

Publications on tick research at University of Antwerp (chronological per subject)

1. Health impact and (lack of) resistance against *Ixodes spp.* infestations in songbirds

Heylen DJA, **Matthysen** E. 2008. Effect of *Ixodes ricinus* on the health status of a passerine bird. *Funct. Ecol.* 22: 1099-1107

Heylen D, **Adriaensen** F, Dauwe T, Eens M, **Matthysen** E. 2009. *Ixodes ricinus* infection load and offspring quality in brood rearing great tits *Parus major*. *Oikos* 118: 1499-1506.

Heylen DJA, Madder M & **Matthysen** E. 2010. Lack of resistance against the tick *Ixodes ricinus* in two related passerine bird species. *Int. J Parasitol* 40: 183-191.

Heylen D, **Matthysen** E. 2011. Differential virulence in two congeneric ticks infesting songbird nestlings. *Parasitology* 138: 1011-1021.

Vergauwen, J., **Heylen**, D., Eens, M. & Muller, W. 2011. Negative Effects of Yolk Testosterone and Ticks on Growth in Canaries. *Journal of Experimental Zoology Part a-Ecological Genetics and Physiology*, 315A, 553-561.

Heylen D, Müller W, Groothuis T, **Matthysen** E. 2012. Female great tits do not alter their yolk androgen deposition when infested with a low-transmittable ectoparasite. *Behav Ecol Sociobiol*, 66: 287-293.

Müller, W., **Heylen**, D., Eens, M., Rivera-Gutierrez, H.F. & Groothuis, T.G.G. 2013. An experimental study on the causal relationships between (ecto-)parasites, testosterone and sexual signalling. *Behavioral Ecology and Sociobiology*, 67, 1791-1798.

Heylen D, Bisaglia B, **Fracasso** G, Prinsen E, Müller W, **Matthysen** E. 2021. Ineffective humoral anti-tick IgY-response in birds: reaction against pathogen constituents? *Open Research Europe*.

Fracasso G, **Matthysen** E, **Heylen** D. Heritable variation in host quality as measured through an ectoparasite's performance. *Oikos in press*

2. Ecology, life history and genetic variation of bird-specific ticks, in particular the tree-hole tick *Ixodes arboricola*

Heylen D, **Matthysen** E. 2010. Contrasting detachment strategies in two related ticks (Ixodidae) parasitizing the same songbird. *Parasitology* 137: 661-667.

Heylen , DJA & **Matthysen** E. 2011. Experimental evidence for host preference in a tick parasitizing songbird nestlings. *Oikos* 120: 1209-1216.

White J, **Heylen** D, **Matthysen** E. 2012. Adaptive timing of detachment in a tick parasitizing hole-nesting birds. *Parasitology* 139: 264-270.

Heylen D, White J, Elst J, Jacobs I, Van de Sande C & Matthysen E. 2012. Nestling development and the timing of tick attachments. *Parasitology* 139: 766-773.

Van Houtte N, Van Oosten AR, Jordaens K, Matthysen E, Backeljau T, Heylen DJA. 2013. Isolation and characterization of ten polymorphic microsatellite loci in *Ixodes arboricola*, and cross-amplification in three other *Ixodes* species. *Exp Appl Acarol.* 61: 327-336.

Van Oosten AR, Heylen DJA, Matthysen E. 2014. Host specificity of a bird-specialised endopholic ectoparasite, the tree-hole tick *Ixodes arboricola*. *Parasitology Research* 113: 4397-4405.

Van Oosten AR, Heylen DJA, Jordaens K, Backeljau T, Matthysen E. 2014. Population genetic structure of the tree-hole tick *Ixodes arboricola* (Acari: Ixodidae) at different spatial scales. *Heredity* 113: 408-415.

Heylen DJA, Van Oosten AR, Devriendt N, Elst J, De Bruyn L, Matthysen E. 2014. Seasonal feeding activity of the tree-hole tick, *Ixodes arboricola*. *Parasitology* 14: 1044-1051.
doi:10.1017/S0031182014000225.

