Within and among population differences in cuticular hydrocarbons in the seabird tick *Ixodes uriae*.

Marlène Dupraz[a]*, Chloe Leroy[b], Thorkell Lindberg Thórarinsson[c], Patrizia d'Ettorre[b], Karen D. McCoy[a].

[a] MIVEGEC, IRD, CNRS, Univ. Montpellier, Domaine La Valette - 900, rue Jean François BRETON 34090 Montpellier, France

[b] Laboratoire d'Ethologie Expérimentale et Comparée UR 4443 (LEEC), Université Sorbonne Paris Nord, F-93430 Villetaneuse, France

[c] Northeast Iceland Nature Research Centre, 640 Húsavík, Iceland

*Corresponding author: marlenedupraz@gmail.com; Tel. +33 4 67 41 61 78;

Abstract

The hydrophobic layer of the arthropod cuticle acts to maintain water balance, but can also serve to transmit chemical signals via cuticular hydrocarbons (CHC), essential mediators of arthropod behavior. CHC signatures typically vary qualitatively among species, but also quantitatively among populations within a species, and have been used as taxonomic tools to differentiate species or populations in a variety of taxa. Most work in this area to date has focused on insects, with little known for other arthropod classes such as ticks. The worldwide distribution and extensive host-range of the seabird tick *Ixodes uriae* make it a good model to study the factors influencing CHC composition. Genetically differentiated host-races of *I. uriae* have evolved across the distribution of this species but the factors promoting sympatric population divergence are still unknown. To test for a potential role of host-associated CHC in population isolation, we collected *I. uriae* specimens from two of its seabird hosts, the Atlantic puffin (*Fratercula arctica)* and the common guillemot (*Uria aalge*) in different colonies in Iceland. Using gas-chromatography and mass-spectrometry, we detected a complex cuticular mixture of 22 hydrocarbons, including *n*-alkanes, methyl-alkanes and alkenes ranging from 17 to 33 carbons in length. We found that each population had a distinct CHC profile. The host group explained the greatest amount of population divergence, with long-chain hydrocarbons being more abundant in puffin tick populations compared to guillemot tick populations. Future work will now be required to test whether the different CHC signals reinforce assortative mating, and thus play a role in generating *I. uriae* population divergence patterns, and to evaluate diverse hypotheses on the origin of distinct population signatures.

Keywords: Host race formation; GC-MS; colonial seabirds; Ixodidae; environmental variation

39 # Introduction

40 The arthropod cuticle acts as both an exoskeleton and a barrier from the external environment
41 (Andersen, 1979). The outermost layer, the epicuticle, is covered by a lipid layer (Lockey, 1988) made-
42 up of esters, carboxylic acids, alcohols, carbonyls and long-chain hydrocarbons (Andersen, 1979) that
43 protects the organism from desiccation (Filshie, 1982). However, cuticular hydrocarbons (CHC) are
44 also involved in chemical communication serving as sex pheromones, kairomones and/or signature
45 mixtures allowing recognition of social identity (van Zweden and d'Ettorre, 2010; Wyatt, 2010). Using
46 analytic techniques such as gas chromatography-mass spectrometry (GC-MS) and MALDI-TOF mass
47 spectrometry, researchers have described hydrocarbons of up 70 carbons in chain length in insects,
48 principally *n*-alkanes, methyl-branched alkanes and alkenes (Blomquist and Bagnères, 2010). The
49 array of CHC on the cuticle constitute a species-specific chemical signature, varying qualitatively
50 between species and quantitatively within species (Lockey, 1988). CHC patterns are genetically
51 controlled, but the relative abundance of particular components can be linked to environmental
52 conditions (Estrada-Peña et al., 1993; Gibbs et al., 1991). CHC patterns have been used as taxonomic
53 tools to characterize hundreds of arthropod species (Howard and Blomquist, 2005), and to
54 discriminate closely-related populations (Bagnères et al., 1991; Bartelt et al., 1986; Jallon and David,
55 1987; Kruger et al., 1991; Simmons et al., 2014).

56 In ticks, hematophagous arthropods widely distributed across the globe and parasitizing a diverse
57 array of vertebrate species (McCoy and Boulanger, 2015), little work has been performed to describe
58 CHC profiles and their variation among species and populations. The only studies to date have used
59 CHC profiles in an attempt to differentiate closely-related taxa (Estrada-Peña et al., 1992, 1994, 1996;
60 Hunt, 1986; Estrada-Peña and Dusbabek, 1993). However, tick CHCs may play essential roles in several
61 aspects of tick life histories. First, the tick epicuticle is perforated with numerous channels providing

