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Genetic structure of a raccoon population (*Procyon lotor*) in Müritz National Park – a result of landscape resistance or space-use behaviour?

Schlagworte/key words: Waschbär, raccoon, *Procyon lotor*, landscape genetics, microsatellites, landscape resistance, Brownian bridge, utilization distribution overlap index, Mantel test

Introduction

Understanding the mechanisms shaping the genetic population structure is important for addressing many questions in evolution, ecology, and practical wildlife management (e.g., EPPS et al. 2007, SEGELBACHER et al. 2010). Current studies often focus on testing for landscape-genetic relationships, because the heterogeneity of the environment can influence the occurrence, abundance, dispersal, and thus, gene flow, in plants and animals (MANEL et al. 2003, HOLDEREGGER & WAGNER 2008).

Among the most popular approaches for such studies is the statistical comparison of genetic and ‘effective’ landscape distances. While the genetic distances measure how close individual animals are genetically, the effective distances estimate how close they are in the landscape, while accounting for potential movement barriers or varying landscape resistances to gene flow. If a significant association is found between these two distances, it is concluded that landscape resistance, as estimated from the effective distances, influences gene flow and resulting genetic structures.

Despite the current popularity of landscape genetics, genetic population structure can actually be influenced by a multitude of factors other than landscape heterogeneity, for example space-use behaviour or reproductive strategies. While some of these influences might be landscape-dependent, others are intrinsic (i.e., landscape-independent) and highly species-specific. Thus, in order to fully understand genetic structures arising in natural wildlife populations, studies should not only focus on testing for landscape-genetic relationships, but also consider alternative causes behind observed genetic structures.

Here, we compare the effects of landscape resistance versus socially-induced space-use behaviour on genetic structures in a population of raccoons (*Procyon lotor*).

First, we test whether genetic structure in the raccoon population has been impacted by landscape resistances, which we estimated from movement paths gathered from telemetry data. Second, we test whether genetic structure is associated with territorial behaviour of raccoons, which we measured through an index of home range overlap.

Material & Methods

The study was conducted in the Müritz national park in northwest Germany, and was part of an intensive effort to study the life-history of raccoons in this region (www.projekt-waschbaer.de). Raccoons were captured and fitted with telemetry collars within the 'Serrahn' part of the park. Detailed information on the study area, capturing and handling of raccoons can be found in KÖHNEMANN & MICHLER (2009). From each captured raccoon, we sampled either a small tissue sample, or hair for genetic analyses. Samples were genotyped at ten microsatellite loci. The genetic analyses are described in detail by GRAMLICH et al. (this issue). To estimate genetic population structure, we calculated a genetic distance among all individuals. Specifically, we chose the kinship coefficient of RITLAND (1996), where higher values indicate higher genetic relatedness. The kinship coefficient was calculated in software SPAGeDi 1.3 (HARDY & VEKEMANS 2002).

Effects of landscape resistance on the genetic population structure

To test the hypothesis that landscape heterogeneity influences genetic structures, we calculated effective distances among all raccoons. For this, we had to model the resistance of the landscape for raccoon movement and gene flow. Modelling such resistance layers is often done based on expert-opinion or 'best guesses'. Alternatively, independent (i.e., non-genetic) data can be used to define landscape resistances empirically. Here, we chose the latter approach and quantified landscape resistances based on the telemetry data gathered for individual raccoons. Specifically, we quantified individual movements using so-called Brownian bridges, which account for the movement speed of individuals (HORNE et al. 2007). This approach has previously been used to define movement corridors for mule deer (*Odocoileus hemionus*) in Wisconsin, USA (SAWYER et al. 2009). In low resistance landscapes, movements should be relatively fast and linear, so that Brownian bridges become narrow and have high intensity-of-use values. In contrast, high resistance landscapes

should lead to wide Brownian bridges with low intensity-of-use values. Brownian bridge calculations were conducted in the *R* statistical environment using the adehabitat package (CALENGE 2007).

