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Summary

Zusammenfassung

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The raccoon (*Procyon lotor*) as potential rabies reservoir species in Germany: a risk assessment

Der Waschbär (Procyon lotor) als potenzielle Tollwutreservoirspezies in Deutschland: eine Risikobewertung

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Frank Michler²

Terrestrial wildlife rabies has been successfully eliminated from Germany predominantly as a result of the distribution of oral rabies vaccine baits. In case that wildlife rabies would re-emerge among its known reservoir species in Germany, swift action based on previous experiences could spatially and temporally limit and subsequently control such an outbreak. However, if rabies emerged in the raccoon population in Germany (*Procyon lotor*), there are no tools or local experience available to cope with this situation. This is especially worrisome for urban areas like Kassel (Hesse) due to the extremely high raccoon population density. A rabies outbreak among this potential reservoir host species in these urban settings could have a significant impact on public and animal health.

Keywords: susceptibility, oral vaccination, vaccine, baits, raccoon, Germany

Die terrestrische Tollwut wurde in Deutschland vor allem durch das Auslegen von oralen Impfstoffködern erfolgreich getilgt. Falls sich die Trägerspezies in Deutschland wieder mit dem Tollwutvirus re-infizieren, kann aufgrund der vorhandenen Erfahrungen schnell sowie gezielt reagiert und der Ausbruch rasch unter Kontrolle gebracht werden. Allerdings gibt es bislang keine Mittel und Erfahrungen mit der Bekämpfung von mit Tollwut infizierten Waschbären (*Procyon lotor*) in Deutschland. Dies ist insbesondere für Städte wie Kassel (Hessen) bedeutsam, in denen die Waschbären eine extrem hohe Populationsdichte erreichen. Ein Tollwutausbruch bei dieser potenziellen Trägerspezies in städtischen Gebieten stellt deswegen ein Risiko für die Gesundheit von Mensch und Tier dar.

Schlüsselwörter: Empfindlichkeit, orale Immunisierung, Impfstoff, Köder, Waschbär, Deutschland

Introduction

On World Rabies Day, 28 September 2008, Germany was declared rabies free; since 2006 no indigenous terrestrial rabies cases had been reported (Anonymous, 2008). The last sylvatic epizootic entered Germany from Poland when an infected animal crossed the Odra river in 1947 (Müller et al., 2004b). The outbreak was fox-mediated; 73% of all cases reported involved foxes (*Vulpes vulpes*). The highest annual number of cases reported occurred in 1983 with 9160 rabies cases (Müller et al., 2004b); the same year that the first field trials with oral vaccination of foxes against rabies took place in Germany. The distribution of these vaccine baits led to the ultimate elimination of terrestrial rabies in this country. Although many animal species other than foxes became infected no other terrestrial animal species acted as reservoir during this outbreak. Recently, the raccoon dog (*Nyctereutes procyonoides*) has also emerged as a reservoir species in North-eastern Europe. Fortunately, the available oral rabies vaccine baits developed for foxes are also efficacious in raccoon dogs (Schuster et al., 2001; Cliquet et al., 2006). Oral vaccination of wildlife has changed the rabies landscape to a great extent and most of Europe is now considered free of terrestrial wildlife rabies. However, vigilance is still required. Terrestrial rabies can be reintroduced through direct entry from rabies-infected wildlife in neighbouring countries as recently occurred in Italy. Alternatively, rabies can also be reintroduced through importation of infected animals incubating rabies (Johnson et al., 2011). In the last decade, at least five cases of imported dog rabies were reported from Germany (Johnson et al., 2011). Sometimes these importations occur through ignorance of regulations or active disregard of importation requirements (Le Roux and van Gucht, 2008). The re-introduction of rabies in Germany through infected wildlife or pets could lead to a spill-over infection into the reservoir species resulting in a new outbreak. Another possibility is a spill-over infection from bats infected with European Bat Lyssavirus Type 1 or 2 (EBLV-1 and -2). Such spill-over infections are relatively rare but have been reported on several occasions like in a stone marten (*Martes foina*) and domestic cats (*Felis catus*) (Müller et al., 2004a; Dacheux et al., 2009). Typically, these spill-over infections are so-called dead-ends and do not progress beyond the first infected terrestrial host. On rare occasions these spill-over infections develop into independent new sustainable infection cycles within the new host species, like recently has been observed in a skunk population in Arizona infected with a bat variant of the rabies virus (Leslie et al., 2006). Most likely these carnivores have preyed on bats and came in contact with an infected animal. Raccoons (*Procyon lotor*, Fig. 1) in (semi-) urban settings may use attics as resting – or den sites, which can also be occupied by bats. Considering that the serotine bat (*Eptesicus serotinus*), the reservoir host of EBLV-1 responsible for more than 90% of bat rabies cases reported in Germany, is a bat species that typically uses buildings as roosts, encounters between serotine bats and raccoons cannot be excluded. A rabies outbreak

among raccoons especially in extremely densely populated urban settings would pose a serious risk for public and animal health. The recent outbreak among raccoons in Central Park, Manhattan – New York City (USA), clearly underscores the potential risk and the difficulties resolving this problem; 121 raccoons found in and around Central Park were reported rabid in 2010 (source: <http://www.nyc.gov/html/doh/html/cd/cdrab-cp.shtml>). On first thought, one would suggest using the highly successful approach of oral rabies vaccination for raccoons. Unfortunately, this approach used so successfully for foxes cannot simply be copied for raccoons for several reasons. First of all, there is only limited experience with distribution of baits containing live replication competent virus vaccines in urban areas. Secondly, no local experience in distributing baits targeted for animals living at extremely high densities is available. Finally and most importantly, the licensed oral rabies vaccine baits in Germany are most likely not suitable for raccoons. Hence, the responsible authorities in Germany would not only be completely unprepared in case of emergence of rabies in the raccoon population but would also have no or limited tools available to address such an outbreak. In this paper we will try to assess the risks associated with the raccoon population in Germany as a potential rabies reservoir species and to identify possible methods to intervene in case rabies would infect the raccoon population.

