

Population biology of the North American raccoon (*Procyon lotor*) in a Northern German lowland beech forest (Müritz National Park)

This study considers questions concerning the spatial and social behaviour, reproduction, population structure and dynamics of the alien North American raccoon (*Procyon lotor*) in Germany. The investigations took place within the framework of a comprehensive raccoon research project (www.projekt-waschbaer.de) over a period of nearly six years in a close-to-nature lowland beech forest in the Müritz National Park (Mecklenburg-West Pomerania). The National Park has been verifiably colonized by raccoons since the end of the 1970s, and due to its abundance of water and its old deciduous tree population it represents an ideal habitat for this mammal.

Between 2006 and 2011, 145 individual raccoons (62 ♀♀ and 83 ♂♂) were captured, genetically sampled, measured and individually tagged. Sampling took place within a 1,114 hectare area of the National Park, at 53 trap sites and with 489 trappings. 51 adult raccoons (23 ♀♀, 28 ♂♂) and 18 juveniles (10 ♀♀, 8 ♂♂) were also fitted with radio collars and located a total of 31,202 times as part of the telemetric survey ($\bar{x}=452$ localisations per individual). Camera trap monitoring was carried out at 36 baited locations of the main investigation area (1,628 ha): 18,721 camera trap pictures were taken of 183 different raccoons over a monitoring period of 5,365 nights. 82 % of all the raccoon pictures showed individually tagged animals. All 145 of the trapped raccoons were successfully genotyped as part of a subproject with highly polymorphic microsatellites. Both the familial relationships and the individual reproductive success of the subject animals could be determined with the genotyping results. For the analyses of the population structure, classic morphometric and phenotypical characteristics, as well as the cause of mortality of 120 raccoon carcasses in the immediate vicinity of the National Park, were recorded.

This thesis established the following main results:

Daytime resting site investigations

Using radio telemetry from 11,241 den site checks for 69 collared raccoons, detailed data on daytime resting site patterns, the habitat characteristics of the dens, the phenology and status group dependent differences, as well as data on the winter dens were recorded. A total of 1,804 different resting sites were identified. Of all the den sites, trees were visited 61 %, ground resting sites and burrows 38 %, and other hideouts 1 % (e.g. buildings). Copper beech (*Fagus sylvatica*) represented the most significant tree for resting with 50 % of all visits, followed by the oak (*Quercus* spp., 34 %) and spruce (*Picea abies*, 5 %). The raccoons used 17 different species of tree for their daytime den. Considering tree den sites, the collared animals were located 80 % of the time in cavities, although tree hollows represented only 36 % of all tree den sites. Therefore, tree cavities were frequently revisited by raccoons (on average 19 repeated visits) whereas other sites such as tree forks, tops of spruces or nests were only visited once or a few times (repeated visits 1.5 to 3.5). The average den site height was 9.7 m (range 0 m to 31 m). 97 % of all ground resting sites were either entirely in or on wet areas (moorland, lakes, ponds) or on islands. Structures in reeds (36 %), under willows (29 %)

and on or in hummocks (10 %) played the most important role. Hideouts on the ground were chosen by the raccoons particularly during the summer (56 % of all den site visits) and autumn (67 %), while tree den sites tended to be chosen in the winter (79 %) and spring (80 %). An average raccoon in the Müritz National Park used between 40 and 80 different daytime resting sites in one year. Each year 20 to 60 new hideouts were added meaning that a 5 year old animal will have slept in 150 to 300 different daytime resting sites. The animals investigated were located in winter on a total of 1,686 days in 25 different winter dens. The dens comprised 17 trees (9 beech, 8 oak) and 7 burrows and/or in a hummock. In 68 % of cases, several collared animals (2-5 raccoons) shared the winter dens. The longest uninterrupted documented use of a winter den by a collared animal was 84 days.