Van Oosten AR, Matthysen E, Heylen DJA. 2016. The more the merrier - experimental evidence for density-dependent feeding facilitation in the bird-specialised tick *Ixodes arboricola*. *Int J Parasitol* 46: 187-193

Van Oosten AR, Heylen DJA, Matthysen E. 2016. Mating strategies and multiple paternity, assessed by microsatellites, of the dispersal-limited, ectoparasitic tree-hole tick *Ixodes arboricola*. *International J Parasitol* 46: 593-602.

Van Oosten AR, Heylen DJA, Elst J, Philtjens S, Matthysen E. 2016. An experimental test to compare potential and realised specificity in ticks with different ecologies. *Evolutionary Ecology* 30: 487-501.

Van Oosten, A.R., Duron, O. & Heylen, D.J.A. (2018). Sex ratios of the tick *Ixodes arboricola* are strongly female-biased, but there are no indications of sex-distorting bacteria. *Ticks Tick-Borne Dis.*, 9, 307-313.

Fracasso G, Matthysen E, Dhondt AA, Heylen D. 2019. Experimental study of micro-habitat selection in ixodid ticks feeding on avian hosts. *Int J Parasitol*, 49: 1005-1014 DOI: 10.1016/j.ijpara.2019.09.003.

Fracasso G, Heylen D, Van Dongen S, Elst J, Matthysen E. Predictors of individual performance and evolutionary potential of life-history traits in a hematophagous ectoparasite. *Evolution, under revision*

3. Ecology and distribution of the generalist sheep tick *Ixodes ricinus*

Kempf, F., De Meeus, T., Vaumourin, E., Noel, V., Taragel'ova, V., Plantard, O., **Heylen, D. J. A.**, Eraud, C., Chevillon, C. & McCoy, K.D. (2011). Host races in *Ixodes ricinus*, the European vector of Lyme borreliosis. *Infect. Genet. Evol.*, 11, 2043-2048.

Møller AP, ... **Heylen D**, ... **Matthysen E** (15th and 22nd of 37 authors), et al. 2013. Assessing the effects of climate on host-parasite interactions: a comparative study of European birds and their parasites. *PLoS ONE* 8(12): e82886.

Heylen D, Adriaensen F, Van Dongen S, Sprong H & Matthysen E. 2013. Ecological factors that determine *Ixodes ricinus* tick burden in the great tit (*Parus major*), an important avian *Borrelia burgdorferi* s.l. reservoir. *Int J Parasitol* 43: 603-611

Ruyts SC, Ampoorter E, Coipan ED, Baeten L, **Heylen D**, Sprong H, **Matthysen E**, Verheyen K. 2016. Diversifying forest communities may change Lyme disease risk: extra dimension to the dilution effect in Europe. *Parasitology* 143: 1310-1319

Ruyts S, Tack W, Ampoorter E, Coipan E, **Matthysen E**, **Heylen D**, Sprong H, Verheyen K. 2018. Year-to-year variation in the density of *Ixodes ricinus* ticks and the prevalence of the rodent-associated human pathogens *Borrelia afzelii* and *B. miyamotoi* in different forest types. *Ticks and Tick-borne diseases* 9:141-145.

Ruyts SC, Landuyt D, Ampoorter E, **Heylen D**, Ehrmann S, Coipan EC, **Matthysen E**, Sprong H, Verheyen K. 2018. Low probability of a dilution effect for Lyme borreliosis in Belgian forests. *Ticks and Tick-borne diseases* 9: 1143-1152.

Heylen DJA, Lasters R, **Adriaensen F**, Fonville M, Sprong H & **Matthysen E**. 2019. Ticks and tick-borne diseases in the city: role of landscape connectivity and green space characteristics in a metropolitan area. *Science of the Total Environment*, 670: 941-949.