Raccoons in Germany

The first free-living raccoons were observed in Germany approximately 80 years ago. Today Germany accommodates the largest raccoon population within Central Europe. In the late 1920s raccoons were precious fur bearers and during this period escapes from enclosures and attempts to introduce the animals in the wild were documented for the first time (Müller-Using, 1956). However, these early escapees and deliberate efforts to introduce raccoons failed. The first successful introduction took place in 1934, when four raccoon (two females and two males) were abandoned at Edersee, Hesse. This



FIGURE 1: Raccoon – *Procyon lotor* (photograph and copyright: Roman Vitt).

event is regarded as the “initiation” of the free-ranging raccoon population in Central Europe. The second introduction took place in Wolfshagen (East Brandenburg). During the turmoil of the Second World war 20–30 animals were released from a raccoon farm in 1945 (K. Allner, pers. comm.) and formed the basis for the raccoon population in Eastern Brandenburg and Western Pomerania (Stubbe, 1993). Raccoons are difficult to contain in captivity; hence, constantly additional captive animals escaped and entered the raccoon populations established by these two original events. In spite of this constant influx of new individuals into the German raccoon population genetic diversity is relatively low compared to several raccoon populations studied in the USA, underscoring the “founder-effect” in the German raccoon population (Gramlich et al., 2011). The main foci for range expansion are still limited to these original sites in the middle and northeastern part of Germany (Fig. 2). The reason for this is the relatively conservative dispersal behaviour. Raccoons disperse actively and exploratively with a distinct gender difference. Due to very strong philopatric behaviour the females remain near their birthplace their entire life, while male raccoons almost always leave the maternal area (Gehrt, 2003; Michler and Köhnemann, 2010).

In 1954, hunting efforts started with the aim of extirpation. However, despite efforts and the use of methods like steel traps or gassing of burrows, hunting never succeeded in having the desired effect. The annual hunting bag increased continuously and showed an exponential increase in the mid 1990s reaching over 50 000 killed raccoons (Fig. 3). Raccoons expanded their range during the last few decades and now occur at varying population densities in all 16 federal states in Germany. According to the Federal Nature Conservation Act (BNatSchG; § 7 Abs. 2 Nr. 7), the raccoon is considered nowadays an indigenous species.

Although being highly adaptable, raccoons are dependant on certain habitats. These are primarily mixed woodland and the presence of wetland (lakes, streams, swamps). Raccoons tend to urbanisation as almost no other wild animals. They are able to successfully utilise human settlement areas because of their extraordinary adaptability and complex and variable social system with distinct intraspecific tolerance (no territorial behaviour). Besides this, the climbing abilities and tactile manipulating skills of raccoons enable the use of resources that are not accessible to most other terrestrial wild animals. (Sub-) Urban habitats provide a markedly superior supply of resources than most woodland habitats, often

allowing population densities of raccoons in (sub-) urban areas to reach up to ten times higher than in rural areas. In Germany, the population density in forested habitats is generally well below ten animals/km² but in certain urban areas population densities of approximately 100 animals/km² have been documented (Kassel – 90 animals/km² and Bad Karlshof – 110 animals/km²; Hohmann 1998; Hohmann et al., 2001; Michler 2004, 2007).

Raccoon and rabies

This New World species can be found almost everywhere in North and Central America, from southern Canada to central Panama. Also, raccoon rabies is widespread especially in the eastern USA; rabid raccoons have been reported from 25 states during 2009 in the USA (Blanton et al., 2010). In the same year, 2327 (34.8%) of the total reported 6841 rabies cases in the USA were raccoons, making it the most often reported rabies infected animal species in North America (Blanton et al., 2010). Rabies can cause high mortality rates during an initial epizootic, with up to 80% of the population succumbing to infection (Clavette, 1996). Some of the most common rabies symptoms or behaviours observed among infected raccoons are aggression, appearance of being sick or unhealthy, impaired mobility or ataxia, fighting with dogs, and abnormal vocalizations. However, extremely aggressive behaviour is far less common in rabies infected raccoons than in rabid foxes (Kappus et al., 1970), and some rabid raccoons display no abnormal behaviour at all. Several authors have indicated that in contrast to fox rabies there is no