Home Ranges

After the increment plot analyses, 26 valid total datasets, 95 valid annual datasets, and 377 valid seasonal datasets were available. The area calculation was done according to 95 % fixed kernel estimation (WORTON 1989). The size of the total ranges of 26 raccoons observed over several years (observational period 569 to 1,947 days) was on average $1,063 \pm 520$ hectares for males and 529 ± 282 hectares for females. Established males covered in one year an annual range of 583 ± 264 hectares on average as compared to 309 ± 181 hectares for the adult females. Thus the range areas of the adult males were significantly larger than those of the adult females. Juvenile raccoons also used considerably smaller range areas ($\bar{x} = 261 \pm 142$ hectares). Extreme annual range areas of up to 3,824 hectares were determined for adult males that were not resident (floaters). The areas covered in a season by the collared raccoons (adult males: $\bar{x} = 390$ hectares, adult females: $\bar{x} = 171$ hectares) were on average 60 % of the range areas covered annually, meaning that they were significantly smaller. The size of the winter ranges correlated clearly with the weather conditions. In the cold and very snowy winter of 2009/10, the adult raccoons covered average areas of only 59 hectares ($\sigma\sigma$) and 41 hectares ($\phi\phi$), whereas there was hardly a difference in the winter ranges in the mild winter of 2006/07 with an average of 525 hectares ($\sigma\sigma$) and 168 hectares ($\phi\phi$) compared to the summer ranges.

Activity rhythm

The assessed raccoons in the Müritz National Park showed a predominantly nocturnal behaviour. 97 % of all localisations in which the animals investigated showed locomotive activity were during the night ($n = 16,892$ localisations). Diurnal activity was particularly observed in summer: The raccoons were active for 14 % of all daytime localisations ($\sigma\sigma$: 4 %, $\phi\phi$: 21 %). Mothers with cubs particularly demonstrated daytime active range behaviour with 27 % of all daytime localisations. Especially during littering phases, many females demonstrated exceptionally cathemeral behaviour in which the raccoons were predominantly active in protected habitat structures such as fens or reed beds during the daytime. During the short summer nights, the animals demonstrated locomotive behaviour for 99 % of all night localisations, whereas the value dropped to 73 % in the winter. During snowy phases, raccoons were fully immobile in their winter dens for up to several weeks at a time (dormancy).

Dispersal patterns

The analyses of dispersal behaviour in juvenile raccoons (natal dispersal) were performed based on 35 males and 55 females captured and tagged verifiably within their natal territory. The results revealed marked intersexual differences in dispersal behaviour. While all the males left the natal territory (male-biased natal dispersal), all female offspring remained in the immediate vicinity of their own natal territory (female-biased natal philopatry). The average dispersal distance (linear distance) was 42 km (range 3 km to 285 km) for males and only 922 m (range 64 m to 3.479 m) for females. The documented maximal distance of 285 km is the longest dispersal distance that has ever been published for raccoons. The collared male left his natal territory at an age of 7 ½ months and covered a calculated total distance of over 1,600 km in 112 days.

The males dispersed in all directions, with no specific direction being preferred or avoided. The average emigration age for the males was 10 months (5-27 months), and the main dispersal times occurred in autumn (40 %) and spring (32 %). The dispersal period lasted on average 3.8 months. The subsequent main immigration period started in the spring during the transition from the first to the second year of life and lasted as far as into the autumn of the second year of life. With the collared juveniles, the immediate dispersal behaviour could be observed over several weeks. The documented dispersal of three adult males from a previously established home range (adult dispersal) was an anomaly.

