer population density ( $N = 450$ ,  $p < 0.001$ ). Nevertheless, the regression model explained only 4% of the total observed variation in the percentage of the mandible marrow fat. The increase in the population density from 2.6 to 7.7 ind./km<sup>2</sup> corresponded to a decline from the average 74% to 69% of mandible marrow fat.

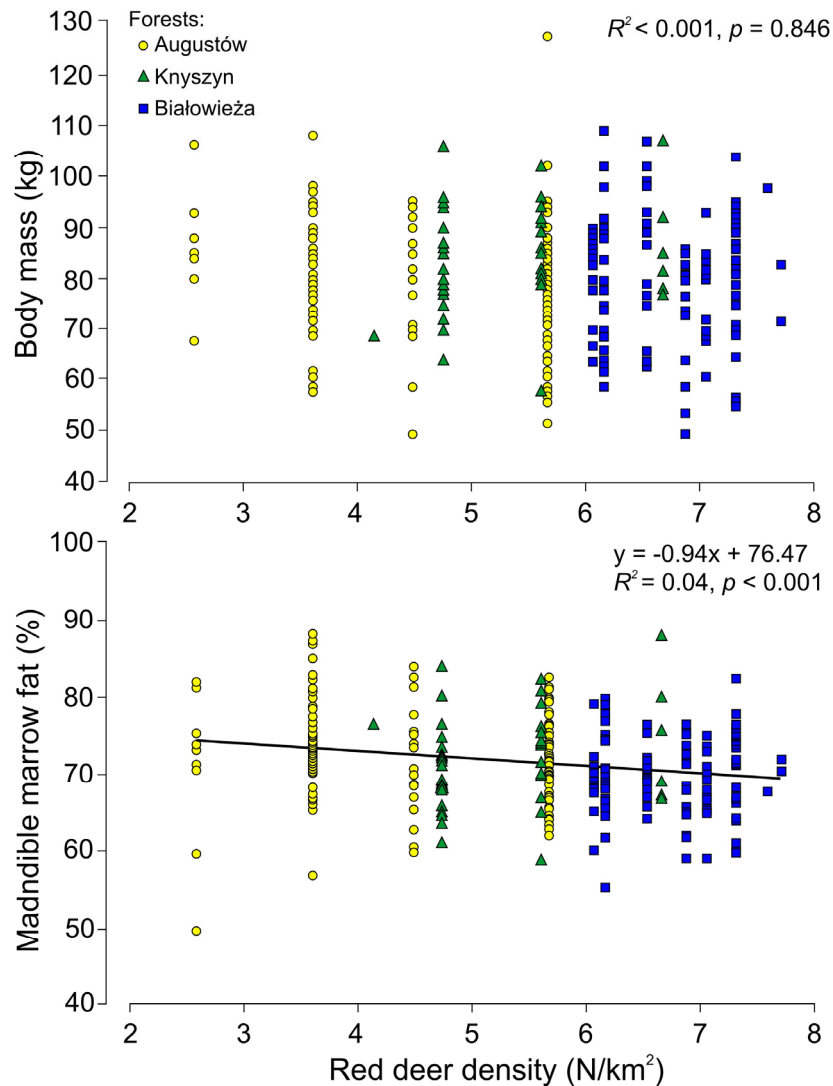


Fig. 9. Relationship between body condition indices of hinds and population density in forest districts during 2006-2011.

The mean ( $\pm$  SE) body mass increased with the age of hinds, from  $67.0 \pm 1.6$  kg for 1-year-old to  $87.5 \pm 1.6$  kg for 9-11-year-old females and then decreased to  $82.8 \pm 2.1$  kg for 11-19-year-old hinds (Fig. 10). The most intensive growth of body mass occurred in hinds between 1 and 4 years old, from  $67.0 \pm 1.6$  kg to  $78.0 \pm 1.4$  kg. The mean body mass of hinds differed significantly between age classes (ANOVA,  $p < 0.001$ ) (Appendix 2: Table A2.1). The mean value of this parameter for 1-year-old females was significantly lower than the mean body mass of hinds from older age classes (Tukey HSD,  $p < 0.001$ ), whereas the mean body mass of 9-11 year old hinds was significantly higher than the mean body mass of 1, 2, and 3-year-old females (Tukey HSD,  $p$  from  $<0.001$  to 0.008). Furthermore, the mean

body mass of 2-year-old females was significantly lower than the body mass of 7-8-year-old hinds (Tukey HSD,  $p = 0.044$ ) (Appendix 2: Table A2.1).

The mean ( $\pm$  SE) percentage of mandible marrow fat increased with the age of females in the first four years of their lives from  $65.9 \pm 0.7\%$  for 1-year-old to  $72.7 \pm 0.8\%$  in 4-year-old hinds (Fig. 10). The steepest growth in marrow fat was observed between the first and the second year of females' life – from  $65.9 \pm 0.7\%$  to  $70.4 \pm 0.8\%$ . A percentage of mandible marrow fat differed significantly among age classes (ANOVA,  $p < 0.001$ ). One-year-old females had significantly lower fat content compared to hinds from all older age classes (Tukey HSD,  $p < 0.001$ ) (Appendix 2: Table A2.1).

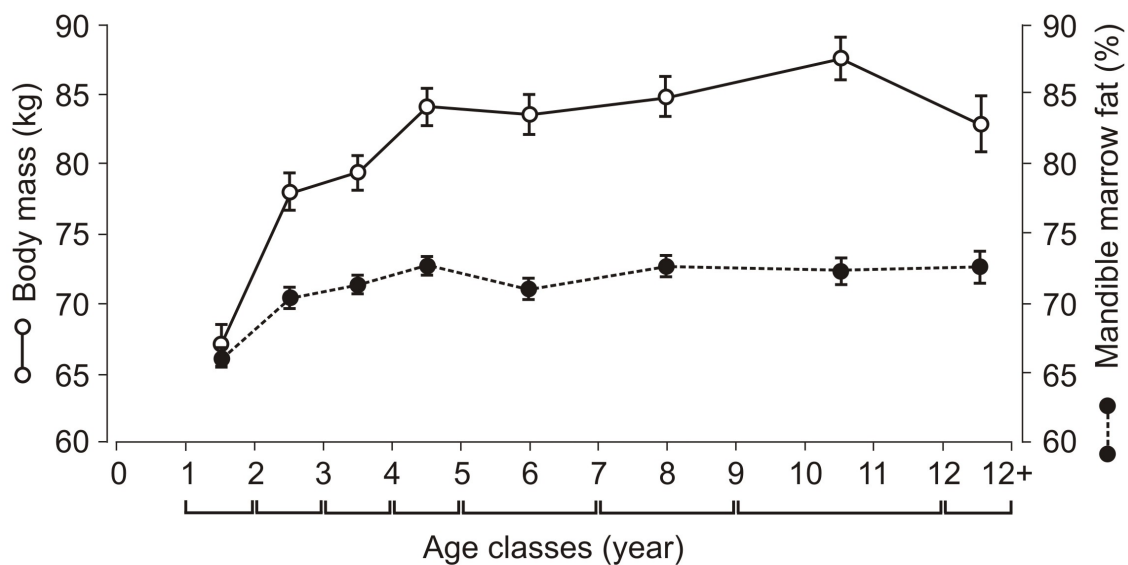


Fig. 10. Body condition indices of hinds in relation to their age (pooled data). Solid points represent mean values of mandible marrow fat; open points – mean body mass. Whiskers denote standard errors.

In order to compare the body mass indices of hinds among the studied forests, I grouped the data into 5 wider age classes. In AF and BF, the mean body mass ( $\pm$  SE) of hinds grew with their age (AF: from  $63.8 \pm 1.8$  kg for 1-year-old to  $87.2 \pm 1.9$  kg for 7-11-year-old hinds, BF: from  $69.1 \pm 2.7$  kg for 1-year-old to  $85.1 \pm 1.6$  kg for 7-11-year-old hinds) and then declined in 12-19-year-old females (AF:  $85.6 \pm 2.7$  kg, BF:  $81.0 \pm 2.9$  kg) (Fig. 11). In KF, the highest mean body mass ( $87.9 \pm 2.7$  kg) was reported for 4-6-year-old females. In AF, the most intensive growth of mean body mass was recorded between the first and the third year of females' life, whereas in BF, the intensive growth was prolonged to 4-6 years of age. The mean body mass varied significantly between the age classes in AF and

BF (ANOVA,  $p < 0.001$ ) (Appendix 2: Table A2.2). In both forests, the mean body mass of 1-year-old females was significantly lower compared to hinds from all older age classes (Tukey HSD,  $p$  from  $< 0.001$  to  $0.008$ ) and the mean body mass of 7-11-year-old hinds was significantly higher than the body mass of 1 and 2-3-year-old females (Tukey HSD,  $p$  from  $< 0.001$  to  $0.042$ ). In BF, the mean body mass in 2-3-year-old hinds was significantly lower compared to 4-6-year-old females (Tukey HSD,  $p = 0.047$ ) (Appendix 2: Table A2.1).

The mean body mass differed significantly between the studied forests only for 4-6-year-old females (ANOVA,  $p = 0.043$ ) – females from KF were significantly heavier than those from AF (Tukey HSD,  $p = 0.047$ ) (Fig. 11, Appendix 2: Tables A2.3 and A2.4). The highest absolute difference (however, not significant) in mean body mass was found between AF and BF for 1-year-old (Tukey HSD,  $p = 0.104$ ) and 12-19-year-old females (Tukey HSD,  $p = 0.287$ ). One-year-old hinds from less productive AF were on average 5.3 kg (8% of their mean body mass) lighter than females from most productive BF, while 12-19-year-old females from AF, were 4.6 kg (6% of their mean body mass) heavier than hinds from BF (Fig. 11).

In AF, the mean ( $\pm$  SE) percentage of mandible marrow fat increased with age of females – from  $68.1 \pm 1.1\%$  for 1-year-old to  $74.8 \pm 0.7\%$  for 4-6-year-old hinds, whereas in BF, values of this index constantly increased with age of hinds from  $63.5 \pm 0.7\%$  for 1-year-old to  $71.6 \pm 1.3\%$  for 12-19-year-old females (Fig. 11). In KF, the highest values of mandible marrow fat had 7-11-year-old females –  $72.3 \pm 2.0\%$ . Both in AF and BF, the most considerable increase in percentage of mandible marrow fat was reported between 1 to 2-3 years of age. The marrow fat content varied significantly among age classes in AF and BF (ANOVA,  $p < 0.001$ ) (Appendix 2: Table A2.1). In both forests, the percentage of mandible marrow fat in 1-year-old females was significantly lower compared to hinds from older age classes (Tukey HSD,  $p$  from  $< 0.001$  to  $0.027$ ) (Appendix 2: Table A2.2).

The percentage of mandible marrow fat differed significantly among the studied forests for females younger than 6 years (ANOVA,  $p$  from  $< 0.001$  to  $0.010$ ) (Appendix 2: Table A2.3). For all age classes, females from AF had a higher level of mandible marrow fat than females from BF, however, the difference was significant only for 1-year-old ( $p = 0.002$ ), 2-3-year-old ( $p = 0.014$ ), and 4-6-year-old females ( $p < 0.001$ ), whereas between AF and KF for 4-6-year-old hinds (Tukey HSD,  $p < 0.001$ ) (Fig. 11, Appendix 2: Tables A2.3 and A2.4). To sum up, females from less productive AF, which occurred at lowest densities,

had on average lower body mass but higher percentage of mandible fat content compared to hinds from BF.

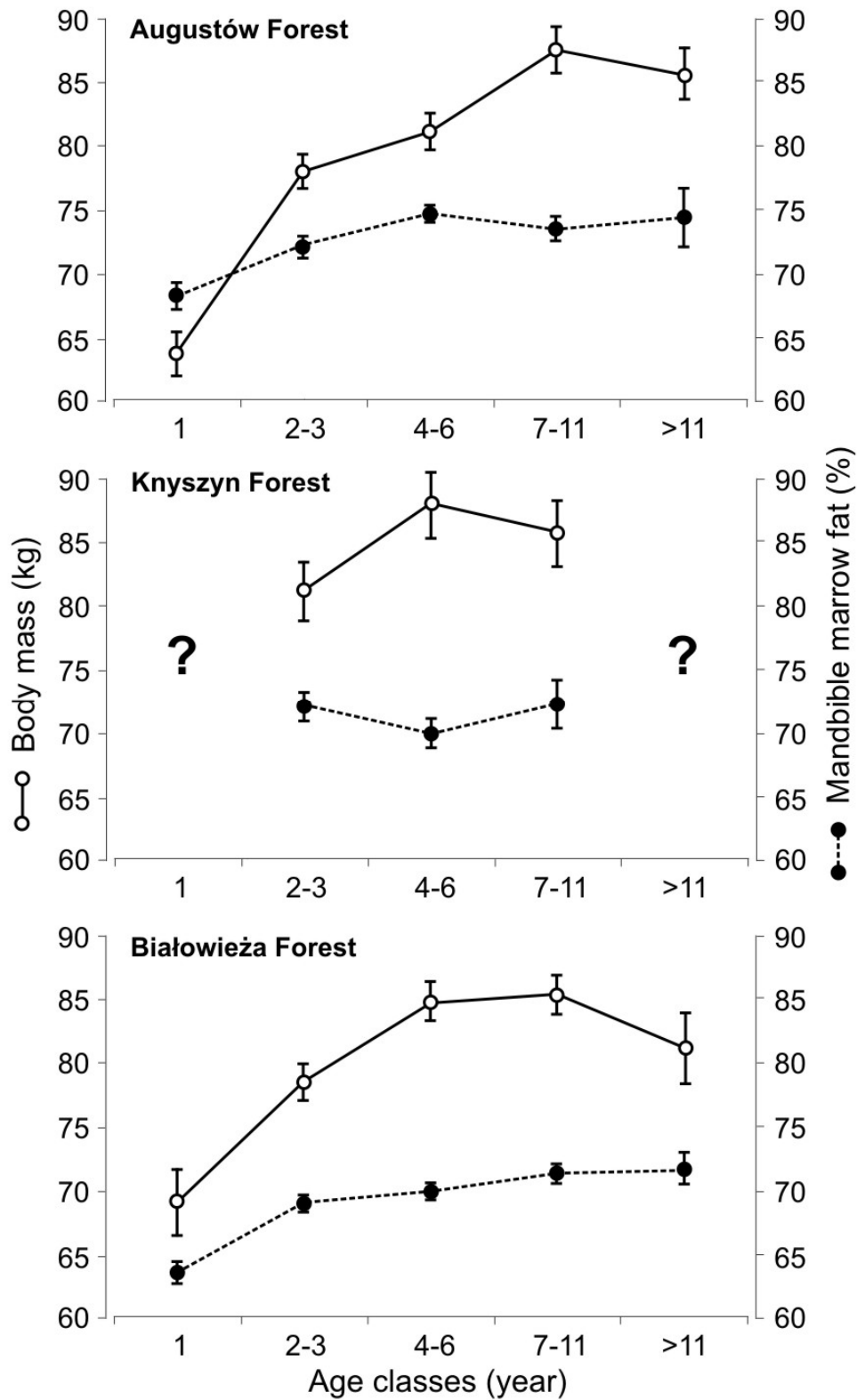


Fig. 11. Body condition indices of hinds in relation to their age in each of the studied forests. ? – no data available. Other denotations as in Fig. 10.

The best model describing the individual variation in the percentage of mandible marrow fat, which explained 23% of the total variation, indicated a positive relationships between the marrow fat content and the mean temperature of the summer (June-August) preceding the sample collection ( $p < 0.001$ ), the body mass ( $p < 0.001$ ) and the age of hinds ( $p = 0.06$ ), as well as a negative relationship with the total amount of summer (June-August) precipitation ( $p < 0.001$ ) (Tables 2 and 3, Fig. 12). Parameter estimates of the best model are presented in Table 3.

Increasing body mass of hinds (from 50 to 127 kg) caused a growth of the percentage of mandible marrow fat by 9.2% (Fig. 12).

Table 2. Model selection (based on the  $AIC_c$  criteria) for the examined multiple regression models with mandible marrow fat (MF) as a dependent variable and body mass (BM), the total summer precipitation (SP), mean summer temperature (ST), age (A), and deer population density (D) as explanatory variables. Only models with  $\Delta AIC_c \leq 4$  are presented. The model (top of the list) representing the highest parsimony (the lowest  $AIC_c$  scores) was the best model.  $K$  – the number of estimated parameters;  $AIC_c$  – Akaike’s information criterion with a second order correction for small sample sizes;  $\Delta AIC_c$  – difference in  $AIC_c$  between a given model and the most parsimonious model;  $\omega_i$  – weight of a model.

Model	$K$	$R^2$	$\Delta AIC_c$	$\omega_i$
<b>BM + SP + ST + A</b>	<b>6</b>	<b>0.23</b>	<b>0</b>	<b>0.470</b>
BM + SP + ST	5	0.22	1.47	0.226
BM + SP + ST + A + D	7	0.23	1.64	0.208
BM + SP + ST + D	6	0.22	3.18	0.096

Table 3. Parameter estimates for the multiple regression model describing factors affecting the percentage of mandible marrow fat in female deer. Significant effects are shown in bold.