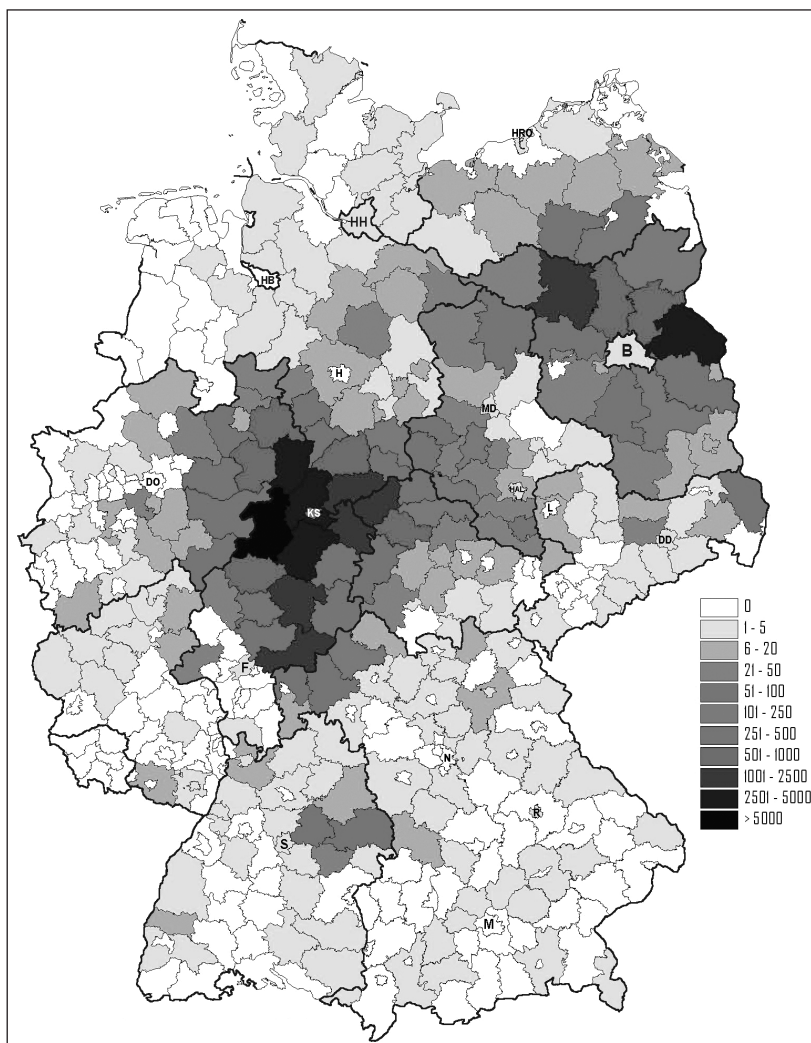


FIGURE 2: Distribution of the raccoon in Germany according to average annual hunting bag, 2001–2003 (animals killed by hunters or found dead per county).

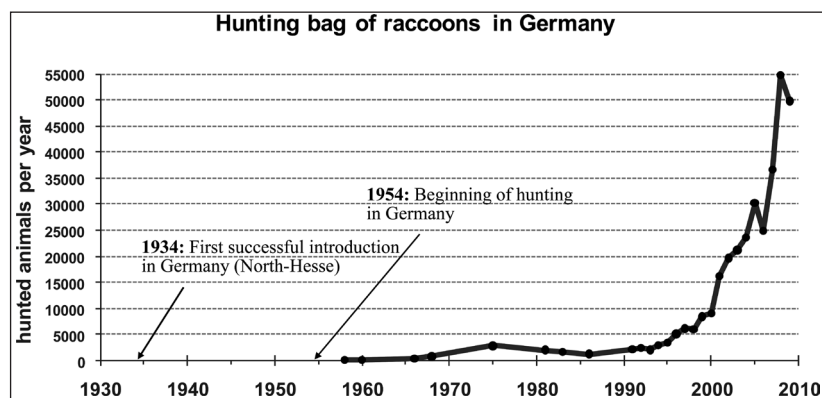


FIGURE 3: Annual number of raccoons killed by hunters in Germany.

distinct temporal pattern in raccoon rabies (Rupprecht, 1992). Torrence et al. (1992) reported on a bimodal pattern with peaks in late winter and early fall whereby the highest and lowest incidence was observed in late winter and the summer months, respectively. These two peaks are very similar to the fox rabies incidence and have been associated with the mating season (January to March) and dispersal of the juveniles in autumn, two periods with increased intraspecific contact rates and aggression.

Raccoon rabies in Germany

During the most recent rabies epizootic, only 15 rabies cases in raccoons were reported from former West Germany between 1960 and 1975 (Rojahn, 1977); most of these cases from the northern part of Hesse. Also several cases were reported from former East-Germany.

However, these cases were all temporarily-spatially isolated and the raccoon had no role in the emergence or spread of wildlife rabies in Germany (Tschirch, 2001). This low number of rabies cases in raccoons is rather remarkable. Some people claimed that rabid raccoons tend to withdraw in their hide-outs (Kampmann, 1975) and therefore are most of the times not found and reported. However, we know from the surveillance data in the USA that this is most likely not the case. Another explanation for the low rabies incidence among German raccoons was the low population density during the last fox rabies outbreak. The exponential increase did not occur until the mid 1990s when fox rabies was already restricted to some isolated residual foci. Therefore, in 1970s and 1980s during the peak of the rabies outbreak the number of raccoons may have been too low for the development of an independent transmission cycle. However, one would have expected more isolated spill-over infections from foxes to raccoons or even self-limited local outbreaks among raccoons after such a spill-over event. There are two other possible explanations. First of all, raccoons may not be very susceptible for the fox rabies virus variant present in Germany. Interspecific variability in susceptibility for different rabies variants is well documented (Blancou, 1988). For example, during an experimental study, raccoons were about thousand-fold more resistant than foxes to infection with a rabies virus isolated from the salivary gland of a rabid fox (Winkler and Jenkins, 1995). Furthermore, it is suggested that raccoons can survive a rabies infection as indicated by the prevalence of seropositive raccoons in rabies