To calculate effective distances among individual raccoons, we had to define landscape resistance for the entire sampling region, but Brownian bridges were only calculated along the movement paths of individual animals. Thus, we constructed a combined Brownian bridge layer by adding up intensity-of-use values from all individuals. We then used the resulting layer to estimate the contribution of different landscape variables to movement resistance. For this, we used GIS data available for the national park at a 1:10,000 scale. These data include different habitat classes that we here grouped into four general habitat types of potential relevance for raccoons. We distinguished forested habitat, riparian areas, agricultural fields and human settlements, and created a GIS-layer for each variable that quantified the distance of each 100 meter cell in the landscape to the closest edge of each of these four habitat types. This distance-to-nearest-habitat approach is often used in habitat selection studies, and accounts for possible inaccuracies in the GIS-data (CONNER & PLOWMAN 2001). We next constructed different models to explain the Brownian bridge layer as a function of the four explanatory landscape variables. Since the Brownian bridge layer is spatially autocorrelated, we could not use standard regression for this step. Rather, we used spatial autoregressive models, which are an analogue of linear regression, but account for the spatial autocorrelation of the dependent data. We used an information-theoretic approach to compare all possible models that can be constructed with four independent variables ($N = 14$). Spatial autoregressive models were calculated in software SAM (RANGEL et al. 2010) and the best model was chosen based on lowest AIC values corrected for small sample sizes (AICc, BURNHAM & ANDERSON 2002). Parameters of this model were then used to estimate a resistance layer for the entire study region. This layer reflects the resistance of the landscape to raccoon movements as estimated from the telemetry data. Finally, effective distances among individual raccoon home range centres were calculated

from this GIS-layer using software Circuitscape (MCRAE & BEIER 2007). This software estimates the effective resistance among sampling locations based on all possible pathways between the locations.

Effects of space use behaviour on the genetic population structure

To test the hypothesis that space-use behaviour influences genetic structure of raccoons, we quantified territoriality by calculating the overlap of home ranges among individual raccoons. Specifically, we estimated the utilization distribution overlap index (UDOI) for 95 % kernel home ranges using the adehabitat package in R. UDOIs are an alternative to the overlap statistics used by MUSCHIK et al. (this issue), and the index has been recommended by FIEBERG & KOCHANNY (2005), because it accounts for varying intensities of use within shared home range areas. The result of this analysis is a pair-wise data matrix that shows the intensity of space-sharing among all individual raccoons. A UDOI-value of zero indicates that two raccoons have no home range overlap, while increasing values indicate that two individuals share larger parts of their home ranges with higher intensity.

Statistical data analysis

To statistically evaluate the two different hypotheses, we needed to account for the fact that kinship coefficients, effective distances and UDOIs are pair-wise data. Thus, we analyzed the data using the Mantel statistic, a widely-used method to assess the significance of correlations between pair-wise data matrices using permutations (MANTEL 1969). If landscape resistance as modelled from the Brownian bridges has impacted genetic population structure, we would expect to see a significant *negative* correlation between effective landscape distances and kinship coefficients (smaller effective landscape distances should be associated with higher kinship values). Similarly, if social space-use behaviour has influenced genetic structure, we should see a significant *positive* correlation between UDOI values and kinship coefficients (increased space-use should occur

between individuals that are more closely related). If both tests yield insignificant results, this would support the null hypothesis of no landscape or social influences. Mantel statistics were calculated in the R package ecodist (GOSLEE & URBAN 2007) using 9,999 permutations to assess significance.

Results

In total, 141 individuals were successfully genotyped and available for genetic data analyses. See GRAMLICH et al. (this issue) for basic population genetic summary statistics. Telemetry data could be gathered for a subset of 69 individual raccoons (32 females and 37 males). The best model explaining movement patterns of Brownian bridges involved distance to forest habitat (dFor) and distance to agricultural areas (dAgr) and accounted for approximately 36.5 % of the variation (Table 1). While the full model involving all four landscape variables explained a slightly higher amount of the variation ($R^2 = 0.366$), it was not the most parsimonious model with an AICc value of 6.95 (Table 1). All other models had even higher AICc values and explained less variation (data not shown). Parameters for the best model estimated landscape resistance as $0.309 * dFor - 0.127 * dAgr$. Thus, landscape resistance decreased with decreasing distance from forests, but increased with decreasing distance to agricultural fields. Effective distances calculated from this model did not significantly correlate with the

Table 1 Coefficients of determination (R^2) and delta AICc values for spatial autoregressive models explaining raccoon movement paths as a function of habitat variables. dFor = distance to forest habitat, dAgr = distance to agricultural fields, dRip = distance to riparian habitat, dSet = distance to human settlement. Only the four best models are shown, as all other models had R^2 values > 0.1 .

Model	R^2	delta AICc
dFor+dAgr	0.365	0
dFor+dAgr+dRip+dSet	0.366	6,95
dAgr	0,344	17,92
dFor	0,211	40,63

genetic distances ($p > 0.05$; Table 2). In contrast, genetic distances were significantly and positively correlated with the home range overlap index UDOI for all data and for females (Table 2). However, Mantel tests were only marginally significant when analyzing only males ($p = 0.057$).

Table 2 Results of Mantel statistics for correlations between kinship coefficients and A) effective landscape distances and B) utilization distribution overlap index. P-values are based on 9,999 permutations.