62 a large surface for exchange with the external environment. As most tick species spend the major
63 part of their life cycle in the off-host environment, maintaining water balance across this surface
64 under different environmental conditions will directly dictate survival (Randolph and Storey, 1999);
65 the presence of CHCs likely plays an important role in this. Second, as obligate parasites, access to
66 the vertebrate host for the bloodmeal is a key aspect of the tick life cycle and, as such, ticks have
67 adapted key traits to locate and successfully exploit their host (McCoy and Boulanger, 2015), as for
68 example Haller's organ, a unique chemosensory structure located on the 1st pairs of legs (Leonovich,
69 2004). Shimshoni et al. (2013) found *Rhipicephalus* tick species had different cuticular fatty acid
70 compositions in relation to host use. However, whether these differences are linked to adaptive
71 survival or by-product variation due to the host resource is unknown as yet. Finally, ticks aggregate
72 both on hosts and in the off-host environment (Randolph, 1998). This behavior is thought to facilitate
73 blood feeding on the host and increase survival in the off-host environment. It may also enable ticks
74 to find appropriate mates for reproduction. Some ticks, such as the tropical bont tick *Amblyomma*
75 *variegatum*, produce a multicomponent pheromone to provoke aggregation (Schöni et al., 1984) but
76 the potential role of these pheromones in assortative mating has never been examined.

77 Seabird ticks are generally nidicolous, exploiting different local host species that use diverse micro-
78 habitats within the colony (Dietrich et al., 2011). Due to this diversity, these ticks may experience
79 diverse selective pressures coming from both the hosts and from the temperature and humidity
80 conditions of the nest micro-habitat. In particular, *Ixodes uriae*, a tick associated with seabird colonies
81 in the polar regions of both hemispheres, is known to form host-specific races that show genetic
82 (McCoy et al., 2005, 2003, 2001) and morphological (Dietrich et al., 2013) differences in relation to
83 host use. Differential performance on alternative hosts has also been experimentally demonstrated
84 (Dietrich et al., 2014). Nevertheless, the factors driving divergence within this species have yet to be

specifically identified. A potential role for isolating mechanisms that lead to assortative mating based on host use have been suggested (McCoy et al., 2013).

Here, we examine the degree of cuticular hydrocarbon diversity in *I. uriae* and the factors influencing these chemical signatures. Based on current knowledge, we predicted that cuticular hydrocarbon patterns could vary in ticks 1) exploiting different host species and 2) sampled in different geographic locations. If host exploitation modifies CHC diversity and abundance, we expected that signatures in ticks from the same seabird host in different locations should be more similar than signatures in ticks from different host species in the same geographic location. To test these predictions, we collected *I. uriae* specimens in the nesting area of two seabird host species, the common guillemot (CG) *Uria aalge,* and the Atlantic puffin (PF) *Fratercula arctica,* at three locations in Iceland. We then extracted cuticular hydrocarbons and analyzed them using gas chromatography-mass spectrometry (GC-MS).

Material and methods

Population samples

Flat adult female ticks were collected off-host in three sites in Iceland in June 2016: common guillemot ticks (CG) were collected under rocks in the middle of the colony in Langanes (L) (66°22'07.2"N 14°38'33.0"W) and on Grimsey Island (GRI) (66°32'57.3"N 17°59'31.1"W); puffin ticks (PF) were collected in burrows on Lundey Island (LI) (66°06'53.2"N 17°22'13.1"W) and on Grimsey Island (GRI) (66°32'39.1"N 18°01'12.9"W) (Fig.1). Ticks were kept alive in plastic tubes before hydrocarbon extraction. Four replicates of 10 flat ticks were extracted for each host species at each site.