Social organisation

The raccoons' social behaviour was studied using static (overlap) and nonparametric dynamic interaction analyses (Jacobs index). Characteristic socioethological patterns were seen within maternal families, between adult females from individual matriline, as well as within male-social-groups. The development of eleven maternal families was continuously documented from parturition (natal territory phase) through adolescence (juvenile stage, incipient dissolution of familial bonds, dispersion, establishing) up to the first reproduction of their own young (parenthood analyses). The splitting of the families in the Müritzer National Park began, at the earliest, after five months in September and continued in some families until the next reproduction period in March. A strictly female-biased natal philopatry led to the formation of widely spread matrilineal groups, which demonstrated highly static overlapping due to favourable resources. The intrasexual interactions were evident through the communal use of different requisites such as daytime resting sites, food sources and winter dens. However, females did not engage in closer social connections with each other (neutral dynamic interaction behaviour). This resource-oriented spatial behaviour corresponded to a characteristic fission-fusion social system. Presumably due to the clumped spatial distribution of the adult females (female aggregations), male coalitions comprising two (dual coalition) or more adult males (up to 5 \triangleq group coalitions) formed regularly in the study area. The partners in dual coalitions (male dyads) demonstrated very high static (mean overlapping value 92±10 %) and dynamic interaction values (Jacobs indices: 0.81-1.00), remaining together on average for 10.5±4.0 months (7-22 months). In contrast, adjacent adult males demonstrated neutral interaction behaviour.

This study investigated, for the first time, the molecular biologically documented individual reproductive success of an adult male in conjunction with his affiliation to a male coalition.

Reproduction

The main mating season in the Müritz National Park took place between January 12th and March 13th depending on weather conditions. 13.2 % of all litters came from a second and/or later breeding cycle (April 25th to June 8th). The raccoons demonstrated promiscuous mating behaviour. 50 % of all genotyped litters showed multiple paternities, whereby females mated exclusively with males belonging to the same coalition. Corresponding to the variability of the main mating season, the documented births occurred between March 19th and May 12th, with more than two-thirds of all births taking place in April. The births that resulted from a later mating season took place between July 1st and August 6th. This study documented a total of 37 natal dens, which were all in tree cavities. The copper beech was the most frequently used tree (70 % of natal dens). The litter hollows were found at an average height of 6.3 ± 4.4 m and had an average volume of 153 ± 139 dm³. The litter sites were used on average for 55 ± 18 days. Thereafter all the female groups went to a so-called successional nursery in which the juveniles stayed for an average of 14 ± 16 days before they changed their den sites with their mother daily (average age of the juveniles 78 days). Based on analysis of 49 litters an average secondary litter size of 3.14 ± 1.10 was determined. Female yearlings had significantly fewer offspring on average (1.75 ± 0.96) than older females (3.27 ± 1.03). Furthermore, one-year-old females were on average gravid in only 50 % of all cases, whereas the rate of 91 % was observed for older females.

Population structure and dynamics

The population structure analysis was based on 609 datasets (489 captures, 120 carcasses), recorded between 2006 and 2011. The bodyweights of adult raccoons in the Müritz National Park varied on average from 5.0 ± 1.1 kg for females to 6.2 ± 1.3 kg for males. The heaviest documented raccoon was a ten-years-old male weighing 10.65 kg at the end of November. The bodyweights differed significantly according to sex, age and season. The weight of adult animals in the autumn was on average nearly 30 % higher than in spring. The head-body length of adult males was on average 637 ± 56 mm, which was 42 mm longer than adult females which averaged at 595 ± 36 mm. The sex ratio of the juvenile raccoons (primary and secondary sex ratio) was uniformly female-biased across all data sources (1.1 to 1.9 female per male), which is consistent with a promiscuous mating system. However, there was strong dependence for the adult raccoons (tertiary sex ratio) on the sampling technique (0.5 to 1.1 female/male). The primary mortality factors were canine distemper, collisions with vehicles and harvest. A total of 14 different causes of death were documented. Half of the raccoons died from an anthropogenic-related cause. The population density varied from 3.8 raccoons/km² in 2006 to 5.7 raccoons/km² in 2009. During the first years (2006-2008) the population grew annually by approx. 20 % and stagnated during the last years of the study. A relatively high average age (2.34 ± 2.69 years), a high annual survival rate (males: 0.90, females: 0.85) associated with a relatively low annual natality rate of 0.92 and a very low turnover-rate (16.1 years) indicated a stable population close to the carrying capacity in the National Park for the years 2009-2011. In addition to the morphometric data clusters, the population studied was characterised using phenotypical characteristics such as pelage colouration, palate pigmentation, number of nipples, among others.