A)	Data used	Mantel r	p-value
	All data	-0.018	0.103
	Females only	-0.017	0.203
	Males only	-0.019	0.314
B)	Data used	Mantel r	p-value
	All data	0.103	0.003
	Females only	0.092	0.032
	Males only	0.065	0.057

Discussion

Our results suggest that the resistance of the landscape to raccoon movements depends on the spatial distribution of forested and agricultural areas. Landscape resistance for raccoons decreased within or close to forest habitat, while it increased with higher proximity to agricultural fields. These results can partially be explained by general habitat preferences of raccoons in the study area. For the studied raccoon population, HERMES et al. (this issue) showed a slight avoidance of open areas, including agricultural fields. Thus, raccoons traverse through open areas less frequently, even though such areas do not impose a physical movement barrier. Raccoons also showed a slight avoidance of forest habitat, and a clear preference for riparian areas. However, these habitat preferences do not seem to influence movement paths estimated through the Brownian bridges. It is possible that some of the telemetry relocations were too far apart in time to accurately estimate intensity-of-use values for all movement paths. This would lead to 'flat' Brownian bridges and could

dilute effects of some landscape characteristics on raccoon movement paths. Furthermore, as noted by HERMES et al. (this issue), the available landscape data is relatively coarse-scaled, and is not suitable to analyze habitat selection at the micro-scale. It is possible that movement paths of raccoons are strongly influenced by habitat characteristics at the micro-scale, so that accurately estimating landscape resistance with the available landscape data is challenging.

This could also be a reason why the varying resistance of the heterogeneous landscape to raccoon movements did not have a significant effect on the genetic structure of the population. There was no significant correlation between effective landscape distances and the kinship coefficients. This suggests that the landscape resistance calculated from the movement data does not reflect the resistance of the landscape for effective gene flow. At this small scale, genetic exchange among individuals is likely not much affected by the landscape, but rather by space-use behaviour associated with mate choice. This conclusion is further supported by the significant correlations between kinship coefficients and home range overlap. According to our results, animals share greater parts of their home ranges (i.e., are less territorial) if they are genetically more closely related. Such patterns have already been observed in other species, including black bears (*Ursus americanus*; MOYER et al. 2006) and swift foxes (*Vulpes velox*; KITCHEN et al. 2005). Interestingly, we observed significant socio-genetic relationships for the entire population and females, but only marginally significant for males. This suggests that the overall structure of the raccoon population is determined by the spatial distribution of matrilineages. As shown by MUSCHIK et al. (this issue), juvenile adults stay in close proximity to their mothers home range, and while all male offspring eventually disperses away from the maternal home range, female offspring often stays in relatively close proximity. Thus, related females are distributed close in space, leading to the significant correlations between kinship and home range overlap. In contrast, GRAMLICH et al. (this issue) showed that male coalitions are not composed of genetically close kin, so that no such correlations were observed for males. Overall, these socially-induced space-

use patterns of male and female raccoons affect the spatial-genetic structure of the studied population.

Study limitations & conclusions

It is important to note that we have used only a single model of landscape resistance to estimate effective distances among sampled raccoons, because more detailed landscape data was not available for the study area. Other studies have compared a much higher number of resistance models, which differed in the way landscape resistance values were derived, and also used different ways for estimating effective distances from these models (CUSHMAN et al. 2006, SHIRK et al. 2010).

Thus, it is possible that we simply have not yet found an adequate model of functional landscape resistance for our study system. Therefore, future analyses should use more fine-scaled landscape data, and use more complex modelling procedures to quantify landscape resistance from the telemetry data. Future studies should also attempt to increase the spatial extend of the sampling, because landscape-genetic relationships are often scale-dependent (ANDERSON et al. 2010).

Based on our current analyses, we conclude that landscape characteristics (i.e., distance to forests and agricultural fields) affect racoon movements, but these characteristics do not seem to influence the genetic structure of the studied population. Instead, genetic population structure seems to be influenced by the space-use behaviour of related raccoons, particularly by that of related females.

Zusammenfassung

Genetische Strukturen einer Waschbärenpopulation (*Procyon lotor* L., 1758) im Müritz-Nationalpark – Landschaftseinflüsse oder barrierefreie Liebe?

Einsicht in genetische Populationsstrukturen und in die Faktoren, von denen diese Strukturen beeinflusst werden, ist Grundlage für eine Vielzahl von Fragestellung in der Evolution, der Ökologie, und dem Management von Wild-

tieren. Viele derzeitige Studien analysieren ausschließlich landschafts-genetische Beziehungen, obwohl genetische Populationsstrukturen von einer Vielzahl anderer Faktoren beeinflusst werden können.