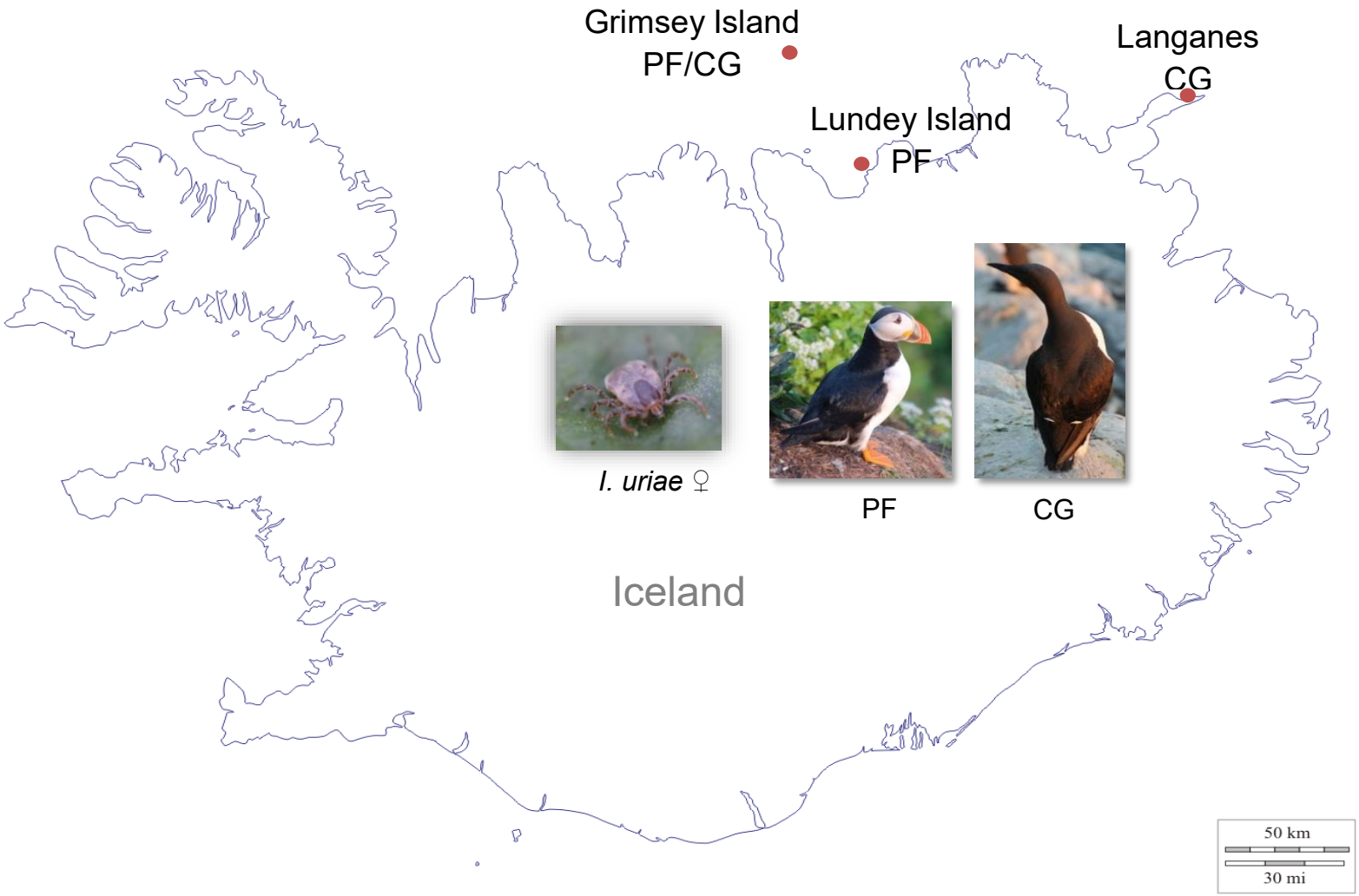


Fig.1: Map showing the sampling locations for *Ixodes uriae* ticks and hosts in Iceland in June 2016. PF refers to the Atlantic puffin (*Fratercula arctica*) and CG to the common guillemot (*Uria aalge*). The acronyms of the sampling locations are as follows: Grimsey Island - G; Lundey Island – Li; Langanes - L.

118 **Hydrocarbon extraction**

119 Several extraction attempts were made with ticks kept alive or stored in alcohol and with only one
120 individual or in batches of five, but the quantities of extracted cuticular compounds were too low to
121 use in analyses. Cuticular compounds were therefore extracted by immersing 10 living flat female
122 ticks in 200 µl of pentane (HPLC grade, Sigma-Aldrich) in glass vials. The vials were agitated for 1
123 minute, set down to rest for 5 minutes and then re-agitated for 1 minute. Ticks were then removed
124 from the vials and preserved in 70% ethanol. The pentane was then evaporated off over 30 minutes
125 to obtain dried eluent and the vials were closed and kept at 4°C until analyses. A negative control
126 containing only 200 µl of pentane was added to each extraction session to control for potential
127 contamination. We did not use an internal standard because the aim of our analysis was not to
128 quantify the absolute amount of CHCs, but to compare the relative proportions of CHCs among
129 samples.

130 **Chemical analyses**

131 Cuticular hydrocarbons are not very volatile, but to reduce variation during the evaporation process,
132 all samples were treated in the same way, placed under the same fume hood in a temperature
133 controlled room. Samples were re-diluted in 40µl of pentane and 3µl were injected into an Agilent
134 Technologies 7890A gas chromatograph (capillary column: Agilent HP-5MS, 30 m × 0.25 mm × 0.25
135 µm; split–splitless injector; carrying helium gas at 1 mL/min) coupled with an Agilent 5975C mass
136 spectrometer with 70 eV electron impact ionization. The oven temperature was programmed at 70°C
137 for 1min, and was increased at 30°C/min to 200°C, then to 320°C at 5°C/min and held for 5 min.
138 Compounds were then identified (raw data available on Zenodo at
139 https://doi.org/10.5281/zenodo.6497483) and sorted on the basis of their mass spectra and
140 retention time by comparison with standards (alkane standard solutions, Sigma-Aldrich, Saint Louis,

141 MO, USA) and published spectra (NIST Library). The abundance of each detected cuticular
142 hydrocarbon was used to build a box plot using the ggplot 2 package with R software (version 4.1.1).
143 The areas under the peaks were extracted using the Agilent MSD ChemStation software
144 (E.02.01.1177) and were used to calculate the relative amount of each hydrocarbon to normalize data
145 coming from different origins and of different qualities. The mean peak area of the four population
146 replicates was calculated for each hydrocarbon to obtain a colony average.