Variables	Estimate	s.e.	$t$ -value	$p$ -value
Intercept	37.01	5.32	6.95	<0.001
<b>Mean summer temperature (ST)</b>	1.47	0.24	6.04	<0.001
<b>Total summer precipitation (SP)</b>	-0.03	0.01	-5.30	<0.001
<b>Body mass (BM)</b>	0.12	0.03	4.42	<0.001
Age (A)	0.16	0.08	1.87	0.06

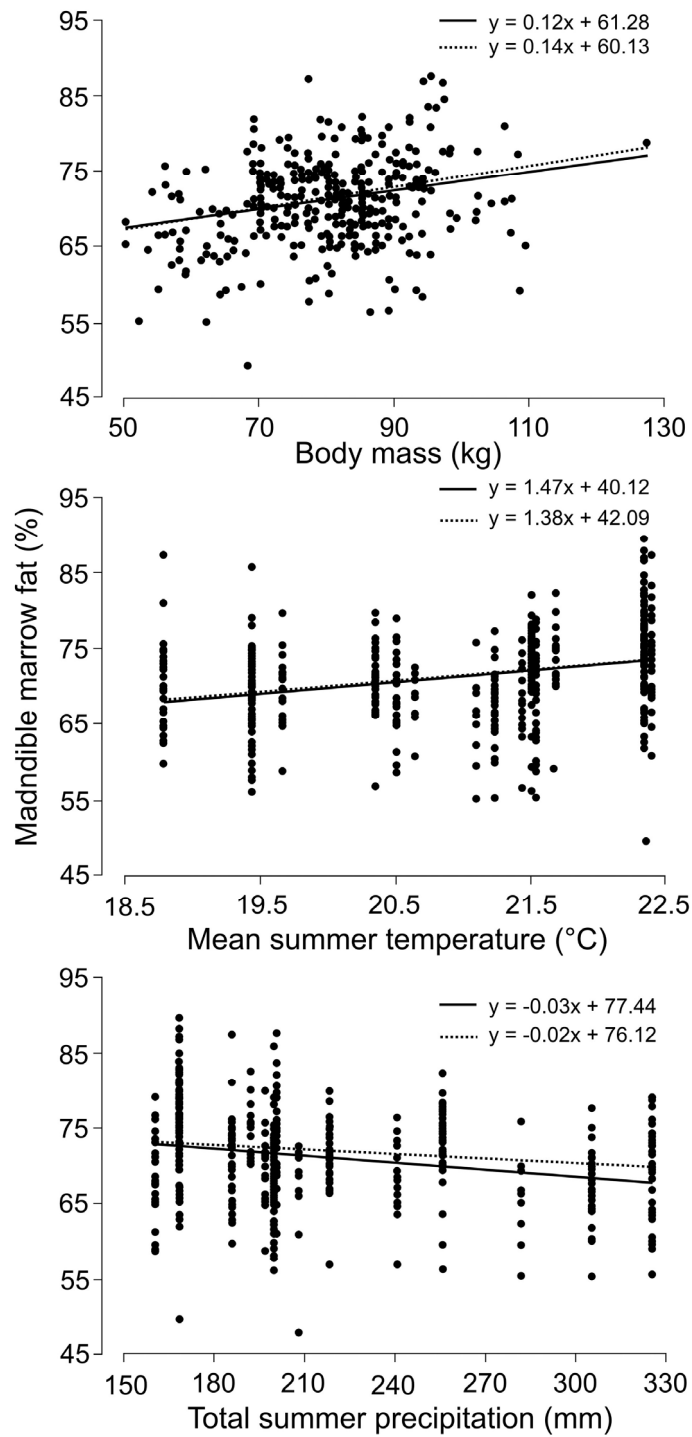


Fig. 12. Percentage of mandible marrow fat in relation to body mass of hinds, mean summer temperature, and the total summer precipitation in 2006-2011. Dotted lines show simple linear regressions. Solid lines show the individual effect of a given explanatory variable with other independent variables held constant at their mean values (body mass – 80.3 kg, mean summer temperature – 21.0°C, total summer precipitation – 217.6 mm). Summer – June-August preceding the date of sampling. See Table 3 for statistical significance of each variable in the complete model.



The increase in mean summer temperature by 1°C accounted for 2.9% of the growth in the marrow fat content, while more rainy summers caused a decrease in the percentage of mandible marrow fat – 3 % per each 100 mm of rain.

#### **4.3. Pregnancy and lactation rates in relation to female age, body mass and marrow fat**

In total, 85% of females in the population aged 1-19 years (N = 541) were found pregnant, while 52% were lactating. Most of the lactating hinds were pregnant (95%); pregnant-lactating females represented 49% of the population. The lowest pregnancy rate (40%) was reported in 1-year-old females; the rate increased to 88% in 2-year-olds (the highest increase), and reached the maximum in 4-year-old females (95%), and then slightly declined with age (91% in 12-19-year-old hinds) (Fig. 13). Pregnancy rates significantly varied with age (Pearson's Chi-squared test,  $\chi^2 = 129.72$ ,  $p < 0.010$ ). However, testing for pairwise differences among age classes (28 pairs) revealed significant differences only between the first class (1-year-old females) and all other age classes (Fisher's exact test,  $p < 0.001$ ) (Appendix 3: Table A3.1).

The share of lactating females among all sampled individuals increased with age from 48% in 2-year-old hinds to a maximum of 84% in 7-8-year-old females, and then decreased to 56% in hinds older than 12 years (Fig. 13). The percentage of lactating females varied significantly among age classes (Pearson's Chi-squared test,  $\chi^2 = 13.34$ ,  $p = 0.038$ ). The highest pairwise differences were found between 7-8-year-old and the three other age classes: 2-year-old, 4-year-old and 12-19-year-old females (Fisher's exact test,  $p$  from 0.002 to 0.045), as well as between 2-year-old and 9-11-year-old hinds (Fisher's exact test,  $p = 0.039$ ) (Appendix 3: Table A3.1).

As the majority of lactating females were pregnant in all age classes (from 87% for 2-year-old females to 100% for 5-6-year-old and 9-11-year-old ones) (Fig. 13), I found a similar variation in the percentage of pregnant-lactating females among the age classes (Pearson's Chi-squared test,  $\chi^2 = 16.46$ ,  $p = 0.011$ ) and pairwise differences in females among the age classes. Significant differences in the share of pregnant-lactating females were observed for the following pairs of females' age classes: 2 and 5-6-year-old, 2 and 7-8-year-old, 2 and 9-11-year-old, 4 and 7-8-year-old, and 7-8 and 12-19-year-old (Fisher's exact test,  $p$  from 0.001 to 0.050) (Appendix 3: Table A3.1).

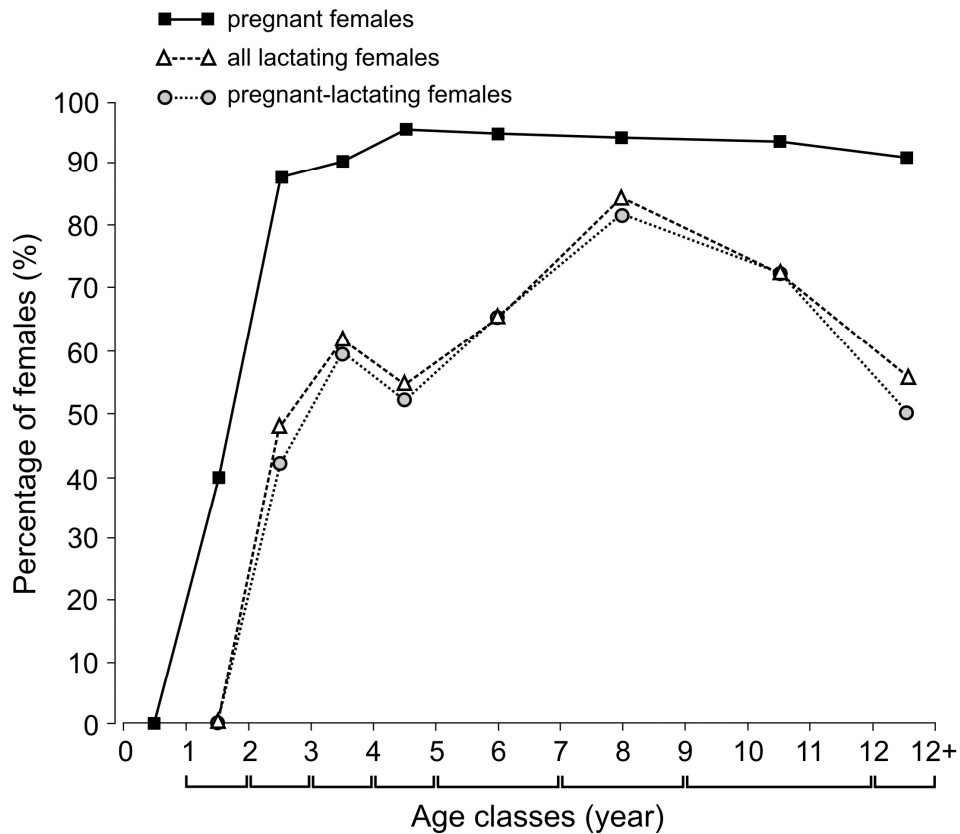


Fig. 13. Percentage of pregnant, all lactating and pregnant-lactating females among all sampled individuals in relation to their age (pooled data). Sample sizes for individual age classes varied from 34 to 75 for pregnant females and from 18 to 48 for all lactating and pregnant-lactating hinds.

Comparison of fertility of hinds among the studied forests was based on 5 wider age classes (Fig. 14). Generally, the age-related variation in the pregnancy rate was the same in the material from AF and BF (where more data were available) (Pearson's Chi-squared,  $p < 0.001$ ): 1-year-old hinds were characterized by significantly lower pregnancy rates compared to older hinds (Fisher's exact test,  $p$  from  $<0.001$  to 0.016) (Appendix 3: Table A3.2). The same pregnancy rate (38%) was observed for 1-year-old females in AF and BF. Pregnancy rates of older age classes did not differ significantly among the studied forests (Pearson's Chi-squared and Fisher's exact tests,  $p$  from 0.239 to 0.965). (Appendix 3: Table A3.5).

In the three forests, most of the lactating females were pregnant (83-100%). In AF and BF, the contribution of both all lactating and pregnant-lactating females in the population increased with age and reached the maximum for 7-11-year-old females, and then decreased for 12-19-year-old hinds (Fig. 14). In both forests, the percentage of all lactating hinds

and pregnant-lactating females was significantly higher among 7-11-year-olds compared to 2-3-year-olds (Fisher's exact test, lactating females – AF:  $p = 0.045$ , BF:  $p = 0.039$ , pregnant-lactating females – AF:  $p = 0.050$ , BF:  $p = 0.019$ ) (Appendix 3: Tables A3.3 and A3.4). I did not find any age-specific differences in the percentage of all lactating and pregnant-lactating females among three forests (Pearson's Chi-squared and Fisher's exact tests,  $p$  from 0.224 to 1) (Appendix 3: Table A3.5).

As the difference in the percentage of pregnant, all lactating and pregnant-lactating females among the studied forests turned out to be insignificant, further analyses were performed for the pooled data.

Pregnant females had significantly higher mean body mass ( $82.3 \pm 0.6$  kg) compared to non-pregnant hinds ( $67.9 \pm 0.8$  kg, ANOVA,  $F = 61.755$ ,  $p < 0.001$ ) (Fig. 15). Pregnant 1-year-old females were on average 5.7 kg heavier than non-pregnant ones (ANOVA,  $F = 7.74$ ,  $p = 0.008$ ). Pregnant 2-3-year-old and 4-19-year-old hinds had higher mean body mass (4.1 kg and 4.9 kg respectively) than non-pregnant females. The observed differences, however, did not reach statistical significance (ANOVA, 2-3-year-old –  $F = 2.027$ ,  $p = 0.157$ , and 4-19-year-old –  $F = 2.878$ ,  $p = 0.091$ ) (Fig. 15).

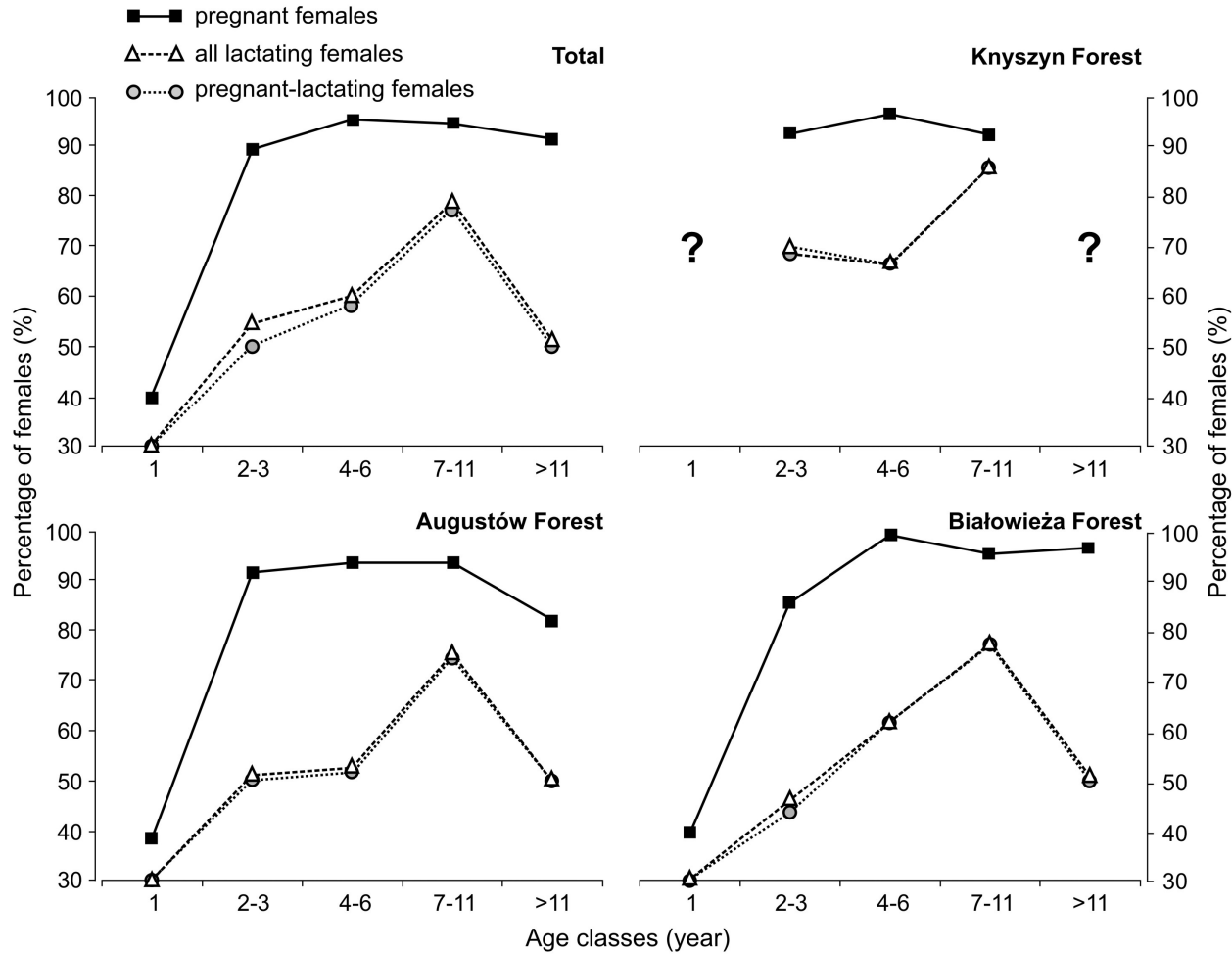


Fig. 14. Percentage of pregnant individuals, all lactating and pregnant-lactating, among all sampled female deer in relation to their age in Augustów, Knyszyn and Białowieża Forests. Sample sizes in forests for individual age classes varied from 11 to 62 – percentage of pregnant females, and from 7 to 41 – percentage of all lactating and pregnant-lactating females. ? – no data available.

The percentage of mandible marrow fat (mean  $\pm$  SE) was significantly higher in pregnant (71.6  $\pm$  0.6%) compared to non-pregnant hinds (67.9  $\pm$  0.8%, ANOVA,  $F = 20.535$ ,  $p < 0.001$ ) (Fig. 15). Having divided the data into separate age classes, the significant difference in the percentage of mandible marrow fat between pregnant and non-pregnant females was found only for 4-19-year-olds, where pregnant females had 4.4% more fat in the mandible marrow compared to non-pregnant ones (ANOVA,  $F = 8.167$ ,  $p = 0.005$ ).

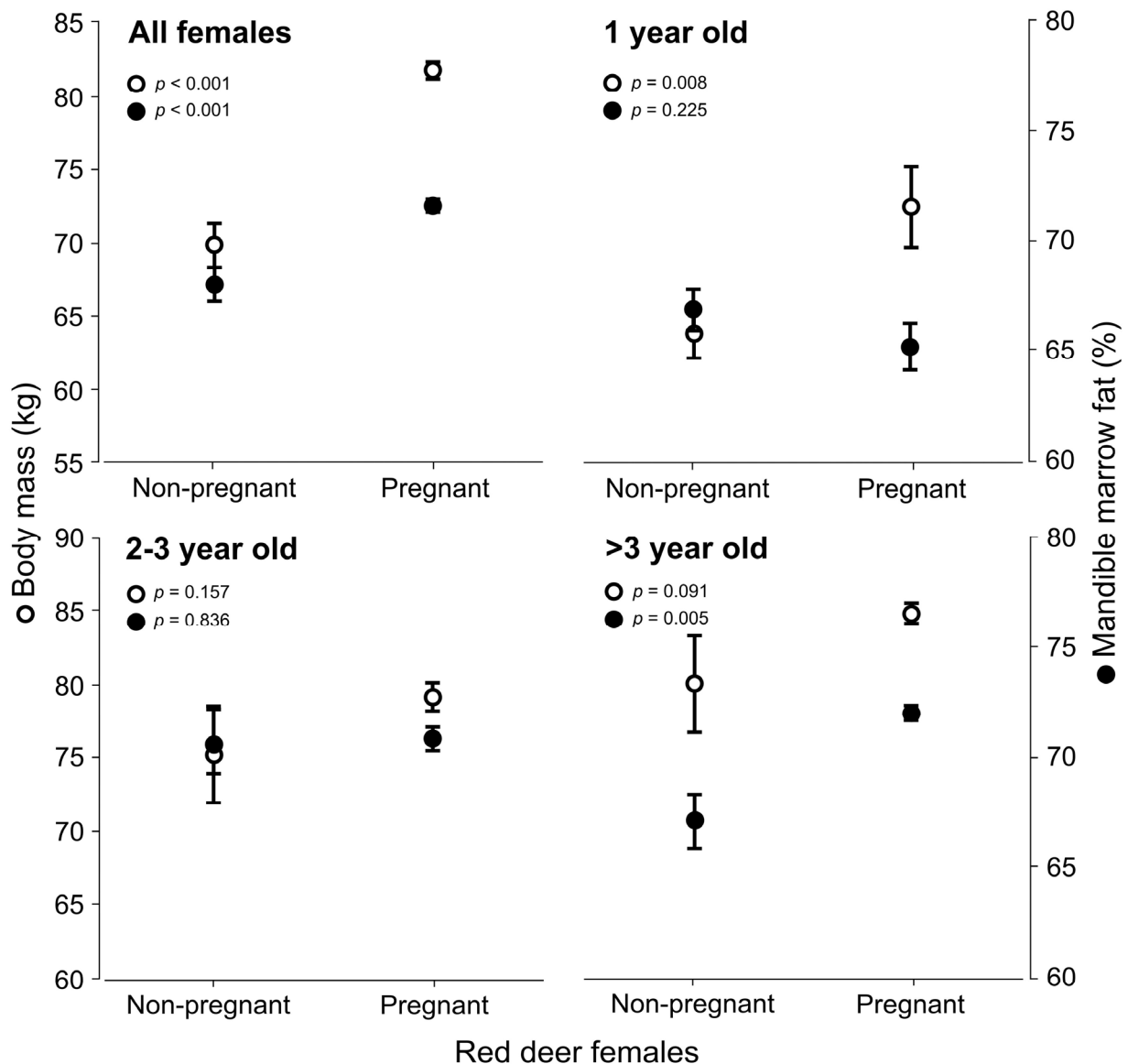


Fig. 15. Mean body mass and percentage of mandible marrow fat of pregnant and non-pregnant females. Differences in mean values tested with one-way ANOVA. Solid dots represent mean mandible marrow fat, open dots – mean body mass. Whiskers denote standard errors.