In der vorliegenden Studie wurde getestet, ob genetische Strukturen innerhalb einer Waschbärenpopulation von Landschaftsstrukturen, oder vom räumlichen Sozialverhalten der Tiere beeinflusst werden. Hierfür wurden 69 Waschbären (32 Fähen, 37 Rüden) mit Telemetrie-Halsbänder ausgestattet. Zusätzlich wurden 141 Waschbären anhand von 10 Mikrosatelliten genotypisiert, und genetische Distanzen zwischen allen Individuen wurden berechnet. Besendungen und genetische Analysen waren Teil einer großangelegten Studie zur Lebensweise von Waschbären im Serrahner Teilgebiet des Müritz-Nationalparks (Mecklenburg-Vorpommern, Deutschland). Bewegungsmuster der besenderten Tiere wurden genutzt, um den Widerstand der Landschaft für Waschbärbewegungen empirisch abzuschätzen. Das so gewonnene Landschaftsmodell wurde verwendet, um effektive Distanzen zwischen allen beprobten Waschbären zu berechnen. Diese effektiven Distanzen wurden statistisch mit den genetischen Distanzen verglichen. Eine signifikante Korrelation zwischen beiden Distanzen würde auf einen Einfluss der Landschaftsstrukturen auf den Genfluss innerhalb der Population hindeuten. Zusätzlich wurde auch das Territorialverhalten der Waschbären über einen Streifgebiets-Überlappungs-Index bestimmt, und dieser wurde ebenfalls mit den genetischen Distanzen verglichen.

Die Ergebnisse zeigen, dass die Bewegungsmuster der besenderten Waschbären von Wald und landwirtschaftlichen Flächen beeinflusst werden. Der Widerstand der Landschaft für Waschbärbewegungen verringerte sich mit zunehmender Nähe zu Wald, und erhöhte sich mit zunehmender Nähe zu landwirtschaftlichen Flächen. Allerdings beeinflussen diese Landschaftswiderstände nicht den Genfluss innerhalb der Population, denn es wurde keine signifikante Korrelation zwischen genetischen und effektiven Distanzen gefunden. Signifikante Korrelationen wurden allerdings zwischen genetischen Distanzen und Streifgebietsüberlappungen gefunden. Waschbären, die einen hö-

heren Verwandtschaftsgrad aufwiesen, teilten sich größere Gebiete ihrer Streifgebiete. Dieser Trend war signifikant für die Gesamtpopulationen, sowie für Fähen, jedoch nicht für Rüden. Insgesamt weisen diese Ergebnisse darauf hin, dass die genetische Struktur der untersuchten Waschbärpopulation nicht von Landschaftsstrukturen beeinflusst wird, sondern von der räumlichen Verteilung der Matrilinien, sowie dem Territorialverhalten der Fähen.

Summary

Understanding genetic population structure and the mechanisms shaping this structure is important for addressing many questions in evolution, ecology, and conservation. Current studies analyzing genetic population structure often focus on testing for landscape-genetic relationships, but genetic structures can actually be influenced by a variety of other, landscape-independent factors. Here, we test whether genetic structure of a raccoon population is affected by landscape resistances to raccoon movement, or by socially-induced space-use patterns. Sixty-nine raccoons (32 females, 37 males) were fitted with telemetry-collars as part of an intensive effort to study the life-history of the species in Müritznational park, Germany.

Movement paths of raccoons were used to empirically estimate the resistance of the landscape to animal movements as a function of various habitat variables. In addition, 141 raccoons were genotyped at ten microsatellite loci, and genetic population structure was estimated through an individual-based genetic distance. Using the empirically-derived landscape resistance model, we then estimated effective separation distances among sampled raccoons, and statistically compared these effective distances with the genetic distances. A significant correlation between genetic and effective distances would indicate an effect of landscape resistance on gene flow. Additionally, we also tested for the effects of territoriality (measured through an index of home range overlap) on observed genetic structures.

Results suggest that raccoon movements in the study area are influenced by forested and agricultural habitats, and that landscape resist-

ance to movement decreases with increasing proximity to forests and decreasing distance to agricultural fields. However, landscape resistance to movement does not influence genetic population structure, as there was no significant correlation between effective and genetic distances. Instead, there was a significant correlation between genetic distances and home range overlap, with genetically more closely-related individuals sharing greater parts of their home ranges. This correlation was significant for the total population, as well as for females, but not for males.

In sum, these results suggest that genetic structure of the studied raccoon population is not influenced by landscape heterogeneity, but rather by the spatial distribution of matrilineages and by the territorial behaviour of females.

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