147 **Multivariate analyses**

148 For analytical purposes, if the relative abundance of a CHC was 0, the value was replaced by 0.00001
149 which is several times lower than the lowest quantity found for a CHC in our dataset. The data were
150 then transformed using a centered log ratio procedure (data available in supplementary materials,
151 Table S1 and on Zenodo at https://doi.org/10.5281/zenodo.5889077) and analyzed by Partial Least
152 Squares coupled with a Discriminant analysis (PLS-DA) using the R software (v 3.4.3) and the
153 "RVAidememoire" package (Hervé, 2014) (https://cran.r-
154 project.org/web/packages/RVAideMemoire/index.html). PLS-DA is an appropriate analysis when the
155 dataset contains fewer groups than explanatory variables, as in the case of the present quantitative
156 dataset. PLS-DA is a supervised technique, meaning that class memberships of the CHCs need to be
157 predefined. Here, we only used the first eight axes produced by the PLS to perform two PLS-DA tests:
158 the first analysis considered the four population samples as four different classes (LCG, GCG, LiPF,
159 GPF, outlined on Fig. 1). The second analysis was based on two classes only, representing the two
160 host types (PF, CG). The number of significant PLS components was determined by cross model
161 validation. We also calculated a numerical value representing the importance of each CHC variable in
162 the projection (VIP), i.e. VIP values larger than 1 are most influential (Hervé, 2014).

163

164 # Results

165 **Hydrocarbon profiles**

166 We detected a complex pattern of 22 hydrocarbons and two non-identified components (I1 and I2)
167 in the cuticle of *I. uriae* ticks. The hydrocarbon mixture was composed of: 14 *n*-alkanes ranging from
168 17 to 33 carbon atoms in length, 4 monomethyl-alkanes with 17 to 24 carbon atoms and 4 alkenes
169 with 21 to 27 carbon atoms (Table 1).

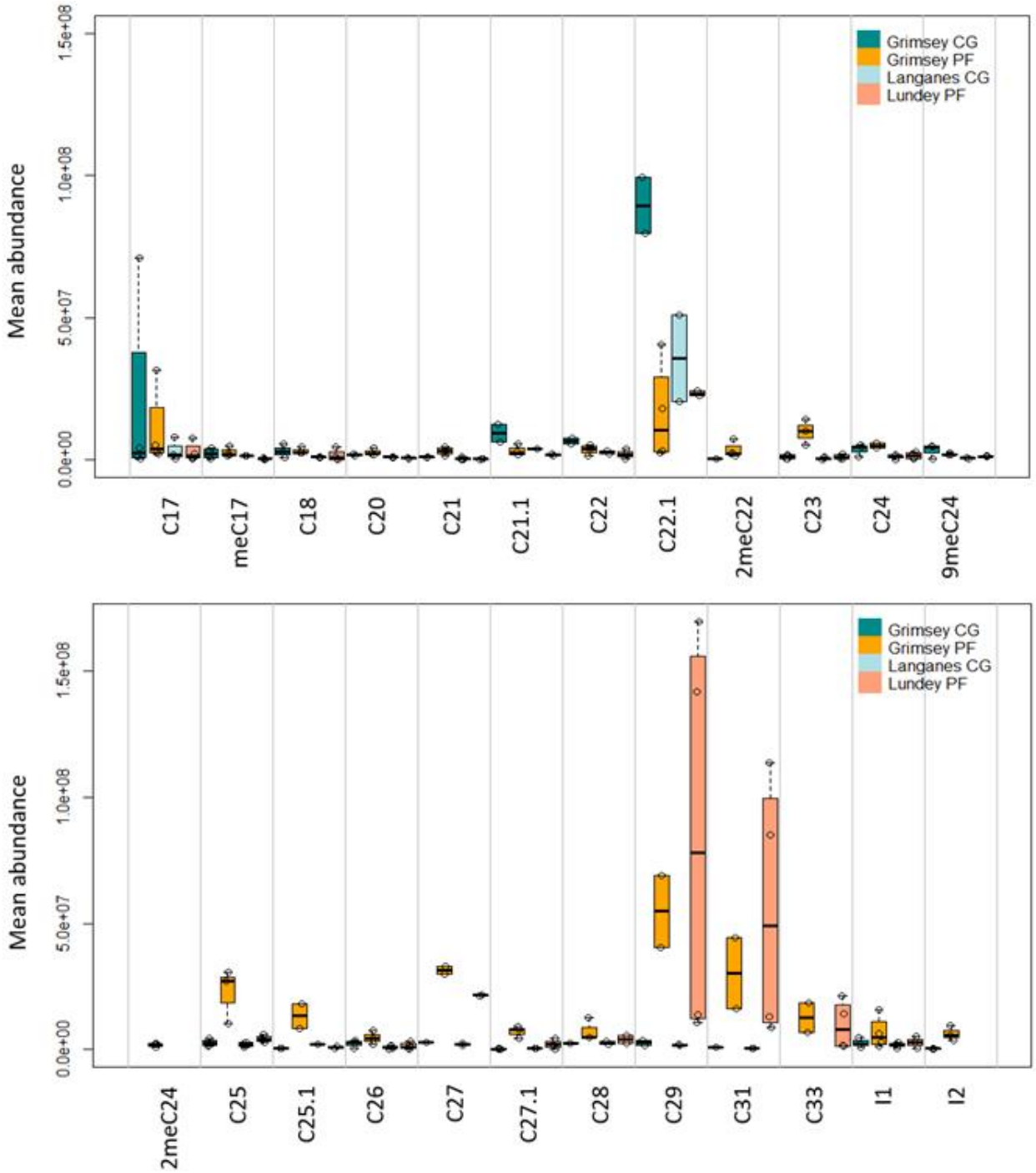
170 **Table 1**: List of detected compounds in the cuticle of *I. uriae* adult female ticks, including name and
171 type.