#### 4.4. Factors explaining the variability in red deer female fertility

Analysis of factors affecting the fertility of all red deer females (aged 1-19 years) provided the set of eight models, including three to five explanatory variables and their interactions. These models explained from 31 to 34% of the total variation in female fertility (Table 4). The age, body mass, percentage of mandible marrow fat and interaction between the age and body mass appeared in all models from the confidence set and had the highest relative importance (Table 5). Almost the same relative importance was shown for the interaction between age and percentage of mandible marrow fat (Table 5). Since the best model in the set had only 32% probability of being the best one, the averaging of 8 models was performed.

The averaged model indicated significant positive effects of body mass and interaction between the age and percentage of mandible marrow on female fertility and significant negative impact of interaction between the age and body mass. Environmental factors (mean temperature of the summer [June-August] preceding the sample collection, the total summer precipitation) and population density did not have significant impact on female fertility (Table 5).

Table 4. The confidence set of generalized linear models (GLMs;  $\Delta AIC_c \leq 5$ ) with the presence (or absence) of red deer pregnancy as a binomial dependent variable and the age of a female (A), body mass (BM), mandible marrow fat (MF), the total summer precipitation (SP), mean summer temperature (ST), and population density (D) as explanatory variables.  $K$  – the number of estimated parameters;  $AIC_c$  – Akaike’s Information Criterion with a second order correction for small sample sizes;  $\Delta AIC_c$  – difference in  $AIC_c$  between a given model and the most parsimonious model;  $\omega_i$  – weight of a model.

Model	$K$	$R^2$	$\Delta AIC_c$	$\omega_i$
A + BM + MF + A×BM + A×MF	6	0.34	0	0.318
A + BM + MF + SP + A×BM + A×MF	7	0.34	1.75	0.132
A + BM + MF + ST + A×BM + A×MF	7	0.34	1.94	0.120
A + BM + MF + D + A×BM + A×MF	7	0.34	2.02	0.116
A + BM + MF + SP + ST + A×BM + A×MF	8	0.34	3.64	0.052
A + BM + MF + D + SP + A×BM + A×MF	8	0.34	3.84	0.047
A + BM + MF + D + ST + A×BM + A×MF	8	0.34	4.03	0.042
A + BM + MF + A×BM	5	0.31	4.94	0.027

Table 5. Relative importance of independent variables for the confidence set of the most parsimonious models predicting the female fertility ( $n = 8$  models,  $\Delta AIC_c \leq 5$ ), with averaged coefficients, unconditional standard errors, and 95% confidence intervals. Significant effects are shown in bold.

Variable	Relative importance in the confidence set of models	Mean coefficient $\pm$ SE	95% confidence intervals	
			Lower	Upper
Intercept	-	-6.61 $\pm$ 3.83	-14.15	0.92
<b>Body mass</b>	1	0.14 $\pm$ 0.02	0.09	0.19
Age	1	0.16 $\pm$ 0.61	-1.04	1.37
Mandible marrow fat	1	-0.03 $\pm$ 0.05	-0.14	0.06
<b>Age <math>\times</math> Body mass</b>	1	-0.02 $\pm$ 0.005	-0.03	-0.01
<b>Age <math>\times</math> Mandible marrow fat</b>	0.97	0.02 $\pm$ 0.01	0.003	0.04
Total summer precipitation	0.27	0.002 $\pm$ 0.004	-0.005	0.01
Mean summer temperature	0.25	-0.05 $\pm$ 0.14	-0.34	0.23
Population density	0.24	0.02 $\pm$ 0.12	-0.22	0.27

To analyse the role of each significant factor (body mass, percentage of mandible marrow, age) on female fertility, the effect of each factor was corrected by the effects of the two other factors. The body mass had the most profound influence (Fig. 16). Within the observed range of body masses, the probability of being a fertile female increased from 0.33 to 1. The shape of the probability curve indicated the highest growth (53%) in the probability of being fertile with the body mass increasing from 52 to 80 kg. Further growth of female mass had a weaker effect. The percentage of mandible marrow fat had an almost linear positive effect on female's probability of being fertile. With mandible marrow fat growing from 50% to 88%, the probability of being fertile increased by 28%. There was a slight positive effect of female age on her probability of being fertile (Fig. 16).

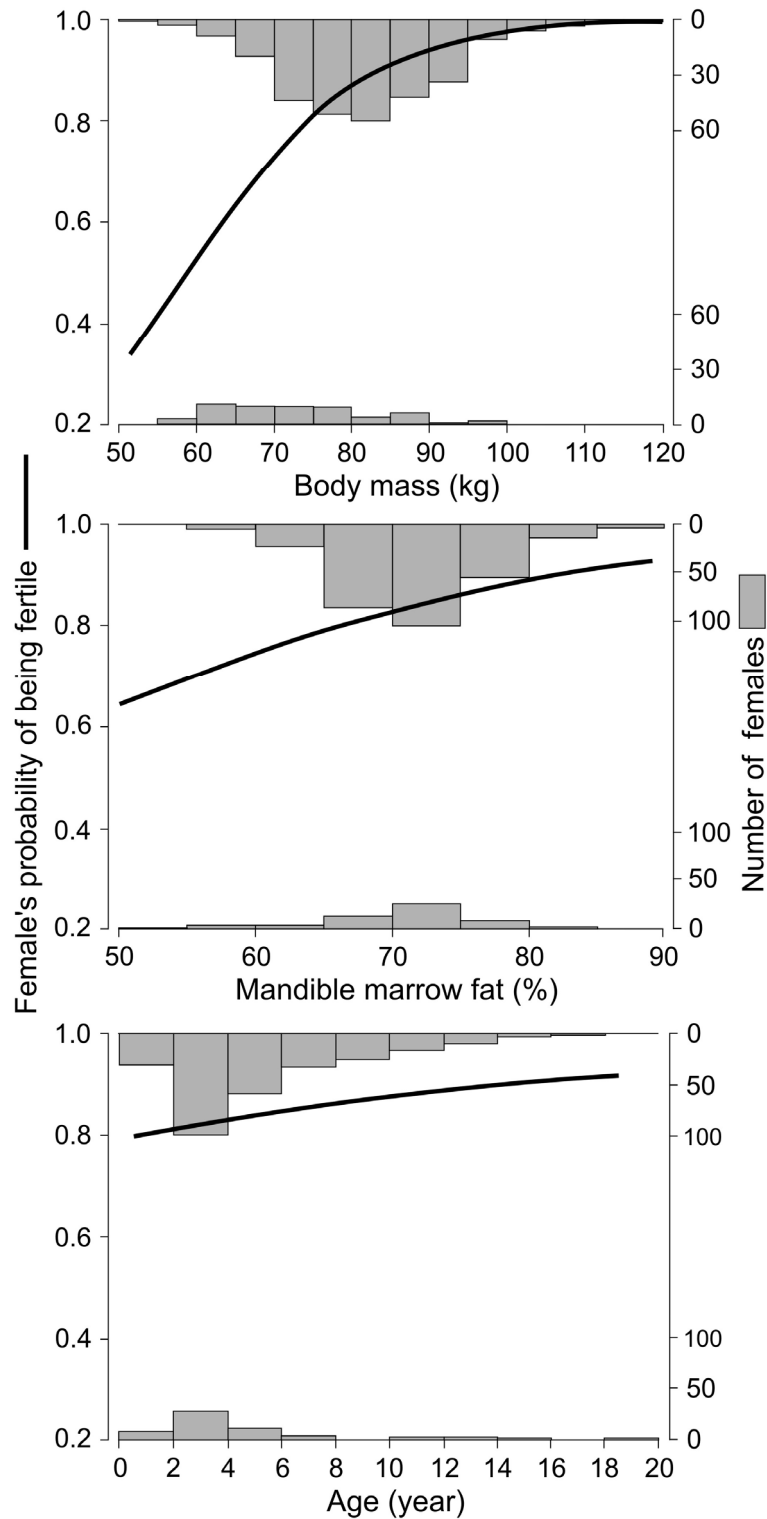


Fig. 16. Female's probability of being fertile in relation to her body mass, the percentage of mandible marrow fat, and age (pooled data). The effect of each factor was corrected by the effects of the two other factors. Histograms on the top and the bottom of each chart represent the number of pregnant (top) and non-pregnant (bottom) females (respectively) in the classes of body mass, percentage of marrow fat, and age.



As the highest variation in fertility was observed in 1-year-old hinds, I attempted to determine factors affecting 1-year-old hinds and all older females (2-19 years old) separately. The model selection procedure performed on models testing the significance of factors affecting the fertility of 1-year-old females indicated the confidence set of 11 models explaining from 21 to 31% of the observed variation in fertility (Appendix 4: Table A4.1). The best model in the set had only 20% probability of being the best one, thus all models were averaged. From all explanatory variables, only body mass was included in all models (the highest relative importance). In the averaged model, this variable had a positive significant effect on hind fertility (Table 6).

Table 6. Relative importance of independent variables for the confidence set of the most parsimonious models ( $n = 11$  models,  $\Delta AIC_c \leq 4$ ) predicting fertility of 1-year-old females, with averaged coefficients, unconditional standard errors, and 95% confidence intervals. Significant effects are shown in bold.

Variable	Relative importance in the confidence set of models	Mean coefficient $\pm$ SE	95% confidence intervals	
			Lower	Upper
Intercept	-	-3.05 $\pm$ 6.77	-16.54	10.45
<b>Body mass</b>	1	0.11 $\pm$ 0.04	0.02	0.20
Mandible marrow fat	0.58	-0.13 $\pm$ 0.08	-0.30	0.03
Population density	0.29	-0.22 $\pm$ 0.27	-0.76	0.31
Total summer precipitation	0.25	0.01 $\pm$ 0.01	-0.01	0.02
Mean summer temperature	0.18	0.13 $\pm$ 0.28	-0.44	0.70

The probability of a 1-year-old female to be fertile increased with the increasing body mass from 0.1 to 0.9 (Fig. 17). The highest effect of the body mass was observed for hinds weighing 60-85 kg; such an increase in the body mass within this range caused an increase in the probability by 47%.

In the case of  $\geq 2$ -year-old females, modelling the probability of being fertile resulted in 26 models, which explained from 3 to 10% of the total observed variation (Appendix 4: Table A4.2). Among explanatory variables, the body mass and percentage of marrow fat had the highest relative importance in the confidence set of the models. As the top model in the set had only 8% probability of being the best one, the averaging of 26 models was applied. The averaged model showed a significant positive effect of interaction between the age and percentage of mandible marrow fat on the female fertility rate (Table 7). The body mass also positively influenced the fertility of  $\geq 2$ -year-old females; its effect, however, was not significant.

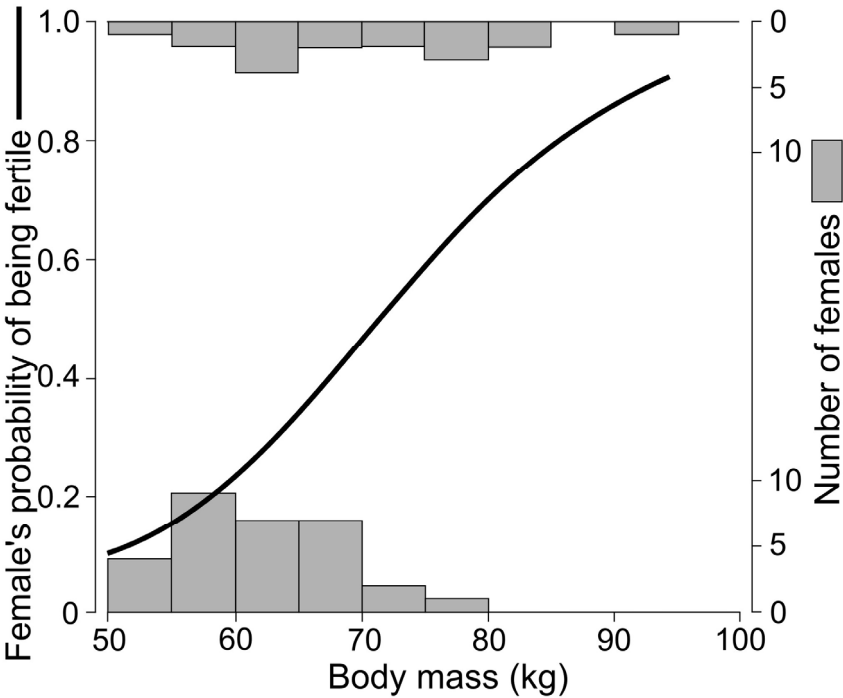


Fig. 17. Probability of a 1-year-old female to be fertile in relation to her body mass. Other explanations as in Fig. 16.

Table 7. Relative importance of independent variables for the confidence set of the most parsimonious models ( $n = 26$  models,  $\Delta AIC_c \leq 4$ ) predicting fertility of  $\geq 2$ -year-old females, with averaged coefficients, unconditional standard errors, and 95% confidence intervals. Significant effects are in bold.

Variable	Relative importance in the confidence set of models	Mean coefficient $\pm$ SE	95% confidence intervals	
			Lower	Upper
Intercept	-	0.20 $\pm$ 5.95	-15.86	11.88
Body mass	0.87	0.05 $\pm$ 0.03	-0.005	0.10
Mandible marrow fat	0.83	-0.02 $\pm$ 0.08	-0.18	0.14
Age	0.63	-0.98 $\pm$ 0.78	-2.52	0.55
<b>Age <math>\times</math> Mandible marrow fat</b>	0.55	0.02 $\pm$ 0.01	0.0003	0.04
Mean summer temperature	0.19	-0.09 $\pm$ 0.19	-0.47	0.28
Population density	0.17	0.06 $\pm$ 0.15	-0.24	0.35
Total summer precipitation	0.17	0.001 $\pm$ 0.005	-0.01	0.01
Age $\times$ Body mass	0.17	-0.01 $\pm$ 0.01	-0.02	0.01

The individual effects of body mass, percentage of mandible marrow, and age on the fertility of  $\geq 2$ -year-old hinds were analysed, with the effect of each factor corrected for the effects of the two other factors. Both the body mass and percentage of mandible marrow had positive effects on hind fertility (Fig. 18). The increasing body mass (from 53 to 120 kg) caused the growth in female's probability of being fertile by 23%; however, the relationship was nonlinear, thus the strongest effect of the body mass was observed in lighter females (50-70 kg). The increase in mandible marrow fat from 50 to 88% resulted in the growing probability of a female to be fertile by 21%. There was a slight negative effect of age on the fertility probability. Between the age of 2 and 19, the probability decreased by 4% (Fig. 18).

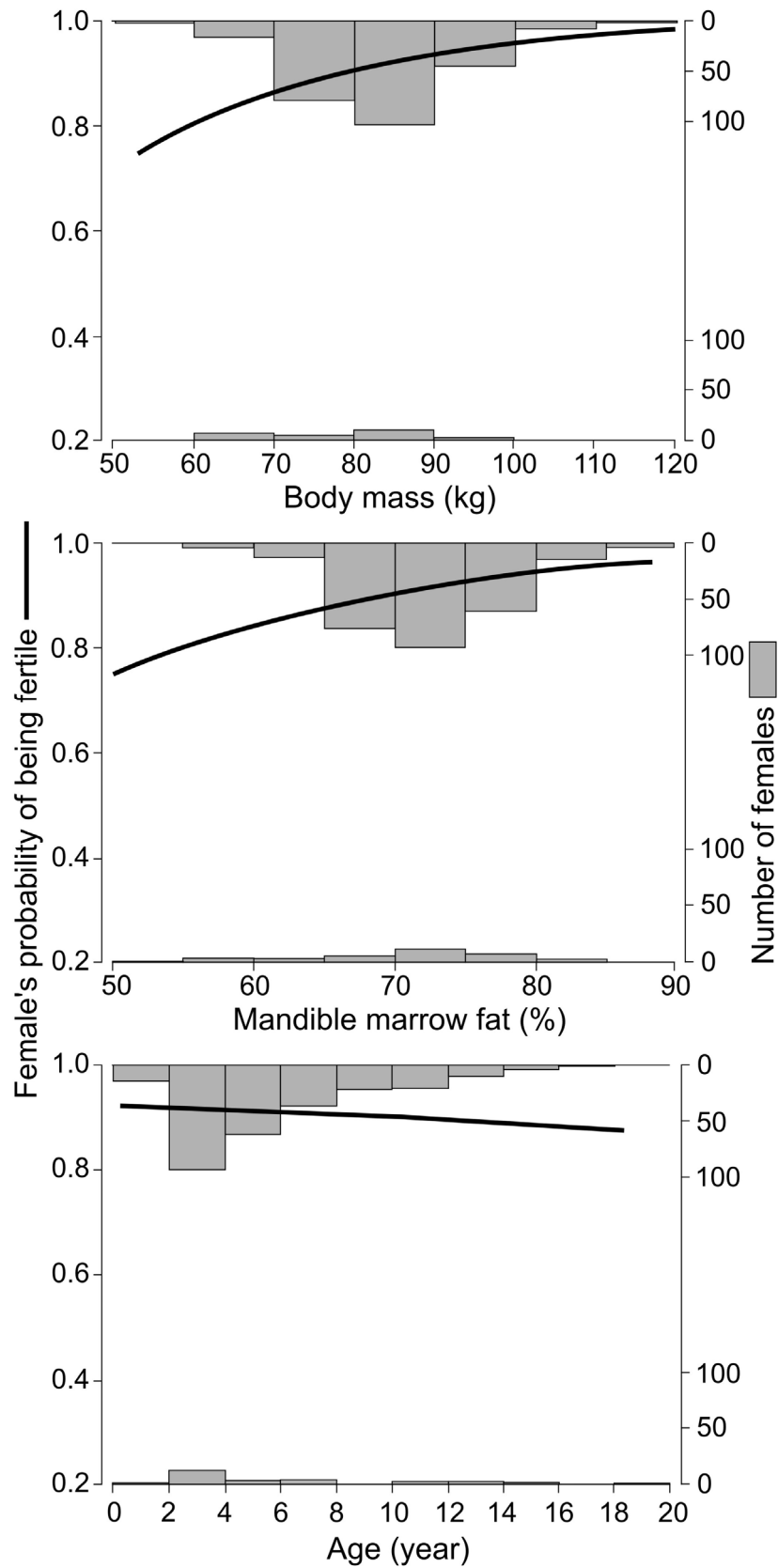


Fig. 18. Probability of  $\geq 2$ -year-old female to be fertile in relation to her body mass, percentage of mandible marrow fat, and age. The effect of each factor was corrected by the effects of two other factors. Other explanations as in Fig. 16.

