

Effects of kin-structure on disease dynamics in raccoons (*Procyon lotor*) inhabiting a fragmented landscape

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Abstract

The spatial aggregation of related individuals can affect disease dynamics by altering contact rates between individuals and/or groups of individuals. However, kin-structure likely affects contact rates in a scale-dependent manner: increasing contact rates within, but decreasing contact rates amongst spatial groups. Thus, the effect of kin-structure on disease exposure risk should depend upon the spatial scale relevant for pathogen transmission. This study was undertaken to test the effects of kin-structure on disease dynamics in raccoons (*Procyon lotor*) inhabiting a highly fragmented agricultural ecosystem. Raccoons ($n = 566$) were trapped at 31 spatially discrete habitat patches (local populations). Trapped individuals were genotyped at 13 microsatellites and their serum screened for antibodies to canine distemper virus (CDV) and multiple *Leptospira* spp. serovars. Our analyses revealed that the effects of kin-structure on transmission dynamics are dependent on both spatial scale and the pathogen under consideration. Thus, in the directly transmitted pathogen (CDV), the probability of pathogen co-exposure (the proportion of individual pairs where both individuals were seropositive for a particular pathogen) was positively correlated with genealogical proximity within local populations. Conversely, in the environmentally transmitted leptospires co-exposure was homogeneous within local populations and was positively correlated with gene flow among these populations. Our analyses also revealed that, after controlling for confounding effects of landscape and demographic variables, the effects of kin-structure on disease exposure risk was pathogen-specific. In particular, increasing kin-structure was associated with increased disease exposure risk in the directly transmitted pathogen (CDV), and alternatively with decreased disease exposure risk in environmentally transmitted leptospires. The potential, scale-dependent, effects of kin-structure on disease exposure risk revealed by our analyses could play an important role in elucidating disease dynamics in natural populations and in planning effective disease mitigation strategies.

Zusammenfassung

Die räumliche Aggregation von verwandten Individuen kann die Seuchendynamik beeinflussen, indem die Kontaktraten zwischen Individuen und/oder Individuengruppen geändert werden. Indessen beeinflusst die Verwandtschaftsstruktur die

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Kontaktraten wahrscheinlich in skalenabhängiger Weise: Die Kontaktraten steigen innerhalb räumlicher Gruppen, sinken aber zwischen diesen. So sollte der Effekt der Verwandtschaftsstruktur auf das Krankheitsrisiko von der räumlichen Skala abhängen, die für die Erregerübertragung maßgeblich ist. Die vorliegende Untersuchung wurde durchgeführt, um den Effekt der Verwandtschaftsstruktur auf die Seuchendynamik bei Waschbären (*Procyon lotor*) zu untersuchen, die eine stark fragmentierte Agrarlandschaft bewohnen. Die Waschbären ($n = 599$) wurden in 31 räumlich getrennten Habitaten (lokale Populationen) gefangen. Die gefangenen Individuen wurden für 13 Mikrosatelliten genotypisiert, und ihr Serum wurde auf Antikörper gegen das Hundestaupavirus (CDV) und verschiedene *Leptospira*-Serotypen untersucht. Unsere Analysen zeigten, dass die Effekte der Verwandtschaftsstruktur auf die Übertragungsdynamik sowohl von der räumlichen Skala als auch vom betrachteten Erregertyp abhängen. So war der Anteil von Individuenpaaren, bei denen beide Individuen seropositiv waren, bei dem direkt übertragenen CDV positiv mit der verwandtschaftlichen Nähe innerhalb der lokalen Populationen korreliert. Dagegen war dieser Anteil bei den indirekt übertragenen Leptospiren innerhalb der lokalen Populationen homogen, aber positiv mit dem Genfluss zwischen diesen Populationen korreliert. Unsere Analysen zeigten auch, dass nach Kontrolle der Konfundierungseffekte von Landschafts- und Demographievariablen der Einfluss der Verwandtschaftsstruktur auf das Expositionsrisiko erregerspezifisch ist. Zunehmende Verwandtschaftsstruktur war bei dem direkt übertragenen CDV mit einem höheren Seuchenexpositionsrisiko assoziiert und mit einem geringeren Risiko bei den indirekt übertragenen Leptospiren. Die bei unseren Analysen festgestellten potentiellen skalenabhängigen Effekte der Verwandtschaftsstruktur auf das Expositionsrisiko könnten eine wichtige Rolle bei der Aufklärung der Seuchendynamik in natürlichen Populationen und bei der Planung von effektiven Seuchenbekämpfungsstrategien spielen.