endemic areas (McLean, 1971; Jenkins et al., 1988). Secondly, in experimental settings not all raccoons die when challenged with rabies virus; nor do all animals effectively seroconvert when vaccinated, suggesting that there is a significant level of variability in the immune response of raccoons to rabies (Hanlon et al., 2002; Szanto, 2009). It is not known if this variability has a genetic basis but genetic variation in susceptibility for certain viral diseases is well documented and has also been suggested for raccoons and rabies (Hedrick, 2002; Sommer, 2005; Srithayakumar et al., 2011). As mentioned above the genetic relatedness among German raccoons is very high. If raccoons in Germany are not (very) susceptible to rabies infection there is a less urgent

need for contingency plans. In the framework of the Lyssavirus research network (<http://lyssavirus.fli.bund.de/Home.aspx>), the susceptibility of German raccoons for several rabies virus variants will be investigated in association with potential re-emergence of terrestrial rabies in Germany.

Control of raccoon rabies

Just as with fox rabies, intensified population reduction schemes alone do not seem to be a sustainable and effective control measure for raccoon rabies, but in combination with other tools it has shown to be highly effective. When raccoon-mediated rabies entered Ontario, Canada, from the USA in July 1999 an integrated emergency control programme was initiated (Rosatte et al., 2009a). Five kilometres around the location of a rabies case, animals were trapped and euthanized to reduce the raccoon population by 80% to 90%. Animals captured in an approximately 5 km radial area around the population reduction zone were vaccinated by the parenteral route using an inactivated vaccine and subsequently released. If more than 60% of the raccoon population in this TVR-zone (Trap-Vaccinate-Release) were vaccinated, the TVR-programme was discontinued. Around the TVR-zone an up to 50 km wide buffer zone was created by distributing oral rabies vaccine baits. As a result of these efforts, the last case of raccoon rabies was reported in Ontario on 23 September, 2005 (Rosatte et al., 2009a). This approach has later also been successfully implemented to control raccoon rabies in Quebec, Canada (Guerin et al., 2008). A special hurdle in implementing such a programme is the fact that the highest raccoon densities are reported from (semi-) urban areas. Population reduction is not only complicated and time and labour consuming, but would also meet considerable opposition from a large part of the public. In Ohio, USA, a similar approach using baiting and TVR but without population reduction was used (Slate et al., 2009). One of the major reasons for these enhanced control efforts, including TVR and population reduction, was that the distribution of the available oral rabies vaccine bait could not reach a sufficient high vaccination level in the raccoon population to control rabies. Furthermore, the efficacy of the oral rabies vaccine used was not as efficacious as the vaccine used for parenteral vaccination (Brown et al., 2011). Another complicating factor is the delivery of baits in urban areas, which is not without difficulties and

there is little or no experience available in Europe with the exception of anthelmintic baiting of foxes against *Echinococcus multilocularis* (Hegglin et al., 2003; König et al., 2008).

Oral vaccination of raccoons

Vaccine

Animals differ greatly in their relative susceptibility to oral vaccination (Hable et al., 1992), and raccoons are more refractory to oral vaccination against rabies than foxes and raccoon dogs. Therefore, it must be determined if the three oral rabies vaccine strains SAD B19, SAD P5/88 and SAG2 registered in Germany are also efficacious in raccoons. The most widely used vaccine in Germany, SAD B19, has been investigated in detail (Rupprecht et al., 1989). Also, the double mutant SAG2 has been tested in raccoons (Hanlon et al., 2002). Both strains showed protective activity in raccoons but at much higher doses than used for foxes. Furthermore, the efficacy was less pronounced when the vaccine was not administered by direct oral instillation but by offering animals vaccine in a bait (Rupprecht et al., 1989).

Presently there is only one oral rabies vaccine licensed for use in raccoons, the recombinant vaccinia virus expressing the rabies glycoprotein (V-RG). During experimental studies this vaccine protected raccoons against a relevant challenge infection (Rupprecht et al., 1986). Unfortunately, field data are inconsistent with results from this and other laboratory efficacy trials where 80% to 100% of raccoons orally immunized with V-RG seroconverted.

The seroconversion rate determined after the distribution of V-RG baits is often much lower (Rosatte et al., 2008; Slate et al., 2009). This low seroconversion rate is not a result of poor bait uptake as indicated by the detection rate of the bait marker, tetracycline. On Parramore Island, Virginia, 1000 baits per km² were distributed during 1990 and only 52% of the raccoons seroconverted although 84% of the raccoons tested positive for the bait marker (Hanlon et al., 1998). Also, in other areas a large discrepancy between bait acceptance (detection of bait marker) and seroconversion rates in raccoons has been observed (Rosatte et al., 2008). In the USA, the average long term post-ORV antibody levels (> 0.05 IU/ml) in raccoons was approximately 30%, much lower in comparison with average levels reported for gray foxes and coyotes using the same vaccine virus and similar baiting strategies (Slate et al., 2009). However, the correlation between seroconversion in terms of the presence of rabies virus neutralizing antibodies (VNA) and protective immunity remains a topic of debate. Hence, animals that consumed a vaccine bait but do not develop detectable levels of VNA can still be protected against a relevant challenge infection (Hanlon et al., 2002).