#### 4.5. Sex ratio of red deer foetuses

All of the surveyed females, except one, had only one foetus; twin foetuses (female and male) were found in one hind (2 years old) (0.2%). Determination of sex in foetuses showed a higher proportion of males in the whole sample (sex ratio 1:0.68) but it did not differ significantly from the 1:1 ratio (odds ratio = 0.678,  $p = 0.111$ ). Having divided the pregnant females into age classes, I observed a higher proportion of female foetuses in 1-year-old mothers with poor body condition (Fig. 19). The opposite relationship was found in older females (2-6 years old). Equal proportion of male to female foetuses was recorded in 7-19 years old females (Fig. 19). However, due to small sample sizes, none of those sex ratios differed significantly from 1:1 (Appendix 5: Table A5.1). I did not find significant differences in the foetus sex ratio among all female age classes ( $\chi^2 = 2.39$ ,  $p = 0.143$ ) and in pairwise combinations of age classes (Appendix 5: Table A5.2).

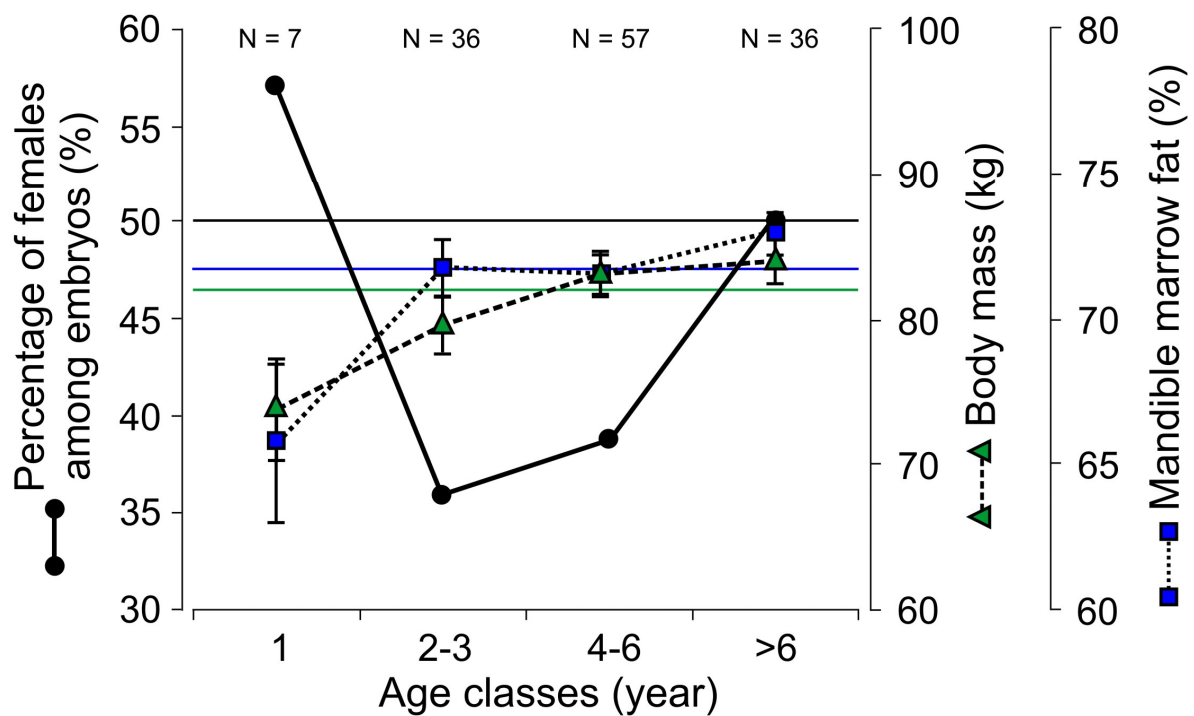


Fig. 19. Relationship between the percentage of females among foetuses and indices of body condition of hinds in different age classes. Horizontal solid lines represent: black – 1:1 sex ratio, green – mean body mass, blue – mean percentage of mandible marrow fat. Whiskers denote standard errors. N – the number of foetuses with determined sex.

Hinds bearing male foetuses were on average heavier (by 3 kg) than those with female foetuses (Fig. 20), however, due to a small sample size, the differences were not significant (Appendix 5: Table A5.3). Interestingly, these differences decreased with the age of mothers. The average mandible marrow fat content did not differ between hinds with female and male foetuses. One-year-old with male foetuses had, on average, somewhat lower percentage of mandible marrow fat than those with daughters (Fig. 20), yet the difference was statistically insignificant (Appendix 5: Table A5.3).

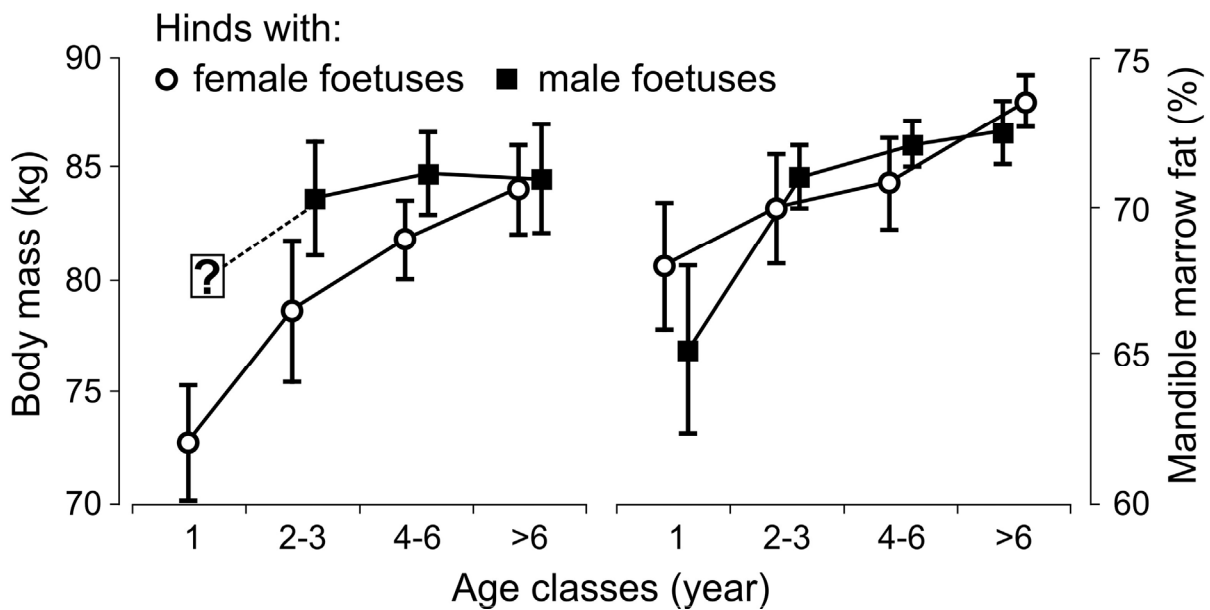


Fig. 20. Body condition indices of hinds bearing foetuses of the opposite sex. Whiskers denote standard errors. ? – no data available.

#### 4.6. Life tables of the deer population

The survivorship table showed that at birth female fawns had life expectancy of 4.3 years. Generally, life expectancy of females showed a slight constant decrease with time – from 3.9 years for 0.5-year-olds to 3.6 years for 11.5-year-olds (Table 8). A steeper decrease in life expectancy of females was observed from birth to the first half of their lives and for >11.5-year-old hinds. About 66% of newborn females survived 1.5 year, 51% – 2.5 year, and only 31% – 4.5 year of life. The survivorship curve indicated almost the same rate of mortality for 0.5-10.5-year-old females (20-25%) (Fig. 21). Somewhat higher mortality rates were observed in newborn females in the first 6 months of lives (14%, which translates to 28% per annum) and in old hinds (11.5-19.5-year-olds – 28%, on average).

Table 8. Survivorship table for females in the red deer population in NE Poland, based on the data from 2006-2011.  $N$  = number of alive females at the beginning of a given age interval,  $n_x$  = number of alive females at the beginning of a given age interval after smoothing,  $l_x$  = survival rate at the begin of an age interval,  $d_x$  = number of dying females within a given age interval,  $q_x$  = rate of mortality,  $p_x$  = rate of survival,  $e_x$  = life expectancy in different years, the number of individuals at birth (age 0) calculated from the fertility rate and the sex ratio of foetuses, number of 0.5-year-old individuals calculated based on the number of offspring which suckled hinds in the autumn-winter season (lactation data). All calculations in each age category were performed on smoothed numbers ( $n_x$ ) which were obtained by fitting the exponential function to the raw frequencies (Appendix 6: Table A6.1).

Age (years) $x$	$N$	Smoothed					
		$n_x$	$l_x$	$d_x$	$q_x$	$p_x$	$e_x$
0	160	140	1.000	20	0.143	0.857	4.282
0.5	107	120	0.857	27	0.225	0.775	3.913
1.5	75	93	0.664	21	0.226	0.774	3.903
2.5	75	72	0.514	16	0.222	0.778	3.896
3.5	71	56	0.400	13	0.232	0.768	3.866
4.5	63	43	0.307	9	0.209	0.791	3.884
5.5	31	34	0.243	8	0.235	0.765	3.779
6.5	28	26	0.186	6	0.231	0.769	3.788
7.5	21	20	0.143	4	0.200	0.800	3.775
8.5	28	16	0.114	4	0.250	0.750	3.594
9.5	10	12	0.086	3	0.250	0.750	3.625
10.5	18	9	0.064	2	0.222	0.778	3.667
11.5	19	7	0.050	1	0.143	0.857	3.571
12.5	6	6	0.043	2	0.333	0.667	3.083
13.5	13	4	0.029	1	0.250	0.750	3.375
14.5	6	3	0.021	0	0	1.000	3.333
15.5	6	3	0.021	1	0.333	0.667	2.333
16.5	1	2	0.014	0	0	1.000	2.250
17.5	0	2	0.014	1	0.500	0.500	1.250
18.5	1	1	0.007	0	0	1.000	1.000
19.5	1	1	0.007	1	1.000	0	0

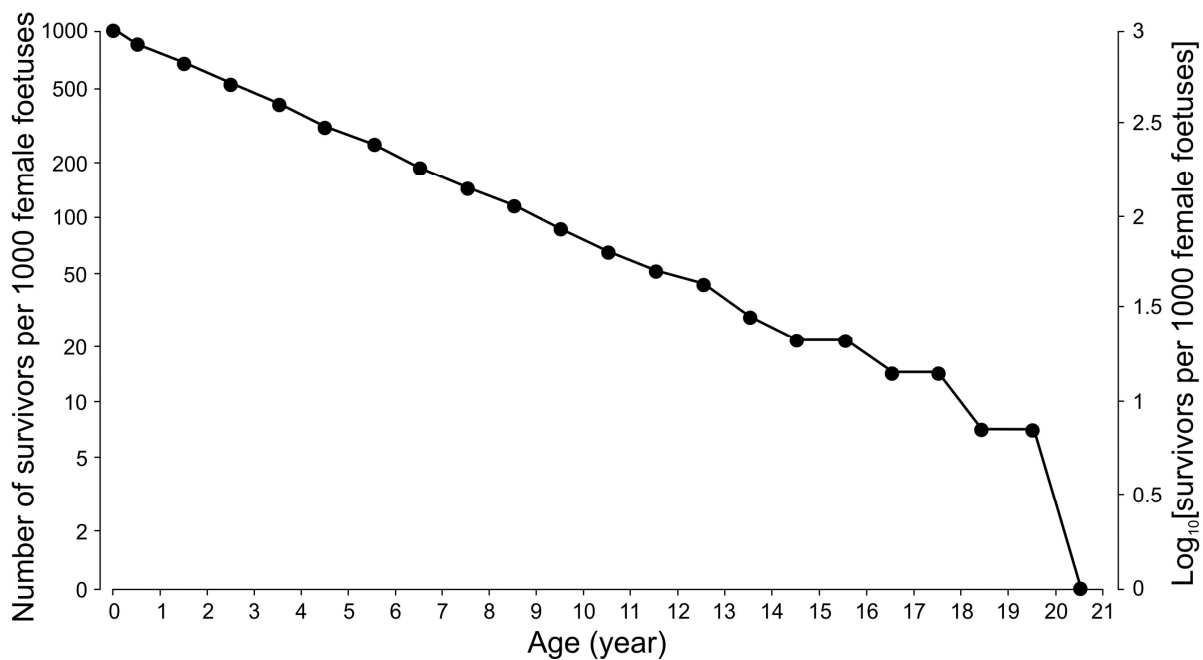


Fig. 21. Survivorship curve for a cohort of 1000 females in the red deer population. Based on the data from Table 8.

The fertility data allowed for calculation of an expected number of offspring produced by a female during her entire life (Table 9). The net reproduction rate (NRR [ $R_0$ ]) of females from the studied deer population was 1.001 individuals. This means that the average female with a mean life expectancy of 4.3 year produced 1.001 female and 1.349 male offspring over the course of her life (in total – 2.35 young). The highest input to the population net reproduction rate was provided by 2.5-year-old females – 0.453 (19.3%); starting from 3.5-year-old hinds, the contribution of individual age classes to NRR gradually decreased (Table 9, Fig. 22). Interestingly, 0.266 of NRR (11.3%) was produced by 1.5-year-old females – the first-time breeders. In total, almost half of NRR (46%) was contributed by 1.5-3.5-year-old females. The estimated intrinsic rate of the population natural growth ( $r$ ) was 0.0002 (Table 9). It indicates that if the reproduction rate, the sex ratio of offspring, and the mortality rate in each age class remain constant, the population of red deer will be stable.



Table 9. Fertility table of females in the studied red deer population.  $m_x$  – calculated based on proportions of pregnant females and sex ratios of foetuses in given age categories of hinds.  $R_0 (\Sigma V_x)$  – the net reproduction rate (average number of offspring produced lifelong by a female with mean life expectancy of 4.3 year). The intrinsic rate of the natural increase ( $r$ ) is the rate at which the population grows in size per individual per unit of time and was assessed according to the equation:  $r \approx \ln R_0/T_c$ . Mean generation length ( $T_c$ ) is the mean period elapsing between the birth of parents and the birth of offspring, calculated as  $T_c = \Sigma l_x m_x x / R_0$ .

Age (years)	Proportion of surviving at the start of age interval	No. of female offspring per female aged $x$ years	Product of $l_x m_x$ – female offspring,	Product of $l_x m_x x$	No. of male offspring per female aged $x$ years,	Product of $l_x m_x$ – male offspring,	No. of all offspring per female aged $x$ years,	Product of $l_x m_x$ – all offspring,
$x$	$l_x$	$m_x$	$V_x$		$m_x$	$V_x$	$m_x$	$V_x$
0	1.000	0	0	0	0	0	0	0
0.5	0.857	0	0	0	0	0	0	0
1.5	0.664	0.229	0.152	0.228	0.171	0.114	0.400	0.266
2.5	0.514	0.318	0.163	0.408	0.562	0.289	0.880	0.453
3.5	0.400	0.325	0.130	0.456	0.576	0.230	0.901	0.361
4.5	0.307	0.368	0.113	0.508	0.585	0.180	0.952	0.293
5.5	0.243	0.366	0.089	0.489	0.583	0.142	0.949	0.231
6.5	0.186	0.366	0.068	0.442	0.583	0.108	0.949	0.176
7.5	0.143	0.469	0.067	0.503	0.469	0.067	0.939	0.134

Table 9. – continued on the next page

Table 9. – concluded.

Age (years)	Proportion of surviving at the start of age interval	No. of female offspring per female aged $x$ years	Product of $l_x m_x$ – female offspring,	Product of $l_x m_x x$	No. of male offspring per female aged $x$ years,	Product of $l_x m_x$ – male offspring,	No. of all offspring per female aged $x$ years,	Product of $l_x m_x$ – all offspring,
$x$	$l_x$	$m_x$	$V_x$		$m_x$	$V_x$	$m_x$	$V_x$
8.5	0.114	0.469	0.054	0.456	0.469	0.054	0.939	0.107
9.5	0.086	0.468	0.040	0.381	0.468	0.040	0.936	0.080
10.5	0.064	0.468	0.030	0.316	0.468	0.030	0.936	0.060
11.5	0.050	0.468	0.023	0.269	0.456	0.023	0.936	0.047
12.5	0.043	0.456	0.020	0.244	0.456	0.020	0.912	0.039
13.5	0.029	0.456	0.013	0.352	0.456	0.013	0.912	0.026
14.5	0.021	0.456	0.010	0.142	0.456	0.010	0.912	0.020
15.5	0.021	0.456	0.010	0.151	0.456	0.010	0.912	0.020
16.5	0.014	0.456	0.007	0.107	0.456	0.007	0.912	0.013
17.5	0.014	0.456	0.007	0.114	0.456	0.007	0.912	0.013
18.5	0.007	0.456	0.003	0.066	0.456	0.003	0.912	0.007
19.5	0.007	0.456	0.003	0.063	0.456	0.003	0.912	0.007
			$R_0 = 1.001$	$T_c = 5.508$	$R_0 = 1.349$	$R_0 = 2.350$		
$r \approx 0.0002$								

Based on the literature data, which reported that prenatal mortality in red deer was minimal (Mitchell and Lincoln 1973), I assumed that mortality of offspring, within the period from the foetus stage (autumn-winter season when fertility of hinds was assessed) till the first 6 months of life (the following autumn when the number of survivors was assessed based on the lactation status of hinds), occurred predominantly after parturition. Therefore, to assess the mortality of offspring during the first 6 months of life, I compared NRR (net reproduction rate) calculated based on the expected number of offspring (2.35) with NRR estimated based on the number of fawns which survived until the age of 0.5 year (lactation data) (1.39) (Fig. 22; Appendix 6: Table A6.1).