Cuticular component	Name	Type
C_{17}	*n*-heptadecane	alkane
meC_{17}	methylheptadecane	methyl-branched alkane
C_{18}	*n*-octadecane	alkane
C_{20}	*n*-eicosane	alkane
$C_{21:1}$	heneicosene	alkene
C_{21}	*n*-heneicosane	alkane
$C_{22:1}$	docosene	alkene
C_{22}	*n*-docosane	alkane
$2meC_{22}$	2methyldocosane	methyl-branched alkane
C_{23}	*n*-tricosane	alkane
C_{24}	*n*-tetracosane	alkane
$9meC_{24}$	9methyltetracosane	methyl-branched alkane
$2meC_{24}$	2methyltetracosane	methyl-branched alkane
$C_{25:1}$	pentacosene	alkene
C_{25}	*n*-pentacosane	alkane
C_{26}	*n*-hexacosane	alkane
$C_{27:1}$	heptacosene	alkene
C_{27}	*n*-heptacosane	alkane
C_{28}	*n*-octacosane	alkane
C_{29}	*n*-nonacosane	alkane
C_{31}	*n*-hentriacontane	alkane
C_{33}	*n*-tritriacontane	alkane
I1	Non-identified	-
I2	Non-identified	-

172

173 All hydrocarbons were shared by the four tick populations, except 2meC_{24} and C_{33} which were only

174 found in puffin ticks (Fig.2).



175

176 **Fig.2**: Boxplot representing the mean abundance of each detected cuticular hydrocarbon from *I. uriae* ticks.
177 Compounds ranged from 17 to 33 carbon atoms in length. Mean abundance was calculated based on values
178 from four replicate tick pools. First and third quartiles, median and data points are shown. See Table 1 for CHC

abbreviations. PF refers to the Atlantic puffin (*Fratercula arctica*) and CG to the Common guillemot (*Uria aalge*).

A high degree of variation among samples in mean abundance of cuticular components was obvious (Fig.2). Hydrocarbons $C_{22:1}$, *n*-C_{29} and *n*-C_{31} were the most predominant, whereas many hydrocarbons were detected in low quantities, as for example *n*-C_{20}, 2meC_{22} and *n*-C_{26}.

The abundance pattern of cuticular hydrocarbons varied between ticks of the two host species (Fig.3), but also among the same host in different colony sites. Nevertheless, results of all pairwise profile comparisons were non-significant. No CHC was specific to CG samples, although *n*-C_{17} and $C_{22:1}$ were highly abundant in the GRI colony (Fig.2 and 3). In contrast, long chain cuticular hydrocarbons tended to be present in both PF samples: *n*-C_{27}, *n*-C_{29} and *n*-C_{31}. CHC components tended to be in lower overall abundance in samples from Langanes (Langanes CG), whereas samples from Lundey Island (Lundey PF) had the highest overall abundance (Fig. 2).