Several other candidate vaccines have been tested in raccoons; including genetically modified rabies virus vaccines, recombinant raccoon pox virus and canine adenovirus type 2 both expressing the rabies virus glycoprotein (Blanton et al., 2007; Henderson et al., 2009; Esposito et al., 1988). Some of these constructs have shown promising experimental results but are most likely not suitable because of pre-existing immunity against the vector virus among the target population in the field (Root et al., 2008). Another not yet licensed

product has already been widely tested in Canada; ONRAB® – a recombinant human adenovirus type 5 expressing the rabies glycoprotein (Rosatte et al., 2009b). Compared to V-RG, ONRAB® vaccine is very immunogenic in raccoons under field conditions (Rosatte et al., 2008). However, it can be expected that in Europe the intentional environmental release of replication-competent recombinant viruses expressing a foreign gene could encounter considerable resistance from the public, especially when it concerns a human pathogen.

Bait

Another possible explanation for the observed poor efficiency in raccoons in the USA is the bait types used. The first bait used was the fish meal polymer bait. During experimental screening experiments and field studies these fish-flavoured baits were preferred over for example baits with a fruit-based or corn oil coating (Linhart et al., 1991, 1994, 2002; Kavanaugh and Linhart, 2000). However, during other studies preference for fish-flavoured baits was less pronounced. In Ontario, Canada, cheese and vanilla-sugar flavoured baits were accepted better by raccoons than for example sea food flavoured baits (Rosatte et al., 1998). Also, initial experimental and field studies in Germany indicated that the present fox bait (fish meal) was not accepted as good as fruit or corn-based baits (unpublished results). Besides bait palatability there are many other bait properties that determine its efficiency in terms of vaccine delivery. For example, a large proportion of discarded sachets within the fish meal polymer baits were not punctured by raccoons after bait uptake (Olson and Werner, 1999; Linhart et al., 2002). In contrast to foxes, raccoons are selective omnivores displaying great ability of manual manipulation of food items, enabling them to selectively remove unfavourable parts of food items. Therefore, it is not uncommon to recover the vaccine capsule intact from a bait of which the matrix has been consumed (Hable et al., 1992).

Hence, other bait types targeted at raccoons were developed like the coated-sachet whereby the sachet containing the vaccine is no longer placed within a bait matrix but simply sprinkled with a fish-meal coating (Linhart et al., 2002). The latest bait developed and used for oral vaccination of raccoons is the UltraLight bait used for the distribution of the ONRAB® vaccine. It consists of an elongated plastic blister coated with a thin bait matrix containing different predominantly sweet attractants (Rosatte et al., 2009b). Both types largely eliminate the risk of selective separation of bait matrix and vaccine container.

Another important factor in determining bait uptake by raccoons is bait competition by non-target species. Especially in urban areas, bait uptake by pets can raise certain concerns by the owners and it may be necessary to develop species-specific baiting techniques. For example, bait distribution in urban settings targeted at red foxes was highly effective when baits were placed at selected sites attractive to foxes and that restricted access to bait competitors (Hegglin et al., 2003; König et al., 2008). The most important bait competitors for foxes in urban areas were dogs, rodents, snails and hedgehogs (Hegglin et al., 2004). Although cats were observed near the baits, they never removed the fish-flavoured baits (Hegglin et al., 2004). However, this does not necessarily apply to different flavoured bait types. It can be expected

that sweet-tasting baits will attract many other animal species.

Another relevant issue is the relationship between raccoon population density and the minimum density of vaccine baits necessary to confer herd immunity. Due to the higher population densities, much higher bait densities must be applied than were used during vaccination campaigns for red foxes. In Toronto, Canada, with a raccoon density of 13–20 animals/km² 400 baits per km² were distributed (Rosatte and Lawson, 2001). So, this would mean that for areas with a raccoon density of 100 animals per km² or more, an unrealistic number of thousands of baits per km² have to be distributed. Therefore, new, innovative bait delivery strategies that could enhance bait uptake efficiency should be developed. Rosatte et al. (2009a) suggest a staggered approach using these extremely high densities only in localized areas and using a lower bait density in surrounding buffer zones. Also cluster baiting at known feeding sites (Hadidian et al., 1989) habitat-targeted baiting (Boyer et al., 2011), or the establishment of artificial feeding stations that are regularly visited by raccoons have been suggested (Boulanger et al., 2008).

Conclusion

The raccoon is not considered a reservoir species for rabies in Germany based on the last terrestrial sylvatic rabies outbreak. However, due to the continuously increasing size of the raccoon population this status could change upon re-emergence and spillover of rabies into raccoons in Germany. Unfortunately, the susceptibility of the German raccoon population for relevant rabies virus variants is unknown. Therefore, it is of utmost importance to determine susceptibility. If shown to be susceptible, all available control measures need to be assessed in detail. The most promising control method is oral rabies vaccination, but no vaccine bait licensed in Germany has been shown to be efficacious in raccoons. Hence, efficacious and safe oral rabies vaccines for raccoons need to be identified and a raccoon-specific bait needs to be developed. Also, effective baiting strategies targeted for raccoons need to be formulated, especially for urban areas with extremely high population densities. Finally, consideration should be given to preparation of conceptual contingency plans to better ensure swift and appropriate intervention in a worst case scenario of emergence of (urban) rabies in raccoons in Germany.