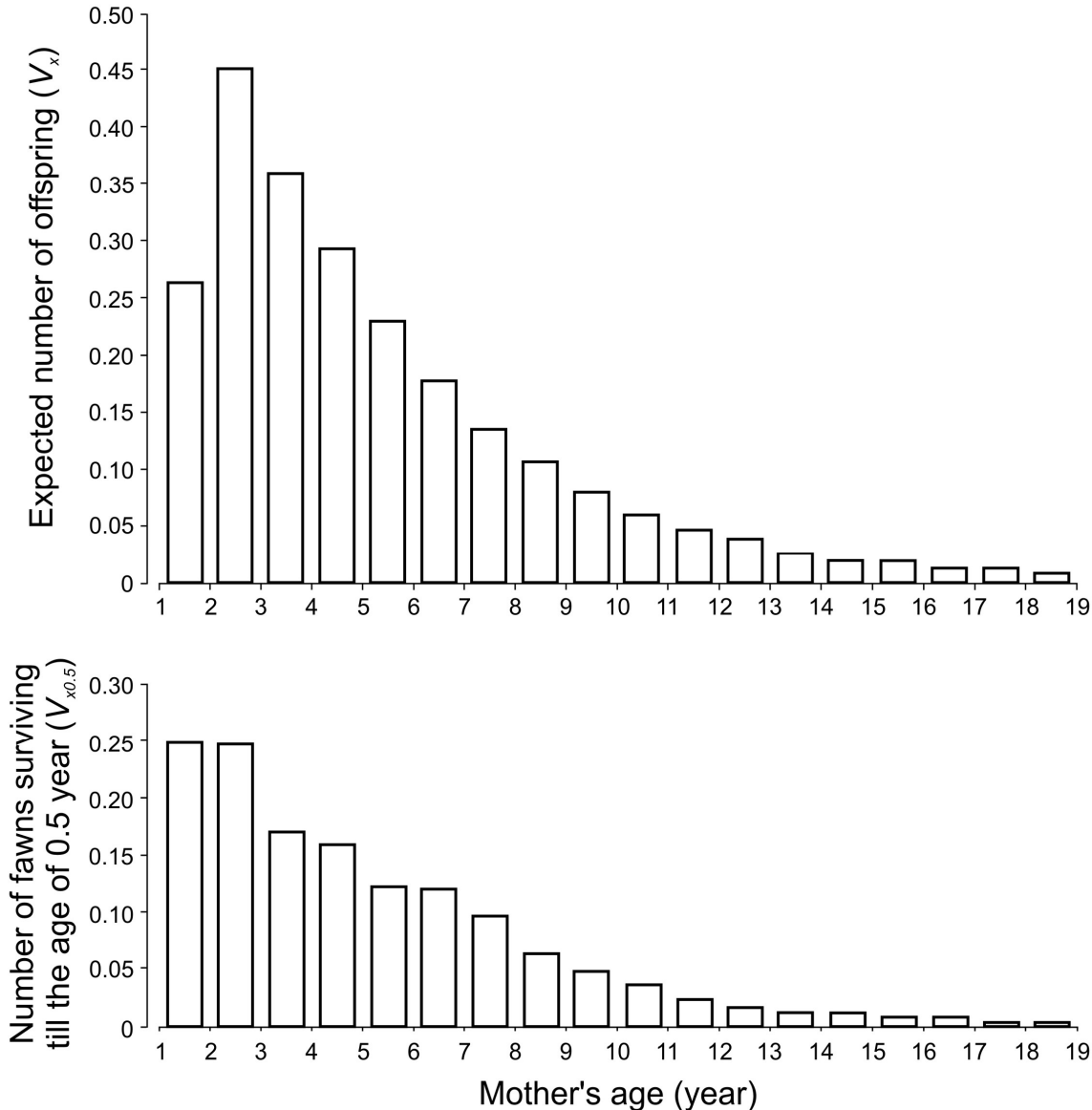


Fig 22. The expected number of offspring ( $V_x$ ) and the corresponding number of fawns which survived until the age of 0.5 year ( $V_{x0.5}$ ) in different age categories of mothers. Numbers based on Table 9 and Table A6.1 in Appendix 6.

The analysed data showed that in the first 6 months of life, due to mortality factors, the number of offspring produced by a female with mean life expectancy (4.3 years) dropped by 41%. The highest contribution to NRR, calculated based on the number of fawns which survived until the age of 0.5 year, was provided by 1.5- and 2.5-year-old females – about 18% each. The input of older females (starting with 3.5-year-olds) gradually decreased with the age of hinds (Fig. 22).

Juxtaposition of the expected number of offspring (at the stage of pregnancy) with the corresponding number of fawns which survived till the age of 0.5 year (lactation in the following year) showed that the percentage of survivors decreased with the age of a mother ( $N = 9$ ,  $p = 0.02$ ) (Fig. 23). On average, the survival rate of fawns (till autumn) in 2-8-year-old mothers was 61%. In older females, the percentage of calves surviving the age of 0.5 year decreased from 59% in 10-year-old mothers to 41% in 18-year-olds (Fig. 23).

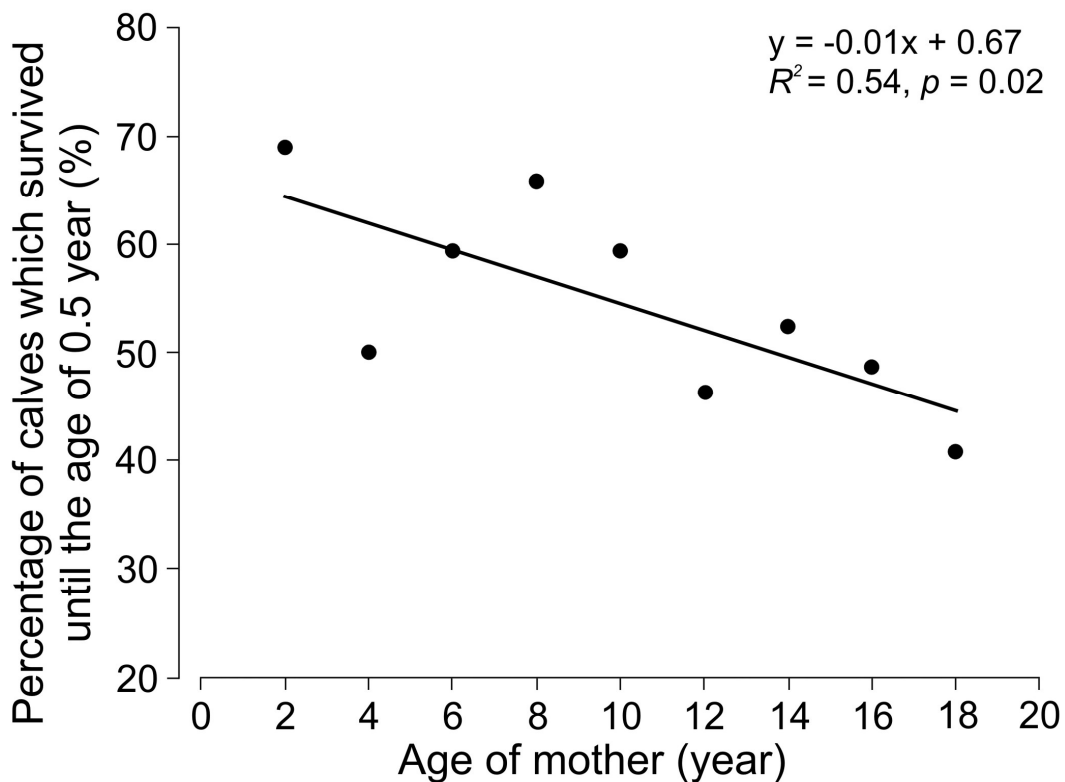


Fig. 23. Percentage of red deer calves that survived until the age of 0.5 year in relation to age of a mother. Percentage of calves was calculated by dividing the expected number of offspring ( $V_x$ ) in each age category by the corresponding number of fawns which survived until the age of 0.5 year ( $V_{x0.5}$ ). The age of mothers is presented in 2-year-long classes.

## 5. DISCUSSION

### 5.1. Recapitulation of the results

In woodlands of NE Poland, the population density of red deer was positively correlated with the habitat productivity expressed as a share of deciduous and mixed tree stands, even though supplementary winter feeding provided by managers for ungulates was most abundant in poor, coniferous-dominated districts (Fig. 24).

Both the body mass and the percentage of mandible marrow fat in hinds increased with their age. However, there was a noticeable decline in mean body mass in females older than 9-11 years. The steepest growth of both indices was observed in the first four years of the females' life. Body condition of 1-year-old females was significantly lower than in older hinds. Moreover, the percentage of mandible marrow fat in hinds was positively correlated with mean summer temperature in the period preceding the sample collection (June-August) and negatively correlated with the total summer precipitation. There was no significant effect of population density on the mandible marrow fat content. Both body condition indices were weakly positively associated (Fig. 24).

Most of the female red deer were found pregnant (85%), while half of them lactating. Almost all of lactating females were pregnant. The pregnancy rate increased with the age of females, from 40% in 1-year-olds to a maximum of 95% in 4-year-olds, and then slightly decreased – 91% in 12-19-year-olds. The percentage of lactating females increased with the age of mothers, from 48% in 2-year-old hinds to a maximum of 84% in 7-8-years-olds, and decreased to 56% in hinds older than 12 years.

Pregnant females had significantly higher body mass and percentage of mandible marrow fat compared to non-pregnant hinds. Having divided the data into separate age classes, only pregnant 4-19-year-old hinds had a higher percentage of mandible marrow fat compared to non-pregnant females, whereas pregnant 1-year-old hinds were heavier than non-pregnant females. The observed age-specific differences in the body condition of females among the studied forests did not result in significant differences in their pregnancy rates.

Fertility of red deer hinds was positively associated with their body mass and the interactive effect of their age and percentage of mandible marrow fat, and negatively correlated with interactive effect of their age and body mass. Environmental and population factors did not affect the female fertility. Fertility of 1-year-old mothers was positively affected by their body mass, while fertility of older females was positively correlated with interactive effect of their age and percentage of mandible marrow fat.

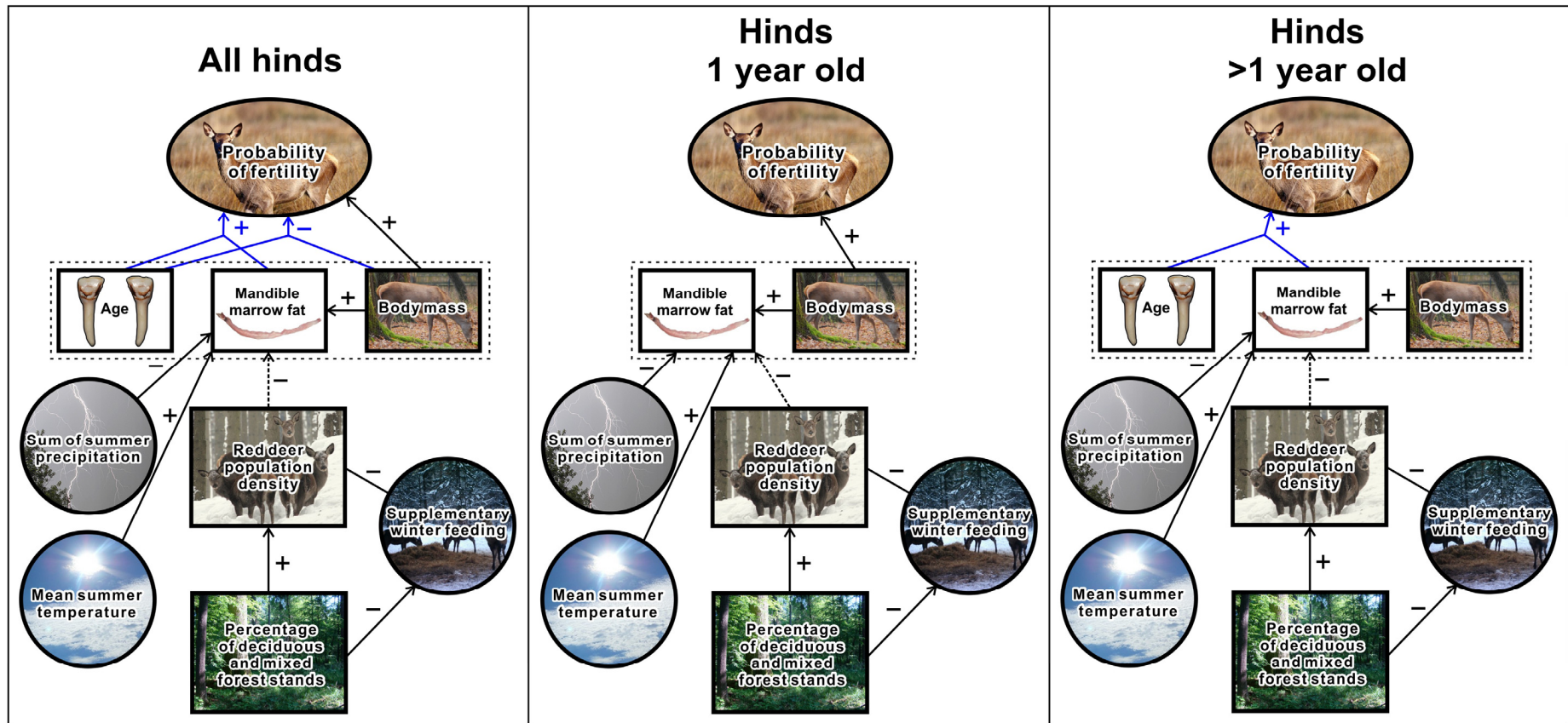


Fig. 24. Summary of factors affecting the fertility of red deer females in Augustów, Knyszyn, and Białowieża Forests. Black solid lines (correlations) and arrows (simple and multiple regression models, generalized linear models [GLMs]) show a significant relationship between the factors; blue solid arrows (GLMs) denote a significant effect of interaction; a black dashed arrow denotes a significant relationship between factors indicated by a simple regression model and not significant in a multiple regression model; “+” – positive relationships, “-” – negative relationships.

The majority of sampled females had one foetus, twins were reported only once. The foetus sex ratio was male-biased (1:0.68). A higher proportion of female foetuses was observed in 1-year-old mothers with worse body condition, the opposite relationship in older females (2-6-year-olds) and equal proportion of sexes among foetuses – for 7-19-year-old hinds. However, none of those sex ratios significantly differed from 1:1. Females bearing male foetuses were on average heavier and exhibited a higher percentage of mandible marrow fat compared to females with female foetuses. The observed differences in the body condition between mothers bearing female versus male foetuses decreased with the age of mothers.

Life expectancy of a female fawn at birth was 4.3 years and steadily decreased with time. Each year, every age class of the red deer female population suffered a similar proportion of losses. On average, an individual hind was expected to produce 1 female and 1.3 male offspring during her lifetime. Younger age classes (1.5-3.5-year-old females) had the highest input (46%) to the total reproduction. Mortality of offspring during the first half year of life averaged 41%. The percentage of calves which survived till the age of 0.5 year decreased with the age of mothers. The studied populations were expected to be stable or grow at a very slow rate.

## **5.2. Reproductive parameters of red deer females in NE Poland compared to other European populations**

Based on the literature review, information on red deer fertility was gathered from 38 populations spread from Scotland and Norway in NW Europe, to Serbia and Ukraine in SE parts of the continent (Fig. 25). Full data are presented in Appendix 7: Table 7.1. In Europe, the red deer population density ranged from 1.5 to 34.4 ind./km<sup>2</sup>. Compared to the whole range of variation, the estimated population densities of red deer in this study were relatively low, markedly below the average value (Table 10). The female fertility rate varied considerably throughout Europe (28-100%). The lowest values were reported in overabundant populations of red deer inhabiting suboptimal habitats in Scottish uplands (Lowe 1969, Mitchell and Lincoln 1973, Mitchell and Crisp 1981) and in the Mesola Nature Reserve, Italy, where the deer population was exposed to high interspecific competition for food resources with fallow deer (*Dama dama*) (Ferretti and Mattioli 2012). The fertility rate of females from populations inhabiting NE Poland was high and above the mean value calculated for this parameter throughout Europe (Table 10).



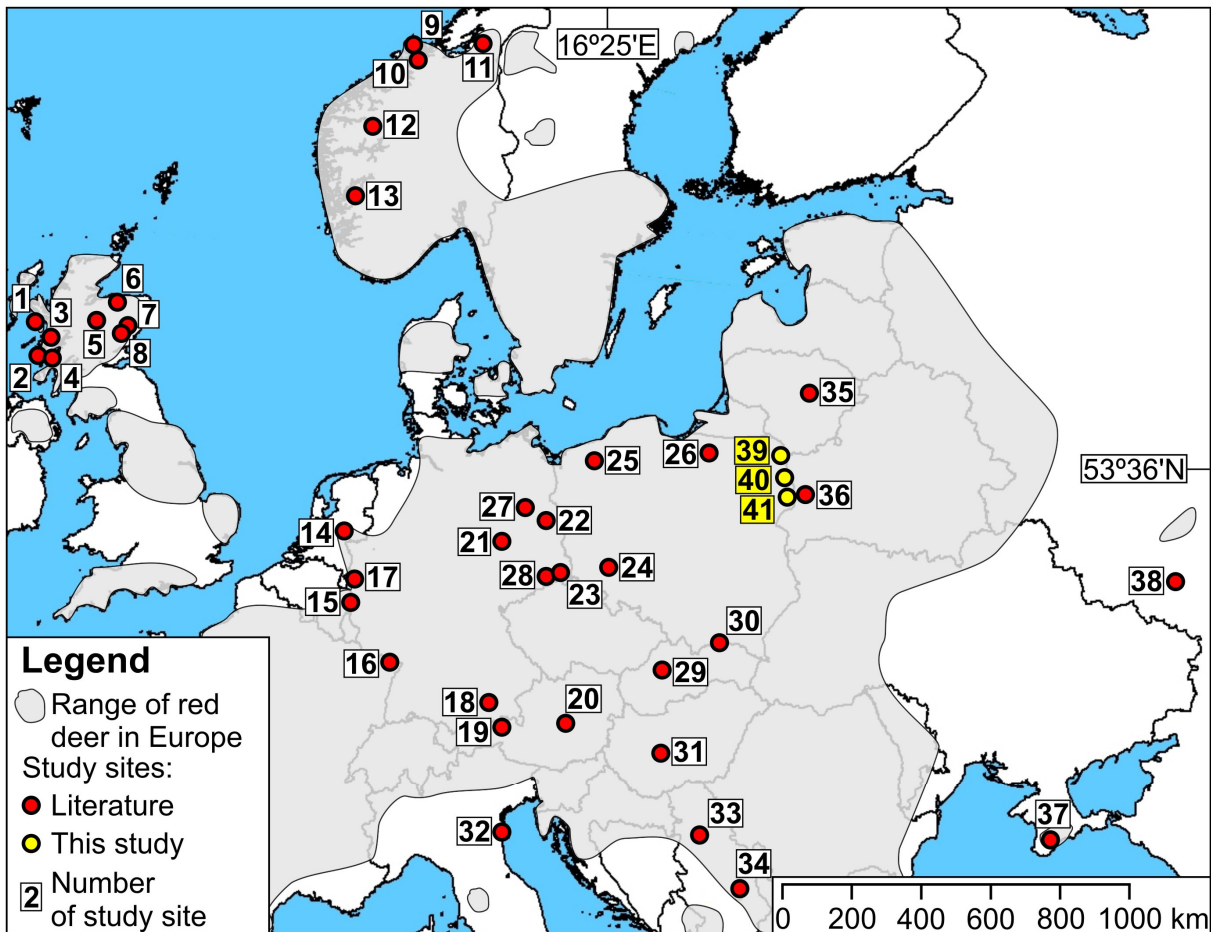


Fig. 25. Distribution of studies on fertility of red deer (*Cervus elaphus*) in Europe conducted in 1939-2011. Detailed overview of the studies in Appendix 7: Table 7.1.