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Introduction

Variance in disease transmission risk in wild populations can be affected by heterogeneity in contact rates between individuals and/or groups of individuals (Cross et al. 2008). Such heterogeneity could be driven by numerous factors such as habitat characteristics, movement patterns and niche overlap (Ostfeld, Glass, & Keesing 2005; Blanchong et al. 2008; Godfrey, Bull, James, & Murray 2009, respectively). Because most natural populations show some form of biological organization (e.g., social or spatial structure), incorporating such ecological heterogeneity into epidemiological analyses is essential to improve our understanding of disease dynamics (Webb, Keeling, & Boots 2007).

The spatial aggregation of related individuals, kin-structure, is a common form of social structure in natural populations (see Hatchwell 2010). The presence of such social structure affects contact rates in a scale-dependent manner: increasing contact rates within but decreasing them between groups of individuals (e.g., Craft, Hawthorne, Packer, & Dobson 2008). Thus, at the individual scale, kin-structure likely increases disease transmission risk because contact rates are expected to be higher between kin vs. non-kin (e.g., Root, Black, Calisher, Wilson, & Beaty 2004; Grear, Samuel, Scribner, Weckworth, & Langenberg 2010; but also see Cullingham et al. 2011). Alternatively, at the group scale, kin-structure is associated with reduced movement of individuals amongst the social groups (see Sugg, Chesser, Dobson, & Hoogland 1996; Banks, Piggott, Stow, & Taylor 2007), and such reduced movement is expected to reduce disease transmission risk between groups (see Hess, 1994, 1996). Consequently, the effect of kin-structure on disease transmission risk, and thus patterns of disease exposure, will depend

upon the spatial scale that is relevant for pathogen transmission.

From an epidemiological perspective, the scale relevant for pathogen transmission depends upon the mode of pathogen transmission (Craft & Caillaud 2011). When transmission is direct (e.g., aerosol), spatial heterogeneity in disease transmission risk will predominantly be affected by contact rates at the individual scale. Thus, in the case of directly transmitted pathogens, kin-structure is likely to increase disease exposure risk because it is associated with increased contact rates at the individual scale. Conversely, when transmission is indirect (e.g., environmental contamination), pathogen exposure rates can be assumed to be homogeneous within a group of individuals inhabiting a common environment and spatial heterogeneity in transmission risk will predominantly be affected by contact rates (movement of individuals) between the groups (Hess, 1994, 1996). Thus, in the case of indirectly transmitted pathogens, kin-structure likely will decrease disease exposure risk because it is associated with the reduced movement of individuals amongst groups.

Despite its importance, empirical data on transmission mode-specific effects of social structure on disease dynamics is limited because the effects of social structure on disease dynamics in microparasites (e.g., bacteria and viruses) have predominantly been studied in single pathogen systems (e.g., Blanchong et al. 2008; Craft et al. 2008; Grear et al. 2010). In this study, we tested if kin-structure and pathogen transmission mode affected disease dynamics in raccoons (*Procyon lotor*; $n = 566$) inhabiting 31 spatially discrete habitat patches (“local populations”) situated in an agricultural ecosystem. The raccoon, an important mesocarnivore in human-dominated landscapes (Prange, Gehrt, & Wiggers 2004; Beasley & Rhodes 2008), was a good model

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