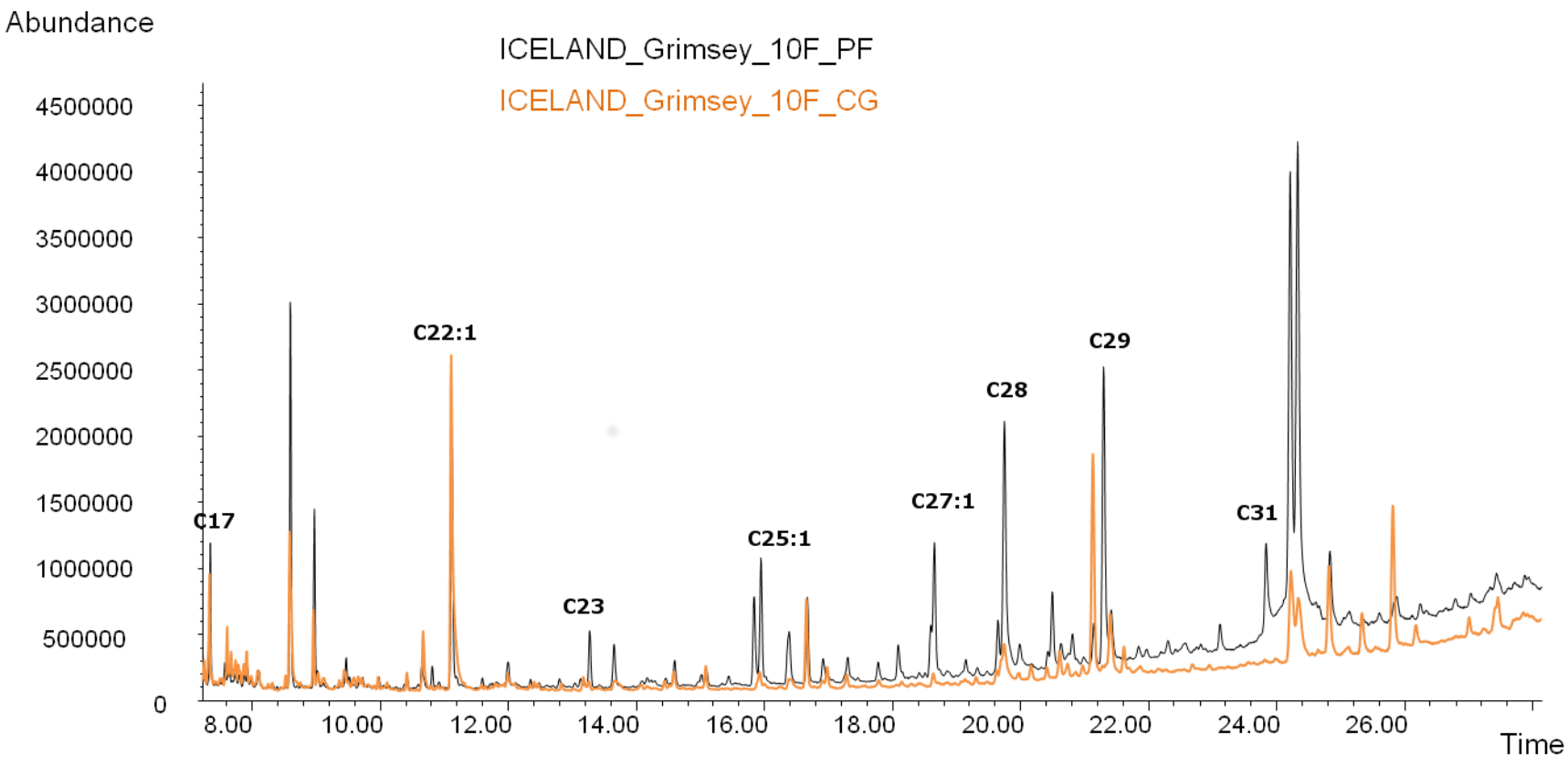
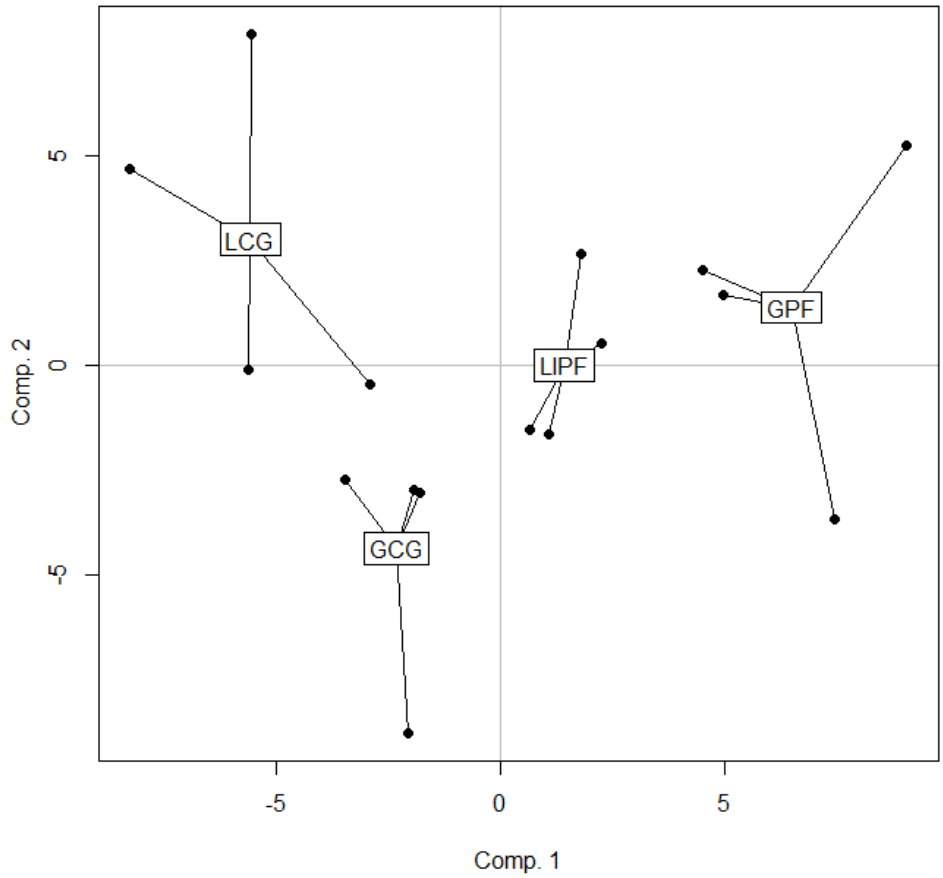