In most of the European populations, females began breeding as yearlings. The exceptions were hinds from the above-mentioned Italian and Scottish populations where hinds reached puberty later (as 5.5 and 2.5-year-olds, respectively), due to the same factors which reduced their fertility rate. The fertility rate of 2.5-year-old hinds from the European populations exhibited a high variation (0-100%), which was on average lower compared to woodlands in NE Poland. For most of the reviewed populations, the female fertility rate increased with age and reached a maximum in >2.5-year-olds (from 69 to 99%). The same trend in the fertility of females was observed in the population from NE Poland – the highest fertility rate was attained by >2.5-year-olds (93.2%) (Table 10).

Interestingly, some researchers reported reproductive senescence in old females. In Belgium, a decline in fertility started in 8-11-year-old hinds (Bertouille and de Crombrughe 2002), while in Scotland and Norway – in >12-year-olds (Guinness et al. 1978a, Langvatn et al. 1996). In this study, I found neither a decreasing fertility nor deterioration of body condition in old hinds. Despite a non-significant decline in their mean body mass compared to prime-aged females, there was no significant decrease in the percentage of mandible marrow fat, which enabled old hinds to reproduce at the same level as prime-aged females. However, the observed decrease in the offspring survival with the increasing age of mothers may be the first symptom of their senescence, which can stem from difficulties in coping with concurrent energetic demands of lactation, caring for young and new pregnancy.

Table 10. Mean fertility parameters of red deer females in European populations of the species studied in 1939-2011. Distribution of the study sites in Figure 25. The list of data and literature resources in Appendix 7: Table 7.1. Fertility rate – percentage of fertile (pregnant) females in the population. N – the number of studies). Percentage of twins among foetuses calculated only for studies where twin foetuses were reported.

Parameter	Average from this study	Data from European populations		
		Mean $\pm$ SE	Min–Max	N
Population density (N/km <sup>2</sup> )	5.4	12.1 $\pm$ 2.1	1.5–34.4	19
Total fertility rate (%)	84.7	81.2 $\pm$ 3.1	28–100	27
Fertility rate of females (%):				
1.5 years old	40.0	28.7 $\pm$ 4.5	0–74	36
2.5 years old	88.0	64.9 $\pm$ 7.4	0–100	16
>2.5 years old	93.2	86.9 $\pm$ 2.5	69–99	15
Percentage of twins among foetuses (%)	0.2	0.8 $\pm$ 0.2	0.1–2.0	8
Percentage of females among calves (%)	40.5	48.7 $\pm$ 1.1	43–57	14

As evidenced by the literature review, multiple pregnancy in red deer occurred occasionally – on average 0.8% of pregnancies (Table 10). At the continental scale, the sex ratio of offspring was slightly male-biased, nevertheless some populations had a female-biased sex ratio (Lowe 1969, Hell et al. 1987, Hetlay et al. 1982, Ferretti and Mattioli 2012).

To sum up, females from the red deer population occurring in NE Poland exhibited high reproductive parameters compared to mean values of these parameters calculated for the whole European range of the species.

### **5.3. Density-dependence in red deer fertility rates**

Red deer in NE Poland, which occur in forest habitats covering the whole productivity gradient, exhibited low variation in the population density. Nevertheless, I found a positive relationship between red deer densities and habitat productivity, which has also been evidenced by other researchers (Bobek et al. 1984, Jędrzejewska and Jędrzejewski 1998). It was explained by the higher and more diverse forage supply in more productive tree stands compared to poorer sites (Dzięciołowski 1969, 1970, Bobek et al. 1975). Interestingly, the influence of habitat productivity on deer population density in my study was not alleviated by supplementary feeding provided by game managers in winter. Richer habitats, despite the lack or little supplementary feeding, still seemed to be more nutritionally attractive to red deer.

The increasing population density was documented to depress female reproduction in many mammalian terrestrial herbivores. For example, negative density-dependence in female reproduction has been reported in roe deer (Gaillard et al. 1992), wild reindeer (*Rangifer tarandus*) (Skogland 1985), moose (Schladweiler and Stevens 1973), European bison (Mysterud et al. 2007), and white-tailed deer (Simard et al. 2010). In the whole gradient of forest habitats occurring in NE Poland, it seems that the red deer population density was markedly below the habitat carrying capacity. Hence, the competition for food resources was most probably negligible and not evident in the body condition and fertility of hinds.

Meta-analysis performed on the literature data showed a clear negative effect of the population density on the hind fertility rate (Fig. 26). The increase in population density from 1.5 to 34.5 ind./km<sup>2</sup> caused a significant decrease in the fertility rate – from 87 to 39% ( $R^2 = 0.50$ ,  $p = 0.001$ ). In the Mesola Nature Reserve (Italy), the population density seemed to reduce the female fertility even more (in Fig. 26 indicated by a black arrow). However, Ferretti and Mattioli (2012) explained such a low fertility rate of red deer females by

a combined effect of red deer and fallow deer population density. As fallow deer exploited the same food resources and their range spatially overlapped with red deer habitats, high interspecific competition was documented. Therefore, after accounting for fallow deer numbers in the Mesola Nature Reserve, the model with population density explained 74% of the observed variation in female fertility across Europe ( $p < 0.001$ ).

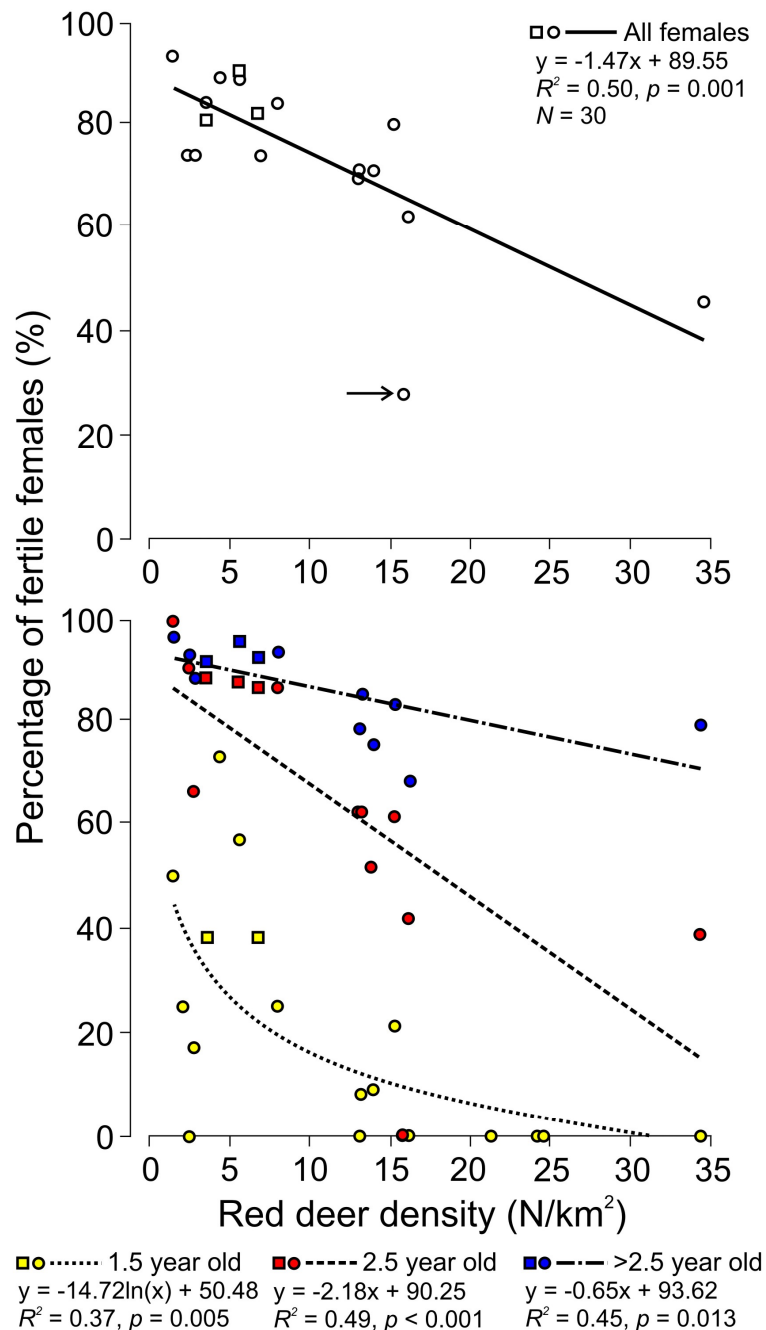


Fig. 26. Density-dependence in fertility of red deer females throughout Europe. Squares – results of this study, circles – other study sites across Europe (for location see Fig. 25). Circle with arrow – see text for explanation.

The strength of density-dependence in female fertility rates was related to female's age (Fig. 26). Negative influence of the increasing population density was most strongly pronounced in 1.5-year-old females, which can be explained by their higher vulnerability to competition for limited food resources. Clutton-Brock et al. (1987) found that the increasing population density of red deer on the Isle of Rhum (Scotland) influenced the fertility of first-breeders to a larger extent than in the case of older hinds, and interpreted it by a subordinate position of young hinds in a female cohort leading to a restricted access to high quality forage. The same conclusion was drawn by Bonenfant et al. (2002), who studied the red deer population in NE France and proved density-dependence in pregnancy rates only in primiparous females.

At the biogeographic scale, 1.5-year-old hinds exhibited the highest variation and a rapid decline in fertility as a response to growing density (Fig. 26). In populations above 16 ind./km<sup>2</sup>, 1.5-year-olds never entered the reproduction. The fertility rate of 2.5-year-olds was more affected by the population density compared to older females. The fertility rate of 2.5-year-old females decreased from 87 to 15% with the increasing population density (from 1.5 to 34.5 ind./km<sup>2</sup>), while in older females – from 93 to 71% (Fig. 26). These findings showed that the weakest density-dependence in fertility occurred in strong, prime-aged hinds.

#### **5.4. Other factors affecting the probability of female fertility**

At the biogeographic scale, high variation in the fertility rate of yearlings at low densities indicated that beside density-dependent factors there are other, density-independent factors, which remarkably influence the fertility rate. For example, weather conditions were proved to influence the parameters of females' reproduction, mainly indirectly – via competition for food resources and then body condition of animals, which determines the ovulation and fertility (Langvatn et al. 2006). Therefore, more productive habitats and favourable weather conditions enhance the food base, which in turn, under a given level of population density, reduces the competition for food. At the population level, this results in a better body condition and a higher fertility rate of hinds, which can be expressed in early breeding, no reproductive senescence in old females, and ability to participate in reproduction in a few consecutive years. In addition, a better body condition of hinds is expected to result in a higher proportion of males (bigger, more costly to produce compared to females) among newborns and better survival of offspring in the first months of lives.

In NE Poland, favourable summer weather (higher mean temperature and lower total precipitation) positively influenced the female body condition, which in turn significantly affected the probability of fertility in females, with the body mass being more important in yearlings, and fat reserves – in fully-grown, older hinds.

Nevertheless, despite apparent significant age-specific effects of the body condition indices, the applied models explained a small proportion of variation in the probability of female to be fertile. It could stem from the low variability in the fertility rate of females in the studied populations. Since the majority of hinds were fertile, the lack of pregnancy was evidenced only for a small group of individuals, which were represented mostly by yearlings. In such a case, when a sample size of non-fertile females was so small, it was highly probable that the lack of fertility could have been related to some stochastic factors (not included in the modelling procedure), which are usually difficult to follow. This could explain why the model created for yearlings, which exhibited a higher variation in the fertility rate, explained a higher proportion of variation in the probability of fertility compared to the model set for adult females.

The indirect influence of weather condition (via food resources and body condition) on the female reproduction was broadly reported. Adams and Dale (1998) showed a negative effect of the increasing late-winter snowfall (in the winter prior to breeding) on the pregnancy rate of the prime-aged female Alaskan caribou (*Rangifer tarandus granti*) occurring at a low population density. Langvatn et al. (1996) showed that independently of the population density, the age of the first reproduction and the pregnancy rate of first-breeding red deer females in two populations living at the edge of the species range (Norway and Scotland) were related to geographical and annual variation in the body weight, which reflected the weather-induced variation in the food resources. Proportions of first-breeders calving in both populations were negatively associated with the variation in May-June degree-days preceding the autumn when conception occurred. The possible explanation assumed that low accumulated degree-days in May-June could have caused a delayed development of vegetation, which enhanced the vegetation digestibility and thus improved the resource base of deer. Interestingly, Coulson et al. (2000) demonstrated very similar associations between the fecundity rate, population density and weather conditions for three different ungulate species (Soya sheep *Ovis aries*, Saiga antelope *Saiga tatarica tatarica*, and red deer). The increasing population density and decreasing winter temperature curbed the female

fecundity in a similar manner. However, in the case of red deer, the relationship was true only for the first-breeding hinds.

Van Vuren and Bray (1986) demonstrated a positive effect of spring precipitation on calf production in bison (*Bison bison*) in semiarid conditions of southern Utah (USA). The same relationship was observed by Kie and White (1985) who indicated a lower reproductive rate of mature white-tailed deer females in the years following the draught periods (low precipitation level). In contrast to the above-mentioned surveys, Bonenfant et al. (2002) (France) and Stewart et al. (2005) (USA) failed to confirm any effect of weather factors on female red deer fertility at any level of the population density.

The available food resources affected also, through body condition, the probability of females to be fertile in two consecutive years i.e. to incur costs of simultaneous lactation and gestation. However, as food resources vary and their accessibility depends on many factors (habitat type, population density and weather), their effect on the recovery of females from previous gestation and lactation was inconsistent across different localities and species of ungulates. The effect of prior reproductive effort on the body condition – fertility association was not confirmed for the female Alaskan caribou occurring at low population density (Adams and Dale 1998) or in Alpine ibex (Toïgo et al. 2002) at any level of the surveyed population densities. The difficulty in detection of the past reproduction costs, which is expected to be reflected in the deteriorated body condition, could be caused by varying female quality and incurred energy expenditure (Toïgo et al. 2002). Dzieciółowski et al. (1995) did not find any relationship between lactation and body condition in hinds occurring in Słowiński National Park (Poland), despite the fact that three different body condition indices were applied.

However, other researchers were able to determine that the costs of prior reproductive activity of females reduced the pregnancy rate in mothers, which weaned the offspring the same year (Yellowstone bison: Kirkpatrick et al. 1996, caribou: Russell et al. 1998). The negative association of prior pregnancy and lactation with the fertility of red deer hinds was widely documented in the population living on the Isle of Rhum and characterized by high population density (Lowe 1969, Mitchell and Lincoln 1973, Mitchell et al. 1976, Guinness et al. 1978a, Albon et al. 1983). Over many years of the study, researchers observed a consistently better body condition and a higher pregnancy rate in mature yield hinds compared to lactating mothers. Interestingly, in most of the adult females, the pause in reproduction lasted no longer than one year.

However, the commonly applied assumption that presence/absence of lactation in females in the autumn-winter period is a good indicator of the past pregnancy can be reliable only under specific conditions. The assumption seems to hold true when postnatal mortality of fawns remains at a very low level. I presumed that in the conditions of woodlands in NE Poland, where predation by wolf and lynx has a significant impact on fawn survival in the first months of life (Okarma et al. 1997, Jędrzejewski et al. 2000), lactation of females facing early losses could have been very difficult to observe a few months later. Therefore, the absence of lactation in females in the autumn-winter period did not necessarily mean that they did not breed in the previous season. Under seminatural conditions, it is an indicator of fawn survival at the beginning of their life rather than the index of female reproductive activity in the previous year.

Finally, the accessibility of food resources as reflected in the body condition of females affects also calf survival in the first months of life. In Norway, Wegge (1975) found higher (than usual) calf mortality in summer and related it to the nutritional failure of pregnant hinds in late winter and spring due to unfavourable weather conditions. On the Isle of Rhum, Guinness et al. (1978b) noted that the mortality rate of calves in the first 6 months of life was higher among offspring of young and old females compared to prime-aged hinds (7-10-year-olds). This was attributed to the optimal parturition time, production of bigger fawns by prime aged-females, as well as their better fat reserves compared to young and old mothers.

My data showed a negative association between the age of mothers and the summer survival of calves. However, I expected the opposite relationship based on female's experience growing with age, which can play a certain role in calf rearing and protecting. An interesting hypothesis, which can serve as a potential explanation for this finding, was put forward by Moyes et al. (2006). They found a positive association between frequent reproduction and mother survival, and explained it by little maternal investment in fawns, which was expected to increase the females' survival probability. I assume, that in populations of NE Poland, old females (>6-year-old) may have experienced gradual deterioration of body condition with age (connected with previous reproductive activity), the effect of which was not yet observed at the stage of early pregnancy (no senescence in the fertility rate) but was apparent at the level of successful rearing of young.

To sum up, under the existing population densities, the available food resources in woodlands of NE Poland allowed red deer females to attain good body condition



and fertility rates. Thus, the studied populations were far from the habitat carrying capacity, and the density-dependent mechanisms, which operate mainly through the female body condition and fertility, were fairly weak. On the other hand, summer weather conditions at the time of the study were stable (no droughts), therefore their indirect effect, which was reflected in the female body condition, explained only a small proportion of the observed variation in the fertility of hinds. The influence of the investigated factors on the female fertility was most pronounced in yearlings.

### **5.5. Body condition of mothers and the sex ratio of foetuses**

According to Trivers-Willard's (1973) hypothesis, better body condition of hinds should result in a higher proportion of males (larger and more costly sex) among newborns. In the red deer populations in NE Poland, the female body condition and age-related changes in the proportion of males among foetuses generally followed the T-W hypothesis, however, the differences in foetus sex ratio were insignificant. Nevertheless, in my opinion the results presented a biologically meaningful trend. A higher proportion of males among foetuses in mothers with the superior body condition was evidenced in the previous studies, and the body condition driven variability in the investment between sexes was proved. Clutton-Brock et al. (1982) associated the offspring sex ratio – mother body condition relationship with the maternal dominance, and showed that dominant females were of superior body condition and invested more in sons compared to subordinate hinds. Kruuk et al. (1999) confirmed this hypothesis but demonstrated that – under unfavourable environmental conditions (a high population density and heavy winter rainfall), which induced nutritional stress – dominant females could not maintain their superior body condition and male-biased offspring sex-ratio. It was suggested that a positive relationship between the maternal quality (expressed as the position of mothers in a cohort) and the contribution of male offspring can occur only in populations below the habitat carrying capacity. However, Bonenfant et al. (2003) did not find any relationship between the maternal quality and the male-biased offspring sex ratio at any level of the population density index. Other researchers (Post and Stenseth 1999, Mysterud et al. 2000) documented that the offspring sex ratio in red deer can be non-adaptively modified post-implementation by the density and weather conditions through foetal mortality. They demonstrated a decreasing proportion of male fawns with the increasing nutritional stress of hinds, caused by the growing population density and severity of weather conditions in Norway.