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References

- Anonymous (2008):** Austria and Germany declared “free from terrestrial rabies”. Rabies Bulletin Europe 32 (3): 7.
- Blancou J (1988):** Ecology and epidemiology of fox rabies. Clin Infect Dis 10: S606–S609.
- Blanton JD, Self J, Niezgoda M, Faber ML, Dietzschold B, Rupprecht C (2007):** Oral vaccination of raccoons (*Procyon lotor*) with genetically modified rabies virus vaccines. Vaccine 25: 7296–7300.
- Blanton JD, Palmer D, Rupprecht CE (2010):** Rabies surveillance in the United States during 2009. J Am Vet Med Assoc 237: 646–657.
- Boulanger JR, Bigler LL, Curtis PD, Lein DH, Lembo AJ (2008):** Comparison of Suburban Vaccine Distribution Strategies to Control Raccoon Rabies. J Wildl Dis 44: 1014–1023.
- Boyer J-P, Canac-Marquis P, Cuérin D, Mainguy J, Pelletier F (2011):** Oral vaccination against raccoon rabies: landscape heterogeneity and timing of distribution influence wildlife contact rates with the ONRAB vaccine bait. J Wildl Dis 47: 593–602.
- Brown LJ, Rosatte RC, Fehner-Gardiner C, Knowles MK, Bachmann P, Davies JC, Wandeler A, Sobey K, Donovan D (2011):** Immunogenicity and efficacy of two rabies vaccines in wild-caught, captive raccoons. J Wildl Dis 47: 182–194.
- Clavette M (1996):** Status of raccoon rabies in Connecticut Wildlife, Connecticut Wildlife 16: 12.
- Cliquet F, Guiot AL, Munier M, Bailly J, Rupprecht CE, Barrat J (2006):** Safety and efficacy of the oral rabies vaccine SAG2 in raccoon dogs. Vaccine 24: 4386–4392.
- Dacheux L, Larrous F, Mailles A, Boisseleau D, Delmas O, Biron C, Bouchier C, Capek I, Muller M, Ilari F, Lefranc T, Raffi F, Goudal M, Bourhy H (2009):** European bat lyssavirus transmission among cats, Europe. Emerg Infect Dis 15: 280–284.
- Esposito JJ, Knight JC, Shaddock JH, Novembre FJ, Baer GM (1988):** Successful oral rabies vaccination of raccoons with raccoon poxvirus recombinants expressing rabies virus glycoprotein. Virology 165: 313–316.
- Gehrt SD (2003):** Raccoons and allies. In: Feldhamer GA, Chapman JA, Thompson BC (eds.), Wild Mammals of North America. 2nd ed., John Hopkins University Press, Baltimore, Maryland USA, 611–634.
- Gramlich S, Schulz H, Köhnemann BA, Michler F-U (2011):** Mater semper certa? – Molekularbiologische Analyse einer Waschbärpopulation (*Procyon lotor* Linné, 1758) in Müritznationalpark. Beiträge zur Jagd- und Wildtierforschung 36: 521–530.
- Guerin D, Jolicoeur H, Canac-Marquis P, Landry F, Gagnier M (2008):** Le contrôle de la rage du raton laveur en Montérégie en 2007: Rapport des interventions terrestre et aérienne. Ministère des Ressources naturelles et de la Faune, Québec, Canada.
- Hable CP, Hamir AN, Snyder DE, Joyner R, French J, Nettles V, Hanlon C, Rupprecht CE (1992):** Prerequisites for oral immunization of free-ranging raccoons (*Procyon lotor*) with a recombinant rabies virus vaccine: study site ecology and bait system development. J Wildl Dis 28: 64–79.
- Hadidian J, Jenkins SR, Johnston DH, Savarie PJ, Nettles VE, Manski D, Baer GM (1989):** Acceptance of simulated oral rabies vaccine baits by urban raccoons. J Wildl Dis 25: 1–9.