Fig.3: Gas-chromatograms showing the comparison of cuticular hydrocarbon profiles for pools of 10 female ticks from Atlantic puffins (PF: black line) and Common guillemots (CG: orange line) on Grimsey Island, Iceland.

196 **PLS-DA analyses**

197 *Population samples*

198 Cross model validation for population samples showed that 50.6% of samples were assigned to the
199 population of origin. PLS-DA analysis showed a discriminating population effect (p=0.008) separating
200 the two host species on first axis (Fig.4). The three first axes explained respectively 11.94, 7.99 and
201 3.99 % of the total variance among samples.



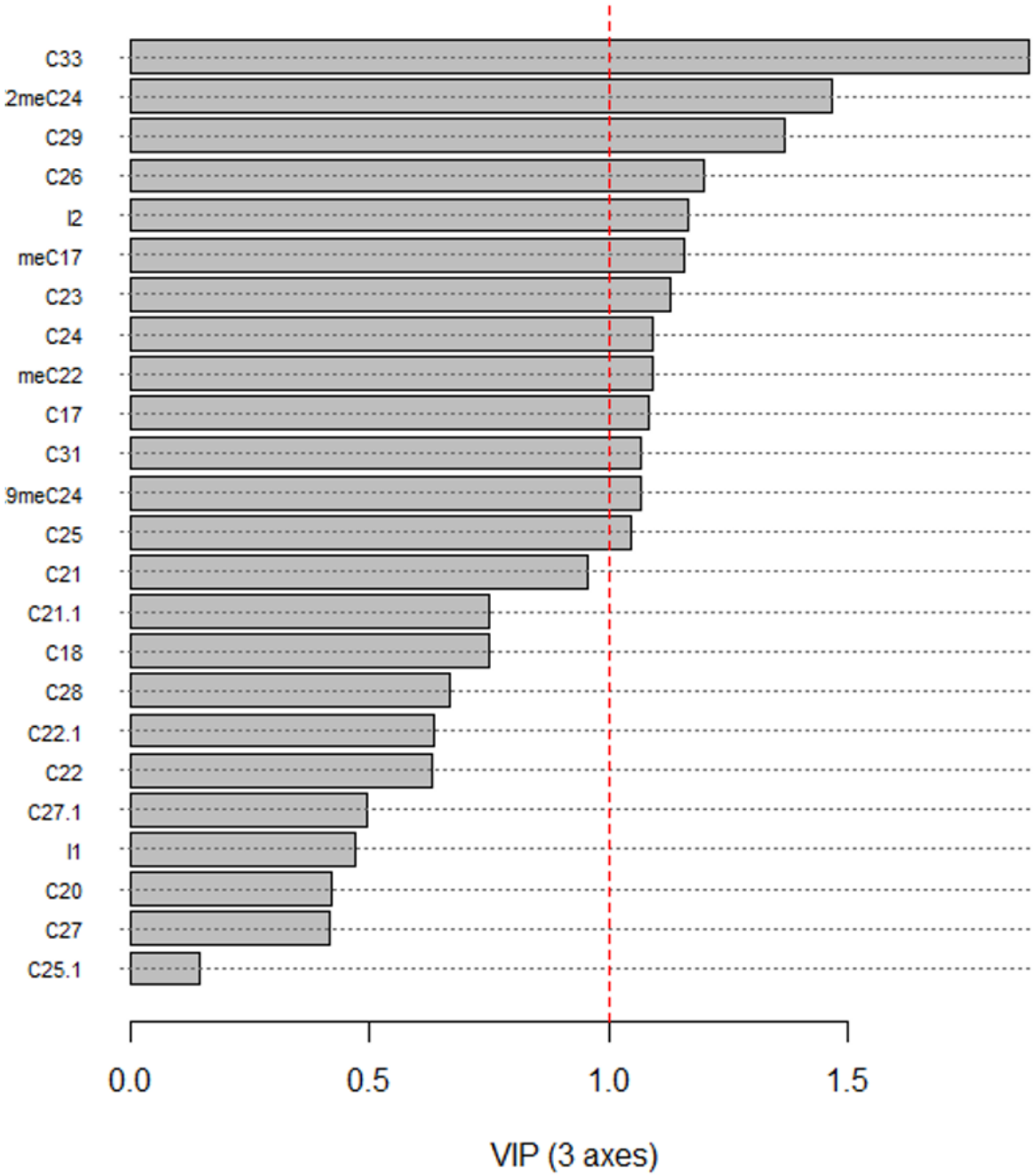
202

203 **Fig.4**: Graphical representation of the four population samples on the two first axes of the PLS-DA analysis. The
204 first and second axes explained respectively 11.94 and 7.99% of the total variance among samples (p=0.008).
205 The acronyms of the sampling locations are as follows: Grimsey - G; Langanes - L; Lundey Island - Li. PF refers
206 to Atlantic puffin (*Fratercula arctica*) and CG to Common guillemot (*Uria aalge*).

207

208 Hydrocarbons *n*-C_{33}, 2meC_{24} and *n*-C_{29} appeared as the most influential components separating the

209 four population samples (Fig.5).



210

211 Fig.5: VIP classification showing the influence of CHC in discriminating the four population samples. VIP values
212 larger than 1 (dashed red line) are most influential. See Table 1 for CHC abbreviations.

213

214

215 *Host types*

216 The cross-validation test for host type revealed that 75% of the tick pools were assigned to the host
217 of origin (PF, CG). However, the PLS-DA analysis revealed no significant difference in CHC profiles
218 between the host types, although a tendency was evident (PLS-DA: p=0.064).

219

220 Discussion

221 **Cuticle composition and function**

222 Cuticular hydrocarbons, including linear and methyl-branched alkanes and alkenes, are
223 biosynthesized from an acetyl-CoA molecule in specialized secretory cells, the oenocytes which are
224 mainly located in the epidermis of insects (Howard and Blomquist, 2005). They are shuttled through
225 the hemolymph to the epicuticular surface via specialized pore canals penetrating the cuticular layers
226 (Holze et al, 2021). Once fixed on the arthropod cuticle within a complex mixture of alcohols, esters,
227 aldehydes, fatty acids, etc, hydrocarbons help prevent desiccation and serve in chemical
228 communication, constituting essential mediators of insect behavior (Blomquist and Bagnères, 2010).
229 Using GC-MS techniques to analyze extracts from female *I. uriae* ticks, we detected a complex mixture