Interestingly, some indication of the influence of population density on the offspring sex ratio was found also at the biogeographic scale. Based on the data from 10 populations (Appendix 7: Table A7.1), I found a nonlinear increasing trend in the percentage of female foetuses with the increasing red deer population density ( $R^2 = 0.30$ ,  $p = 0.102$ ) (Fig. 27). However, a larger sample size would be required to verify the significance of the relationship.

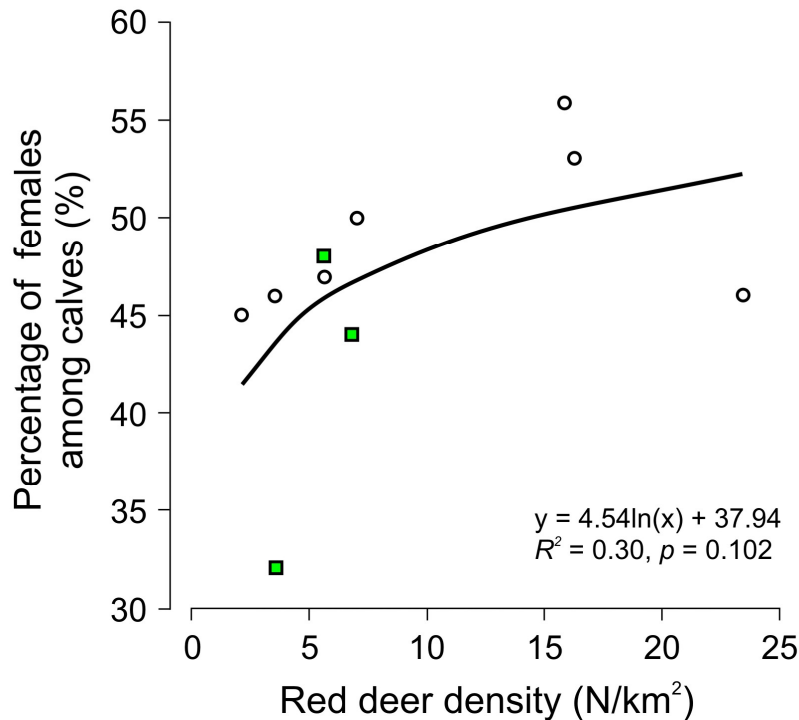


Fig. 27. Relationship between red deer population density and calf sex ratio of foetuses throughout Europe. Green squares – this study; white circles – other study sites in Europe; data in Appendix 7: Table A7.1.

### 5.6. Red deer population dynamics – reproductive input under the existing mortality level

Analysis of life tables showed that under the existing mortality factors (predation by wolf and lynx, hunting harvest, possible poaching and severe winter conditions) females in red deer populations in NE Poland experienced somewhat higher losses in the first months of life and in older age classes (>11.5-year-old) compared to all older age classes of hinds whose mortality rate was almost stable. The age-constant mortality rate for a large part of the lifespan was usually proved for short-lived species with high initial mortality (Krebs and Horperg 1972). Spinage (1972) found such pattern in the age-specific mortality rate for only one out of four studies on African ungulates and attributed it to a high level of postnatal

losses. Contrary to my study, Lowe (1969) showed that in the red deer population on the Isle of Rhum (Scotland), most severe mortality occurred in 8-9 years old females. Moreover, the death rate of prime-aged females was lower compared to hinds from Polish populations.

Unfortunately, the study on the Isle of Rhum did not account for mortality of individuals younger than one year, thus it was impossible to make a comparison between the mortality rate of 0.5-year-olds from NE Poland and the Isle of Rhum. Lowe (1969) found also a different trend in the life expectancy of females. Contrary to my study, yearlings and prime-aged females (2.5-4.5-year-old) on the Isle of Rhum were characterized by higher life expectation (5.19 years and 4.94-3.89 years, respectively). The observed differences in the mortality rate and life expectancy of females can result from different levels of extrinsic mortality imposed on both populations. Compared to the population in NE Poland, the deer population on the Isle of Rhum was exposed only (at the time of data collection) to non-intensive hunting harvest. Lowe (1969) explained the increasing rate of natural mortality in older females by inefficient rumination caused by a reduction of tooth infundibular ridges with age. Almost the same level of mortality among different age classes of adult females in NE Poland most probably resulted from non-selective hunting harvest and similar predator (wolf, lynx) pressure on hinds from all age classes (Okarma et al. 1997, Jędrzejewski et al. 2000).

Both the age-specific mortality and the fertility schedule of females allowed for calculation of the population innate capacity for the increase. The obtained results indicated that the red deer population in NE Poland was nearly stable. It seems that extrinsic and intrinsic mortality imposed on the population was fully balanced by the female reproductive potential. Having applied the same method, Lowe (1969) showed similar population stability for the population at the beginning of his study on the Isle of Rhum. After a few years, however, he reported a decrease in the population innate capacity for the increase and related it to a decline in the female fecundity rate caused by deterioration of food resources after the cessation of muirburn.

To sum up, my study documented the reproduction potential of the red deer population exposed to both natural and human related mortality. Under the existing environmental conditions of large woodlands in NE Poland, females exhibited a high fertility rate, which compensated for losses caused by wolf and lynx predation, hunting harvest and other mortality factors, and ensured the stability of the surveyed populations. The results of this project are important for the deer management, as they can help in long-term planning

of hunting bags according to the established strategy. Nevertheless, an example presented by Lowe (1969) gives a warning that the observed trends can quickly change when extrinsic or intrinsic factors caused a shift in the mortality level or reproductive performance of females. Hence, the obtained results should be treated with caution and applied to red deer management only under the conditions of environmental stability.

## 6. CONCLUSIONS

(1) Red deer females from populations inhabiting three woodlands in NE Poland lived at relatively low densities, and exhibited high reproductive potential (high fertility rate, low age at the first breeding and lack of reproductive senescence) compared to other European populations.

(2) At the population level, the body condition and the fertility rate of yearlings were significantly lower compared to older age classes. Pregnant females had significantly higher body mass and a percentage of mandible marrow fat than non-pregnant hinds. There were no differences in the reproductive potential of females among the studied populations. It could result from a low variation in population densities and similar nutritional conditions in the three woodlands.

(3) At the individual level, the probability of hinds to be fertile depended on their age and body condition. A positive effect of the body mass on the female fertility decreased with mother's age, whereas a positive influence of a percentage of marrow fat content increased with age. The fertility probability in yearlings was positively associated with the body mass. The fertility probability of adult females increased with the growing percentage of marrow fat, and the influence of this factor grew with female's age. Since favourable summer weather positively affected the female's body condition, it may have had an indirect positive effect on female fertility via improved food resources. Population density did not influence the probability of female to be fertile, which could have been caused by relatively low deer abundance. Since the surveyed populations were most probably significantly below the habitat carrying capacity, females did not suffer from considerable competition for food resources, thus could reach good body condition and reproductive potential.

(4) The foetus sex ratio was male-biased. In accordance with Trivers-Willard's hypothesis, younger females with worse body condition had more females among foetuses, while the opposite relationship was proved for prime-aged mothers having better body condition. Mothers bearing male foetuses were on average heavier than females with female foetuses.

(5) The mortality rate of fawns in the first months of life was high and increased with mother's age. These results may indicate the symptoms of reproductive senescence in old mothers, which can be expressed in the decreasing investments in calves after parturition.

(6) Life expectancy of females at birth was low, which seemed to reflect a high level of mortality imposed by natural factors (wolf and lynx predation, harsh winter conditions) and hunting harvest. The population suffered almost equal proportions of losses in all age classes. An average female was expected to produce more male than female offspring during her life. At the population level, younger age classes had the highest contribution to reproduction. Under the current conditions, the reproductive potential of females seemed to compensate for the suffered losses, thus the surveyed populations are expected to be stable. This finding can be applied in deer management, in future planning of hunting bags according to the established strategy.

(7) At the biogeographic (European) scale, density-dependence in female fertility rates was observed, and its strength declined with female's age.

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## **APPENDICES 1-7**

### Appendix 1. Red deer population density in the studied forests

Table A1.1. Red deer population density (N individuals/km<sup>2</sup>) estimated based on driving counts performed in the study area in 2008-2012. Blocks denote forest compartments or a group of forest compartments, which were inventoried by driving counts during winter seasons (December-February).

Season	Augustów Forest			Knyszyn Forest			Białowieża Forest		
	N blocks	% area	N/km <sup>2</sup> ± SE	N blocks	% area	N/km <sup>2</sup> ± SE	N blocks	% area	N/km <sup>2</sup> ± SE
2008/09	45	10.4	4.27±0.68	-	-	-	43	9.9	5.98±0.87
2009/10	-	-	-	-	-	-	46	10.4	7.70±1.21
2010/11	-	-	-	-	-	-	36	8.0	4.67±1.10
2011/12	43	10.5	2.97±0.52	77	9.6	5.61±0.59	44	9.5	6.79±1.38
Mean±SE	44±1.0	10.45±0.05	3.64±0.43	77	9.6	5.61±0.59	42.2±2.2	9.4±1.0	6.84±0.68



**Appendix 2. Body condition indices in relation to the age of red deer females – results of statistical testing**

Table A2.1. Comparison of the body mass and percentage of mandible marrow fat in different age classes of red deer females. Differences among all age classes tested with ANOVA. Pairwise differences between age classes tested with post-hoc Tukey HSD.

Age classes compared (years)	Body mass		Mandible marrow fat	
	<i>ANOVA</i>			
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
All	18.576	<b>&lt;0.001</b>	9.244	<b>&lt;0.001</b>
	<i>Tukey HSD</i>			
	<i>diff</i>	<i>P</i>	<i>diff</i>	<i>p</i>
1 – 2	11.045	<b>&lt;0.001</b>	4.527	<b>&lt;0.001</b>
1 – 3	12.559	<b>&lt;0.001</b>	5.386	<b>&lt;0.001</b>
1 – 4	16.980	<b>&lt;0.001</b>	6.847	<b>&lt;0.001</b>
1 – 5-6	16.519	<b>&lt;0.001</b>	6.094	<b>&lt;0.001</b>
1 – 7-8	17.729	<b>&lt;0.001</b>	6.770	<b>&lt;0.001</b>
1 – 9-11	20.481	<b>&lt;0.001</b>	6.510	<b>&lt;0.001</b>
1 – >11	15.859	<b>&lt;0.001</b>	6.699	<b>&lt;0.001</b>
2 – 3	1.514	0.995	0.856	1
2 – 4	5.935	0.057	2.320	0.340
2 – 5-6	5.474	0.133	1.567	0.825
2 – 7-8	6.684	<b>0.044</b>	2.243	0.488
2 – 9-11	9.436	<b>&lt;0.001</b>	1.983	0.662
2 – >11	4.814	0.521	2.172	0.689
3 – 4	4.442	0.377	1.464	0.860
3 – 5-6	3.960	0.567	0.711	0.998
3 – 7-8	5.170	0.281	1.387	0.924
3 – 9-11	7.922	<b>0.008</b>	1.127	0.977
3 – >11	3.300	0.896	1.316	0.971
4 – 5-6	-0.461	0.991	-0.753	0.997
4 – 7-8	0.749	1	-0.077	1
4 – 9-11	3.501	0.742	-0.337	1
4 – >11	-1.121	1	-0.148	1
5-6 – 7-8	1.210	1	0.676	1
5-6 – 9-11	3.962	0.637	0.416	1
5-6 – >11	-0.660	1	0.605	1
7-8 – 9-11	2.752	0.938	-0.260	1
7-8 – >11	-1.870	1	-0.071	1
9-11 – >11	-4.622	0.649	0.189	1

∞ Table A2.2. Comparison of the body mass and percentage of mandible marrow fat in different age classes of red deer females in Augustów, Knyszyn and Białowieża Forests. Differences among all age classes tested with ANOVA. Pairwise differences between age classes tested with post-hoc Tukey HSD.

Age classes compared (years)	Body mass						Mandible marrow fat					
	Augustów Forest		Knyszyn Forest		Białowieża Forest		Augustów Forest		Knyszyn Forest		Białowieża Forest	
	<i>ANOVA</i>											
All	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
	23.720	<0.001	2.113	0.133	9.945	<0.001	6.667	<0.001	0.946	0.394	12.147	<0.001
	<i>Tukey HSD</i>											
	<i>diff</i>	<i>p</i>	<i>diff</i>	<i>p</i>	<i>diff</i>	<i>p</i>	<i>diff</i>	<i>p</i>	<i>diff</i>	<i>p</i>	<i>diff</i>	<i>p</i>
1 – 2-3	14.228	<0.001	9.339	0.006	4.037	0.024	5.496	<0.001				
1 – 4-6	17.299	<0.001	15.798	<0.001	6.626	<0.001	7.094	<0.001				
1 – 7-11	23.428	<0.001	16.060	<0.001	5.409	0.002	7.958	<0.001				
1 – >11	21.785	<0.001	11.909	0.009	6.320	0.027	8.099	<0.001				
2-3 – 4-6	3.011	0.631	6.398	0.047	2.589	0.181	1.598	0.568				
2-3 – 7-11	9.140	0.001	6.661	0.042	1.372	0.807	2.462	0.156				
2-3 – >11	7.497	0.202	2.510	0.928	2.283	0.788	2.603	0.282				
4-6 – 7-11	6.129	0.057	0.262	1	1.221	0.869	0.864	0.950				
4-6 – >11	4.686	0.668	-3.889	0.755	0.305	1	1.005	0.953				
7-11 – >11	-1.642	0.990	-4.151	0.718	0.911	0.992	0.141	1				

Table A2.3. Comparison of the body mass and percentage of mandible marrow fat among Augustów, Knyszyn and Białowieża Forests in hinds belonging to the same age classes – results of ANOVA.

Age classes (years)	Body mass		Mandible marrow fat	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
1	2.571	0.104	10.417	<b>0.002</b>
2-3	0.526	0.593	4.763	<b>0.010</b>
4-6	3.261	<b>0.043</b>	11.42	<b>&lt;0.001</b>
7-11	0.383	0.683	1.290	0.280
>11	1.888	0.287	1.349	0.255

Table A2.4. Pairwise comparisons of the body mass and percentage of mandible marrow fat in hinds belonging to the same age classes among Augustów, Knyszyn and Białowieża Forests shown by ANOVA as significantly different (see Table A2.3). Pairwise differences between age classes tested with post-hoc Tukey HSD.

Age classes (years)	Forests	<i>diff</i>	<i>p</i>
<b><i>Body mass</i></b>			
4-6	AF – KF	6.775	<b>0.047</b>
	AF – BF	3.775	0.222
	KF – BF	-3.000	0.558
<b><i>Mandible marrow fat</i></b>			
2-3	AF – KF	-0.042	0.999
	AF – BF	-3.220	<b>0.014</b>
	KF – BF	-3.178	0.069
4-6	AF – KF	-4.756	<b>&lt;0.001</b>
	AF – BF	-4.210	<b>&lt;0.001</b>
	KF – BF	0.546	0.906

### Appendix 3. Reproduction parameters in relation to the age of hinds – results of statistical testing

Table A3.1. Pairwise comparisons of the proportion of pregnant, all lactating and pregnant-lactating red deer females among all age classes – results of Fisher’s exact test.

Age classes compared (years)	Pregnant females		All lactating females		Pregnant and lactating females	
	Odds ratio	<i>p</i>	Odds ratio	<i>p</i>	Odds ratio	<i>p</i>
1 – 2	0.093	< <b>0.001</b>				
1 – 3	0.074	< <b>0.001</b>				
1 – 4	0.034	< <b>0.001</b>				
1 – 5-6	0.037	< <b>0.001</b>				
1 – 7-8	0.045	< <b>0.001</b>				
1 – 9-11	0.047	< <b>0.001</b>				
1 – >11	0.066	< <b>0.001</b>				
2 – 3	0.803	0.793	0.570	0.238	0.490	0.139
2 – 4	0.369	0.224	0.762	0.534	0.652	0.398
2 – 5-6	0.395	0.227	0.502	0.131	0.391	<b>0.049</b>
2 – 7-8	0.481	0.361	0.181	<b>0.002</b>	0.175	<b>0.001</b>
2 – 9-11	0.503	0.367	0.350	<b>0.039</b>	0.272	<b>0.007</b>
2 – >11	0.712	0.750	0.739	0.783	0.718	0.587
3 – 4	0.460	0.334	1.338	0.658	1.332	0.661
3 – 5-6	0.492	0.346	0.882	0.819	0.799	0.650
3 – 7-8	0.599	0.525	0.317	0.066	0.358	0.070
3 – 9-11	0.626	0.738	0.613	0.460	0.556	0.329
3 – >11	0.886	1	1.294	0.775	1.461	0.575
4 – 5-6	1.071	1	0.659	0.491	0.600	0.361
4 – 7-8	1.301	1	0.237	<b>0.012</b>	0.269	<b>0.015</b>
4 – 9-11	1.360	1	0.459	0.150	0.417	0.096
4 – >11	1.921	0.420	0.869	1	1.098	1
5-6 – 7-8	1.215	1	0.360	0.101	0.448	0.182
5-6 – 9-11	1.270	1	0.696	0.608	0.696	0.608
5-6 – >11	1.794	0.665	1.466	0.563	1.825	0.382
7-8 – 9-11	1.045	1	1.930	0.369	1.552	0.560
7-8 – >11	1.477	0.685	4.025	<b>0.045</b>	4.032	<b>0.050</b>
9-11 – >11	1.413	0.692	2.100	0.293	2.612	0.132

Table A3.2. Pairwise comparisons of the proportion of pregnant hinds among all age classes for the pooled data and separately for Augustów, Knyszyn and Białowieża Forests – results of Fisher’s exact test.