Heylen D; Schmidt, O; Dautel, H; Gern, L; Kampen, H; Newton, J; Gray, J. 2019. Host identification in unfed ticks from stable isotope compositions (delta C-13 and delta N-15). *Medical And Veterinary Entomology* 33: 360-366, DOI: 10.1111/mve.12372

Van Gestel M, Verheyen K, **Matthysen E**, **Heylen D**. Danger on the track? 2021. Tick densities near recreation infrastructures in forests. *Urban Forestry & Urban Greening* 59: 126994

4. Prevalence and transmission dynamics of *Borrelia burgdorferi* s.l. and other pathogens in bird-tick systems

Jahfari, S., Fonville, M., Hengeveld, P., Reusken, C., Scholte, E.-J., Takken, W., Heyman, P., Medlock, J.M., **Heylen D.**, Kleve, J., & Sprong, H. (2012). Prevalence of *Neohhrlichia mikurensis* in ticks and rodents from North-west Europe. *Parasites Vectors*, 5.

Heylen D, Tijssse E, Fonville M, **Matthysen E**, Sprong H. 2013. Transmission dynamics of *Borrelia burgdorferi* s.l. in a bird tick community. *Environmental Microbiology*, 15: 663-673.

Heylen D, Sprong H, van Oers K, Fonville M, **Leirs H**, **Matthysen E**. 2014. Are the specialized bird ticks, *Ixodes arboricola* and *I. frontalis*, competent vectors for *Borrelia burgdorferi* sensu lato? *Environmental Microbiology* 16: 1081-1089.

Heylen DJA, **Matthysen E**, Fonville M, Sprong H. 2014. Songbirds as general transmitters but selective amplifiers of *Borrelia burgdorferi* sensu lato genotypes in *Ixodes ricinus* ticks. *Environmental Microbiology* 16: 2859-2868.

Jahfari, S., Coipan, E.C., Fonville, M., Van Leeuwen, A.D., Hengeveld, P., **Heylen D.** et al. (2014). Circulation of four *Anaplasma phagocytophilum* ecotypes in Europe. *Parasites Vectors*, 7.

Heylen DJA, Müller W, Vermeulen A, Sprong H, **Matthysen E**. 2015. Virulence of recurrent infestations with *Borrelia*-infected ticks in a *Borrelia*-amplifying bird. *Scientific Reports* 5:16150

Cochez, C., Heyman, P., **Heylen**, D., Fonville, M., Hengeveld, P., Takken, W. et al. (2015). The Presence of *Borrelia miyamotoi*, A Relapsing Fever Spirochaete, in Questing *Ixodes ricinus* in Belgium and in The Netherlands. *Zoonoses and Public Health*, 62, 331-333.

Heylen, D., Fonville, M., van Leeuwen, A.D. & Sprong, H. (2016). Co-infections and transmission dynamics in a tick-borne bacterium community exposed to songbirds. *Environmental Microbiology*, 18, 988-996.

Heylen, D.J.A. 2016. Ecological interactions between songbirds, ticks, and *Borrelia burgdorferi* s.l. in Europe. In: Ecology and prevention of Lyme borreliosis (Braks M.A.H. et al., eds.). Wageningen Academic Publishers, pp. 91-101.

Heylen, D., Fonville, M., van Leeuwen, A.D., Stroo, A., Duisterwinkel, M., van Wieren, S. et al. (2017a). Pathogen communities of songbird-derived ticks in Europe's low countries. *Parasites Vectors*, 10.

Duron, O., ... **Heylen**, DJA, **Van Oosten** AR (10th and 11th of 19 authors), ... et al. (2017). Evolutionary changes in symbiont community structure in ticks. *Molecular Ecology*, 26, 2905-2921.

Heylen, D., Krawczyk, A., de Carvalho, I.L., Nuncio, M.S., Sprong, H. & Norte, A.C. (2017). Bridging of cryptic *Borrelia* cycles in European songbirds. *Environmental Microbiology*, 19, 1857-1867.

Heylen, D.J.A., Sprong, H., Krawczyk, A., **Van Houtte**, N., Genne, D., Gomez-Chamorro, A. et al. (2017). Inefficient co-feeding transmission of *Borrelia afzelii* in two common European songbirds. *Scientific Reports*, 7.

Norte, A.C., Costantini, D., Araujo, P.M., Eens, M., Ramos, J.A. & **Heylen**, D. (2018). Experimental infection by microparasites affects the oxidative balance in their avian reservoir host the blackbird *Turdus merula*. *Ticks Tick-Borne Dis.*, 9, 720-729.