- Hanlon CA, Niezgoda M, Hamir AN, Schumacher C, Koprowski H, Rupprecht CE (1998):** First North American field release of a vaccinia-rabies glycoprotein recombinant virus. *J Wildl Dis* 34: 228–239.
- Hanlon CA, Niezgoda M, Morrill P, Rupprecht CE (2002):** Oral efficacy of an attenuated rabies virus vaccine in skunks and raccoons. *J Wildl Dis* 38: 420–427.
- Hedrick PW (2002):** Pathogen resistance and genetic variation at MHC loci. *Evolution* 56: 1902–1908.
- Hegglin D, Ward PI, Deplazes P (2003):** Anthelmintic baiting of foxes against urban contamination with *Echinococcus multilocularis*. *Emerg Infect Dis* 54: 439–447.
- Hegglin D, Bontadina F, Gloor S, Romer J, Müller U, Breitenmoser U, Deplazes P (2004):** Baiting red foxes in an urban area: A camera-trap study. *J Wildl Manage* 68: 1010–1017.
- Henderson H, Jackson F, Bean K, Panasuk B, Niezgoda M, Slate D, Li J, Dietzschold B, Mattis J, Rupprecht CE (2009):** Oral immunization of raccoons and skunks with a canine adenovirus recombinant rabies vaccine. *Vaccine* 27: 7194–7197.
- Hohmann U (1998):** Untersuchungen zur Raumnutzung des Waschbären (*Procyon lotor*, L. 1758) im Solling, Südniedersachsen, unter besonderer Berücksichtigung des Sozialverhaltens. University of Göttingen. Göttingen. Dissertation.
- Hohmann U, Voigt S, Andreas U (2001):** Quo vadis raccoon? New visitors in our backyards – on the urbanization of an allochthonous carnivore in Germany. *Naturschutz und Verhalten* 2: 143–148.
- Jenkins SR, Perry BD, Winkler WG (1988):** Ecology and epidemiology of raccoon rabies. *Rev Infect Dis* 10: S620–S625.
- Johnson N, Freuling C, Horton D, Müller T, Fooks AR (2011):** Imported Rabies, European Union and Switzerland, 2001–2010. *Emerg Infect Dis* 17: 753–754.
- Kampmann H (1975):** Der Waschbär. Verbreitung, Ökologie, Lebensweise, Jagd. Paul Parey. Hamburg & Berlin.
- Kavanaugh DM, Linhart SB (2000):** A modified bait for oral delivery of biological agents to raccoons and feral swine. *J Wildl Dis* 36: 86–91.
- Kappus KD, Bigler WJ, McLean RG, Trevino HA (1970):** The Raccoon an Emerging Rabies Host. *J Wildl Dis* 6: 507–509.
- König A, Romig T, Janko C, Hildenbrand R, Holzhofer S, Kotulski Y, Ludt C, Merli M, Eggenhofer S, Thoma D, Vilsmeier J, Zannantonio D (2008):** Integrated baiting concept against *Echinococcus multilocularis* in foxes is successful in southern Bavaria. *Eur J Wildl Res* 54: 439–447.
- Le Roux I, van Gucht S (2008):** Two cases of imported canine rabies in the Brussels area within six months time. *Rabies Bulletin Europe* 32: 5–7.
- Leslie MJ, Messenger S, Rhode RE, Smith J, Cheshier R, Hanlon C, Rupprecht CE (2006):** Bat-associated rabies virus in skunks. *Emerg Infect Dis* 12: 1274–1277.
- Linhart SB, Blom FS, Dasch GJ, Roberts JD, Engeman RM, Esposito JJ, Shaddock JH, Baer GM (1991):** Formulation and evaluation of baits for oral rabies vaccination of raccoons (*Procyon lotor*). *J Wildl Dis* 27: 21–33.
- Linhart SB, Blom FS, Engeman RM, Hill HL, Hon T, Hall DI, Shaddock JH (1994):** A field evaluation of baits for delivering oral rabies vaccines to raccoons (*Procyon lotor*). *J Wildl Dis* 30: 185–194.
- Linhart SB, Wlodkowski JC, Kavanaugh DM, Motes-Kreimeyer L, Montoney AJ, Chipman RB, Slate D, Bigler LL, Fearneyhough MG (2002):** A new flavor-coated sachet bait for delivering oral rabies vaccine to raccoons and coyotes. *J Wildl Dis* 38: 363–377.
- McLean RG (1971):** Rabies in raccoons in the southeastern United States. *J Infect Dis* 123: 680–681.
- Michler F-U (2004):** Waschbären im Stadtgebiet – Wildbiologie International 5/12, Infodienst Wildbiologie & Ökologie, Zurich.
- Michler F-U (2007):** Der Waschbär. In: Stubbe M, Böhning V (eds.), Neubürger auf dem Vormarsch, DLV, München, 36–59.
- Michler F-U, Köhnemann B (2010):** Tierische Spitzenleistung – Abwanderungsverhalten von Waschbären (*Procyon lotor* L., 1758) in Norddeutschland. *Labus* 31: 52–59.
- Müller T, Cox J, Peter W, Schäfer R, Johnson N, McElhinney LM, Geue JL, Tjørnehoj K, Fooks AR (2004a):** Spill-over of European bat lyssavirus type 1 into a stone marten (*Martes foina*) in Germany. *J Vet Med B Infect Dis Vet Public Health* 51: 49–54.
- Müller W, Cox JH, Müller T (2004b):** Rabies in Germany, Denmark and Austria. In: King AA, Fooks AR, Aubert M, Wandeler AI (eds.), Historical perspective of rabies in Europe and the Mediterranean Basin. OIE, Paris, France, 79–92.
- Müller-Using D (1956):** Die Ausbreitung des Waschbären in Westdeutschland. *Z Jagdwissenschaft* 5: 108–109.
- Olson CA, Werner PA (1999):** Oral rabies vaccine contact by raccoons and nontarget species in a field trial in Florida. *J Wildl Dis* 35: 687–695.
- Rojahn A (1977):** Vorkommen der Tollwut in der Bundesrepublik Deutschland. *Berl Münch Tierärztl Wschr* 90: 269–273.
- Root JJ, McLean RG, Slate D, MacCarthy KA, Osorio JE (2008):** Potential effect of prior raccoonpox virus infection in raccoons on vaccinia-based rabies immunization. *BMC Immunol* 9: e57.
- Rosatte RC, Lawson KF, MacInnes CD (1998):** Development of baits to deliver oral rabies vaccine to raccoons in Ontario. *J Wildl Dis* 34: 647–652.
- Rosatte RC, Lawson KF (2001):** Acceptance of baits for delivery of oral rabies vaccines to raccoons. *J Wildl Dis* 37: 730–739.
- Rosatte R, Sobey K, Donovan D, Bruce L, Allan M, Silver A, Bennett K, Gibson M, Simpson H, Davies C, Wandeler A, Muldoon F (2006):** Behavior, movements, and demographics of rabid raccoons in Ontario, Canada: Management implications. *J Wildl Dis* 42: 589–605.
- Rosatte R, Allan M, Bachmann P, Sobey K, Donovan D, Davies JC, Silver A, Bennett K, Brown L, Stevenson B, Buchanan T, Bruce L, Wandeler A, Fehlner-Gardiner C, Beresford A, Beath A, Escobar M, Maki J, Schumacher C (2008):** Prevalence of tetracycline and rabies virus antibody in raccoons, skunks, and foxes following aerial distribution of V-RG baits to control raccoon rabies in Ontario, Canada. *J Wildl Dis* 44: 946–964.
- Rosatte RC, Donovan D, Allan M, Bruce L, Buchanan T, Sobey K, Stevenson B, Gibson M, MacDonald T, Whalen M, Davies JC, Muldoon F, Wandeler A (2009a):** The control of raccoon rabies in Ontario Canada: Proactive and reactive tactics, 1994–2007. *J Wildl Dis* 45: 772–784.
- Rosatte RC, Donovan D, Davies JC, Allan M, Bachmann P, Stevenson B, Sobey K, Brown L, Silver A, Bennett K, Buchanan T, Bruce L, Gibson M, Beresford A, Beath A, Fehlner-Gardiner C, Lawson K (2009b):** Aerial distribution