Age classes compared (years)	Total		Augustów Forest		Knyszyn Forest		Białowieża Forest	
	Odds ratio	<i>p</i>	Odds ratio	<i>p</i>	Odds ratio	<i>p</i>	Odds ratio	<i>p</i>
1 – 2-3	0.083	< <b>0.001</b>	0.060	< <b>0.001</b>			0.105	< <b>0.001</b>
1 – 4-6	0.025	< <b>0.001</b>	0.049	< <b>0.001</b>			0.016	< <b>0.001</b>
1 – 7-11	0.068	< <b>0.001</b>	0.046	< <b>0.001</b>			0.035	< <b>0.001</b>
1 – >11	0.066	< <b>0.001</b>	0.141	<b>0.016</b>			0.029	< <b>0.001</b>
2-3 – 4-6	0.421	0.079	0.817	1	0.507	1	0.149	<b>0.048</b>
2-3 – 7-11	0.543	0.258	0.759	1	1	1	0.330	0.198
2-3 – >11	0.787	1	2.320	0.309			0.271	0.274
4-6 – 7-11	1.287	0.768	0.929	1	1.961	1	2.200	0.606
4-6 – >11	1.862	0.410	2.830	0.254			1.800	1
7-11 – >11	1.447	0.696	3.031	0.251			0.821	1

Table A3.3. Pairwise comparisons of the proportion of all lactating red deer females among all age classes for the pooled data and separately for Augustów, Knyszyn and Białowieża Forests – results of Fisher’s exact test.

Age classes compared (years)	Total		Augustów Forest		Knyszyn Forest		Białowieża Forest	
	Odds ratio	<i>p</i>	Odds ratio	<i>p</i>	Odds ratio	<i>p</i>	Odds ratio	<i>p</i>
2-3 – 4-6	0.861	0.644	0.960	1	1.637	0.686	0.605	0.431
2-3 – 7-11	0.345	<b>0.004</b>	0.329	<b>0.045</b>	0.571	1	0.306	<b>0.039</b>
2-3 – >11	0.980	1	1.109	1			0.673	0.727
4-6 – 7-11	0.401	<b>0.020</b>	0.343	0.049	0.349	0.616	0.507	0.358
4-6 – >11	1.138	0.798	1.154	1			1.108	1
7-11 – >11	2.815	0.073	3.304	0.188			2.169	0.413

Table A3.4. Pairwise comparisons of the proportion of pregnant-lactating hinds among all age classes for the pooled data and separately for Augustów, Knyszyn and Białowieża Forests – results of Fisher’s exact test.

Age classes compared (years)	Total		Augustów Forest		Knyszyn Forest		Białowieża Forest	
	Odds ratio	<i>p</i>	Odds ratio	<i>p</i>	Odds ratio	<i>p</i>	Odds ratio	<i>p</i>
2-3 – 4-6	0.757	0.440	0.953	1	1.120	1	0.491	0.201
2-3 – 7-11	0.315	<b>0.001</b>	0.353	<b>0.050</b>	0.392	0.613	0.248	<b>0.019</b>
2-3 – >11	1.022	1	1.000	1			0.813	1
4-6 – 7-11	0.417	<b>0.021</b>	0.370	0.055	0.349	0.616	0.507	0.358
4-6 – >11	1.349	0.606	1.049	1			1.641	0.704
7-11 – >11	3.213	<b>0.041</b>	2.789	0.221			3.209	0.224

Table A3.5. Comparisons of the proportion of pregnant, all lactating and pregnant-lactating hinds belonging to the same age classes from Augustów, Knyszyn and Białowieża Forests. Significance of differences between two proportions tested with Fisher’s exact test, differences among three proportions tested with Pearson's Chi-squared test.

Age classes (years)	Pregnant females			All lactating females			Pregnant-lactating females		
	Odds ratio	$\chi^2$	<i>p</i>	Odds ratio	$\chi^2$	<i>p</i>	Odds ratio	$\chi^2$	<i>p</i>
1	1.014		1						
2-3		1.413	0.493		2.995	0.224		2.333	0.311
4-6		1.177	0.555		0.966	0.617		1.423	0.491
7-11		0.072	0.965		0.267	0.875		0.426	0.808
>11	0.216		0.239	0.682		1	1		1

**Appendix 4. Factors affecting the red deer female fertility – confidence sets of models (GLMs)**

Table A4.1. The confidence set of generalized linear models (GLMs;  $\Delta AIC_c \leq 4$ ) with the presence (or absence) of pregnancy in 1-year-old females as a binomial dependent variable and body mass (BM), mandible marrow fat (MF), population density (D), the total summer precipitation (SP), and mean summer temperature (ST) as explanatory variables.  $K$  – the number of estimated parameters;  $AIC_c$  – Akaike’s information criterion with a second order correction for small sample sizes;  $\Delta AIC_c$  – a difference in  $AIC_c$  between a given model and the most parsimonious model;  $\omega_i$  – weight of the model.

Model	$K$	$R^2$	$\Delta AIC_c$	$\omega_i$
BM + MF	3	0.28	0	0.198
BM	2	0.21	0.70	0.139
BM + MF + D	4	0.31	1.40	0.098
BM + SP	3	0.25	1.67	0.086
BM + MF + ST	4	0.29	1.98	0.074
BM + MF + SP	4	0.29	2.32	0.062
BM + D	3	0.22	2.73	0.050
BM + ST	3	0.22	2.86	0.047
BM + D + SP	4	0.26	3.31	0.038
BM + MF + D + SP	5	0.31	3.70	0.031
BM + MF + D + ST	5	0.31	3.87	0.028

Table A4.2. The confidence set of generalized linear models (GLMs;  $\Delta\text{AIC}_c \leq 4$ ) with the presence (or absence) of pregnancy in  $\geq 2$ -year-old females as a binomial dependent variable and the age of female (A), body mass (BM), mandible marrow fat (MF), mean summer temperature (ST), the total summer precipitation (SP), population density (D) as explanatory variables. Other explanations as in Table A4.1.

Model	$K$	$R^2$	$\Delta\text{AIC}_c$	$\omega_i$
A + BM + MF + A×MF	5	0.09	0	0.082
BM + MF	3	0.06	0.71	0.058
A + BM + MF + A×BM + A×MF	6	0.10	1.01	0.050
BM	2	0.04	1.20	0.045
A + BM + MF + ST + A×MF	6	0.09	1.94	0.032
A + MF + A × MF	4	0.06	1.94	0.031
A + BM + MF + SP + A×MF	6	0.09	2.01	0.030
A + BM + MF + D + A×MF	6	0.09	2.02	0.030
BM + MF + D	4	0.06	2.25	0.027
BM + MF + ST	4	0.06	2.26	0.027
A + BM + MF	4	0.06	2.52	0.023
BM + MF + SP	4	0.06	2.56	0.023
A + BM + MF + ST + A × BM + A×MF	7	0.10	2.81	0.020
A + BM	3	0.04	2.98	0.019
MF	2	0.03	2.98	0.019
BM + D	3	0.04	3.01	0.018
A + BM + MF + D + A×BM + A×MF	7	0.10	3.01	0.018
A + BM + MF + SP + A×BM + A×MF	7	0.10	3.05	0.018
BM + ST	3	0.04	3.13	0.017
BM + SP	3	0.04	3.19	0.017
A + MF + SP + A×MF	5	0.06	3.72	0.013
A + BM + MF + A×BM	5	0.06	3.84	0.012
A + BM + MF + ST + SP + A×MF	7	0.09	3.84	0.012
A + MF + ST + A×MF	5	0.06	3.88	0.012
A + MF + D + A×MF	5	0.06	3.93	0.012
A + BM + MF + ST + D + A×MF	7	0.09	3.95	0.011



**Appendix 5. The foetus sex ratio in relation to mother's age and body condition – results of statistical testing**

Table A5.1. Departure of the sex ratio of foetuses from the 1:1 ratio for each age class of hinds – results of Fisher's exact test.

Age classes (year)	Odds ratio	<i>p</i>
1	1.308	>0.999
2-3	0.570	<0.341
4-6	0.631	<0.258
>6	–	1

Table A5.2. Pairwise comparisons of the foetus sex ratio between females belonging to different age classes – results of Fisher's exact test.

Age classes compared (years)	Odds ratio	<i>p</i>
1 – 2-3	2.310	0.407
1 – 4-6	2.096	0.428
1 – >6	1.319	>0.999
2-3 – 4-6	0.900	0.830
2-3 – >6	0.571	0.398
4-6 – >6	0.632	0.434

Table A5.3. Comparisons of the body condition indices for hinds bearing foetuses of the opposite sex (male versus female) in each age class of hinds – results of ANOVA.  
? – no data available.

Age classes (years)	Body mass		Mandible marrow fat	
	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>
1	?	?	0.282	0.618
2-3	0.308	0.584	0.452	0.506
4-6	1.246	0.270	0.842	0.363
>6	0.030	0.863	0.428	0.517

**Appendix 6. Life tables – data smoothing and the net reproduction rate of the population**

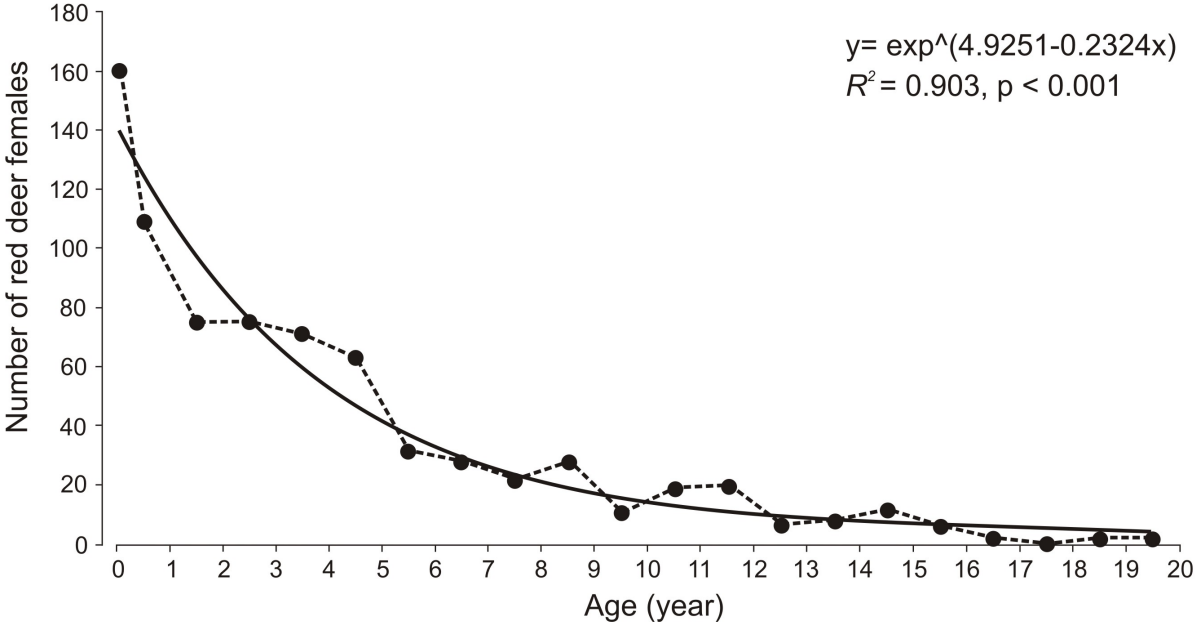


Fig. A6.1. Raw and smoothed frequencies of sampled red deer females in individual age categories. Smoothing performed by fitting the exponential function to raw frequencies.

Table A6.1. The net reproduction rate ( $R_{0.5}$  [ $\Sigma V_{x0.5}$ ]) of the studied red deer population in the autumn-winter season based on the number of 0.5-year-old offspring. The number of 0.5-year-old individuals ( $n_{x0.5}$ ) in different age classes of mothers calculated based on the number of young which suckled hinds in the autumn-winter season (lactation data).

Age (years)	Proportion of surviving at the start of the age interval	No. of 0.5-year-old fawns per female aged $x$ years	Product of $l_x n_{x0.5}$	Percentage of $V_{x0.5}$
$x$	$l_x$	$n_{x0.5}$	$V_{x0.5}$	
0	1.000	0	0	0
0.5	0.857	0	0	0
1.5	0.664	0	0	0
2.5	0.514	0.479	0.246	17.7
3.5	0.400	0.619	0.248	17.8
4.5	0.307	0.548	0.168	12.1
5.5	0.243	0.649	0.158	11.3
6.5	0.186	0.649	0.120	8.7
7.5	0.143	0.839	0.120	8.6
8.5	0.114	0.839	0.096	6.9
9.5	0.086	0.727	0.062	4.5
10.5	0.064	0.727	0.047	3.4
11.5	0.050	0.556	0.036	2.6
12.5	0.043	0.556	0.024	1.7
13.5	0.029	0.556	0.016	1.1
14.5	0.021	0.556	0.012	0.9
15.5	0.021	0.556	0.012	0.9
16.5	0.014	0.556	0.008	0.6
17.5	0.014	0.556	0.008	0.6
18.5	0.007	0.556	0.004	0.3
19.5	0.007	0.556	0.004	0.3
All			$R_{0.5} = 1.389$	$\Sigma = 100$

## Appendix 7. Literature data on fertility of female red deer in Europe

Table A7.1. Data on the red deer female fertility in 41 localities of Europe derived from studies conducted in 1939-2011. The fertility rate – percentage of fertile females in the population.

No.	Location	Years	Fertility rate (%) 1.5 years old	Fertility rate (%) 2.5 years old	Fertility rate (%) >2.5 years old	Total fertility rate (%)	Twin foetuses (%)	Sex ratio of calves (males: females)	Population density (N/km <sup>2</sup> )	Source
1	Scotland, Rhum Island	1958-65	0	42	69	63	0.1	1:1.14	16.2	Lowe 1969
		1966-67	9	52	76	72	–	–	13.9	Mitchell and Lincoln 1973
		1971	0		72	–	–	–	–	Guinness et al. 1978a
		1972	0		92	–	–	–	21.3	” ”
		1973	0		80	–	–	–	24.4	” ”
		1974	0		92	–	–	–	24.6	” ”
		Total (1971-74)	0		81	–	–	1:0.84	23.4	” ”
	1971-97	0	17	72	–	–	–	–	Coulson et al. 2000	
2	Scotland, Ross of Mull	1960	17	67	89	75	–	–	2.8	Mitchell and Lincoln 1973
3	Scotland, Fiunary	1965	8	63	86	72	–	–	13.2	” ”
4	Scotland, Scarba Island	1974	0	39	80	46	–	–	34.4	Mitchell and Crisp 1981

Table A7.1 – continued on the next page

Table A7.1 – concluded.

5	Scotland, Glen Feshie	1966-71	0	63	79	71	–	–	13.1	Mitchell and Lincoln 1973
6	Scotland, Glen Fiddich	1961-65	25	87	94	85	–	–	8.0	” ”
7	Scotland, Invermark	1961-65	21	62	84	81	–	–	15.3	” ”
8	Scotland, Glen Prosen	1960	0	67	91	79	–	–	–	” ”
9	Norway, Hitra	1971-72	0	91	93	75	–	–	2.5	Wegge 1975
10	Norway, Aure	1971-72	50	100	97	94	–	–	1.5	” ”
9-10	Total (Hitra, Aure)	1971-72	12	95	95	83	–	–	–	” ”
11	North Norway	1969-91	71	98	98	91	–	–	–	Langvatn et al. 1996
12	Intermediate Norway	1969-91	64	98	99	89	–	–	–	” ”
13	South Norway	1969-91	57	93	97	83	–	–	–	” ”
11-13	Total (Norway)	1969-91	64	95	98	88	–	–	–	” ”
15	Belgia, Wallonia	1992-99	73	97	90	90	–	–	4.4	Bertouille and de Crombrugge 2002

Table A7.1 – continued on the next page

Table A7.1 – concluded.

16	France, Vosges Mountains	1979-83	6	85	–	–	–	–	Bonenfant et al. 2002
		1984-99	63	85	–	–	–	–	” ”
17	Germany, Westphalia	1939-42	74	–	–	–	–	–	Kröning and Vorreyer 1957
18	Germany, Bavaria	1939-42	31	–	–	–	–	–	” ”
19	Austria, Alps, Karwendel	1939-42	22	–	–	–	–	–	” ”
20	Austria, Alps excluding Karwendel	1939-42	31	–	–	–	–	–	” ”
21	Germany, Lower Saxony	1939-42	49	–	–	–	–	–	” ”
22	Germany, Brandenburg	1939-42	55	–	–	–	–	–	” ”
23	Germany, Saxony	1939-42	17	–	–	–	–	–	” ”
24	Poland, Lower Silesia	1939-42	56	–	–	–	–	–	” ”
25	Poland, Western Pomerania	1939-42	60	–	–	–	–	–	” ”

Table A7.1 continued on the next page

Table A7.1 – concluded

26	Poland, Masuria	1939-42	63	–	–	–	–	–	–	Kröning and Vorreyer 1957
17-26	Total (Germany, Austria, Poland)	1939-42	63	–	–	–	0.6	1:0.98	–	” ”
27	Eastern Germany	1987-91	–	–	–	84 (first breeding in 1.5-year- olds)	–	1:0.89	–	Ahrens 1994
28	Germany, Saxon Switzerland	1991-99	–	–	–	94	–	1:0.82	–	Ansorge et al. 1999
29	Slovakia, Western Carpathians	1981-85	–	–	–	95 (first breeding in 1.5-year- olds)	0.5	1:1.04	–	Hell et al. 1987
30	Poland, Carpathians	1980-92	57	96	90	–	1:0.89	–	5.6	Tomek 2002

Table A7.1 – continued on the next page

Table A7.1 – concluded

31	Hungary, Budavidek	1978-79	–	–	–	91	–	1:0.75	Hetlay et al. 1982	
		1979-80	–	–	–	96	–	1:1.33	–	” ”
		Total (1978-80)	–	–	–	93 (first breeding in 1.5-year- olds)	0.7	–	–	” ”
32	Italy, Mesola Wood	2010	0	0	–	28 (first breeding in 5.5-year- olds)	–	1:1.30	15.8	Ferretti and Mattioli 2012
33	Former Yugoslavia	–	30	98	–	–	–	–	–	Valenticic 1960 after deCrombrugghe 1964
34	Serbia, Belje	–	–	–	–	91	2	–	–	Brna 1969 after Danilkin 1999
35	Lithuania	–	–	–	–	97	0.7	1:0.90	–	Gaross 1985 after Danilkin 1999
36	Belarus, Białowieża Forest	1969-73	–	–	–	85 (first breeding in 2.5-year- olds)	0.8	1:0.85	3.5	Shostak 1975
37	Ukraine, Crimean Reserve	–	–	–	–	75	0.7	1:1	7.0	Yanushko 1958 after Danilkin 1999

Table A7.1 – continued on the next page



Table A7.1 – concluded

38	Russia, Voronezh	–	–	–	–	100	–	–	–	Prostakov 1996 after Danilkin 1999
39	Poland, Augustów Forest	2006-11	38	89	92	82	0	1:0.47	3.6	This study
40	Poland, Knyszyn Forest	2006-11	–	88	96	91	0	1:0.92	5.6	” ”
41	Poland, Białowieża Forest	2006-11	38	87	93	83	0.5	1:0.79	6.8	” ”
39-41	Total (NE Poland)	2006-11	40	88	93	85	0.2	1:0.68	-	” ”