Novakova, M., Heneberg, P., **Heylen**, D.J.A., Medvecký, M., Muñoz-Leal, S., Smajs, D. et al. (2018). Isolated populations of *Ixodes lividus* ticks in the Czech Republic and Belgium host genetically homogeneous *Rickettsia vini*. *Ticks Tick-Borne Dis.*, 9, 479-484.

Mysterud A, **Heylen** DJA, **Matthysen** E, Røer JE, Lopez Garcia A, Jore S & Viljugrein H. 2019. Lyme neuroborreliosis and bird populations in northern Europe. *Proc R Soc B*, 286: 20190759. DOI: 10.1098/rspb.2019.0759

Hepner, S; Fingerle, V; **Heylen**, D; Marosevic, D; Ghaffari, K; Okeyo, M; Sing, A; Margos, G. 2019. First investigations on serum resistance and sensitivity of *Borrelia turcica*. *Ticks And Tick-Borne Diseases* 10: 1157-1161, DOI: 10.1016/j.ttbdis.2019.06.013

Norte AC, Lopes de Carvalho I, Nuncio MS, Araújo PM, **Matthysen** E, Ramos JA, Sprong H & **Heylen** D. 2020. Getting under the birds' skin: tissue tropism of *Borrelia burgdorferi* s.l. in naturally and experimentally infected avian hosts. *Microbial Ecology* 79: 756-769 doi.org/10.1007/s00248-019-01442-3

Al-Khafaji AM, Bell-Sakyi L, Fracasso G, Luul L, **Heylen** D, **Matthysen** E, Oteo JA, Palomar AM. 2020. Isolation of *Candidatus Rickettsia vini* from Belgian *Ixodes arboricola* ticks and propagation in tick cell lines. *Ticks and Tick-borne Diseases* 11: 101511. doi.org/10.1016/j.ttbdis.2020.101511

5. General

Heylen DJA, Jacobs I, **Matthysen** E, Madder M. 2012. Comments on article "First report of *Ixodes frontalis* (Acari: Ixodidae) in Finland, an example of foreign tick species transported by a migratory bird". *Memoranda Soc. Fauna Flora Fennica* 88: 54-55.

Obsomer, V., Wirtgen, M., Linden, A., Claerebout, E., Heyman, P., **Heylen**, D. et al. (2013). Spatial disaggregation of tick occurrence and ecology at a local scale as a preliminary step for spatial surveillance of tick-borne diseases: general framework and health implications in Belgium. *Parasites Vectors*, 6.

Heylen, D., De Coninck, E., Jansen, F. & Madder, M. (2014). Differential diagnosis of three common *Ixodes* spp. ticks infesting songbirds of Western Europe: *Ixodes arboricola*, *I. frontalis* and *I. ricinus*. *Ticks Tick-Borne Dis.*, 5, 693-700.

Estrada-Pena, A., D'Amico, G., Palomar, A.M., Dupraz, M., Fonville, M., **Heylen**, D. et al. (2017). A comparative test of ixodid tick identification by a network of European researchers. *Ticks Tick-Borne Dis.*, 8, 540-546.

Charrier, NP; Hermouet, A; Hervet, C; Agoulon, A; Barker, SC; **Heylen**, D; Toty, C; McCoy, KD; Plantard, O; Rispe, C. 2019. A transcriptome-based phylogenetic study of hard ticks (Ixodidae). *Scientific Reports* 9: 12923, DOI: 10.1038/s41598-019-49641-9

6. PhD theses

Heylen, D.J.A. 2011. Parasite-host interactions between ticks and hole-breeding songbirds. Promotor E. Matthysen, University of Antwerp.

Van Oosten, R.A. 2015. Adaptations to an endophilic lifestyle in the tree-hole tick. Promotors E. Matthysen & D.J.A. Heylen, University of Antwerp.

Ruyts, S. 2017. Ecological interactions between ticks, hosts and forest types and the impact on Lyme borreliosis risk. Promotors K. Verheyen, E. Ampoorter, E. Matthysen, H. Sprong, University of Gent.