- of ONRAB® baits as a tactic to control rabies in raccoons and striped skunks in Ontario, Canada. *J Wildl Dis* 45: 363–374.
- Roscoe DE, Holste WC, Sorhage FE, Campbell C, Niezgoda M, Buchannan R, Diehl D, Niu HS, Rupprecht CE (1998):** Efficacy of an oral vaccinia-rabies glycoprotein recombinant vaccine in controlling epidemic raccoon rabies in New Jersey. *J Wildl Dis* 34: 752–763.
- Rupprecht CE, Wiktor TJ, Johnston DH, Hamir AN, Dietzschold B, Wunner WH, Koprowski H (1986):** Oral immunization and protection of raccoons (*Procyon lotor*) with a vaccinia rabies glycoprotein recombinant virus vaccine. *Proc Nat Acad Sci* 83: 7947–7950.
- Rupprecht CE, Dietzschold B, Cox JH, Schneider LG (1989):** Oral vaccination of raccoons (*Procyon lotor*) with an attenuated (SAD-B19) rabies virus vaccine *J Wildl Dis* 25: 548–554.
- Rupprecht CE (1992):** Epidemiology of raccoon rabies. In: Bögel K, Meslin FX, Kaplan M, (eds.), *Wildlife Rabies Control*. Wells medical Ltd, Kent, UK, 22–24.
- Schuster P, Müller T, Vos A, Selhorst T, Neubert L, Pommerening E (2001):** Comparative immunogenicity and efficacy studies with oral rabies virus vaccine SAD P5/88 in raccoon dogs and red foxes. *Acta Vet Hung* 49: 285–290.
- Slate D, Algeo TP, Nelson KM, Chipman RB, Donovan D, Blanton JD, Niezgoda M, Rupprecht CE (2009):** Oral rabies vaccination in North America: Opportunities, complexities, and challenges. *PLoS Negl Trop Dis* 3: e549.
- Sommer S (2005):** The importance of immune gene variability (MHC) in evolutionary ecology and conservation. *Frontiers Zool* 2: e16.
- Srithayakumar V, Castillo S, Rosatte RC, Kyle CJ (2011):** MHC class II DRB diversity in raccoons (*Procyon lotor*) reveals associations with raccoon rabies virus (Lyssavirus). *Immunogenetics* 63: 103–113.
- Stubbe M (1993):** Waschbär – *Procyon lotor* (Linné, 1758). In: Niethammer J, Krapp F (eds), *Handbuch der Säugetiere Europas* – 5/1, Aula-Verlag, Wiesbaden, 331–364.
- Szanto A (2009):** Molecular genetics of the raccoon rabies virus. Peterborough, Ontario, Canada, Trent University, diss.
- Torrence ME, Jenkins SR, Glickman LT (1992):** Epidemiology of raccoon rabies in Virginia, 1984 to 1989. *J Wildl Dis* 28: 369–376.
- Tschirch W (2001):** Die Bedeutung von Luchs, Wildkatze, Waschbär und Marderhund in der Tollwut-Epidemiologie. *Beitr Jagd-Wildforsch* 26: 281–298.
- Wilson M, Bretsky P, Cooper G, Egbertson S, van Kruiningen H, Cartier M (1997):** Emergence of raccoon rabies in Connecticut 1991–1994: Spatial and temporal characteristics of animal infection and human contact. *Am J Trop Med Hyg* 57: 457–463.
- Winkler WG, Jenkins SR (1995):** Raccoon rabies. In: Baer GM (ed.) *The natural history of rabies*, second edition. CRC Press, Boca Raton, USA, 326–340.

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