230 of cuticular hydrocarbons containing linear and monomethyl-alkanes and alkenes ranging from 17 to
231 33 carbon atoms. The qualitative composition is similar to that reported for many other arthropods,
232 comprising predominantly linear alkanes (n-C_{23}, n-C_{25}, n-C_{27}, n-C_{29} and n-C_{31}) (Howard and Blomquist,
233 2005; Lockey, 1988). A majority of the detected cuticular hydrocarbons were already reported in
234 other hard ticks: *I. persulcatus* (Tkachev et al., 2000), *Amblyomma variegatum* (Estrada-Peña et al.,
235 1994) and *Rhipicephalus* spp. (Estrada-Peña et al., 1992). Nevertheless, alkenes were only detected
236 once in low quantities in *Rhipicephalus* spp. (Estrada-Peña et al., 1992). Here, we report the presence

237 of alkenes as heneicosene, pentacosene, heptacosene and a high quantity of docosene, particularly
238 in one of the CG samples. Alkenes were demonstrated to act as sex pheromones in the Alfalfa leaf-
239 cutter bee *Megachile rotundata* and the rove beetle *Aleochara curtula* (Paulmier et al., 1999; Peschke
240 and Metzler, 1987). Heneicosene is also described as an aggregation pheromone in *Drosophila* species
241 (Bartelt et al., 1988; Bartelt and Jackson, 1984). Pentacosene is implicated in the mating process of
242 different fly species as a stimulant pheromone (Uebel et al., 1978). The presence of these alkenes in
243 *I. uriae* could corresponds to the biological state of the female ticks when they were collected.
244 However, as mating in this tick species frequently takes place prior to feeding on the host, and in
245 particular when nymphal ticks emerge as flat females (McCoy and Tirard, 2002), we cannot conclude
246 on the mating status of collected females. Indeed, some of the profile variation in our data may be
247 due to the inclusion of females in different reproductive states. Experimental studies will now be
248 necessary to determine the potential role of the observed CHC compounds in mating behavior.

249 We found also large amount of long-chain hydrocarbons in PF samples (n-C_{29}, n-C_{31} and n-C_{33}). Mixed
250 with other compounds, n-C_{31} was demonstrated to induce copulation in males of the stable fly
251 *Stomoxys calcitrans* (Uebel et al., 1975). Other long chain hydrocarbons, including n-C_{23} to n-C_{31},
252 produced in large quantities and acting in combination, were found to serve in colony recognition by
253 bumblebees *Bombus terrestris* (Rottler et al., 2013). Studies have also highlighted the importance of
254 the environment in the acquisition of new hydrocarbons (d'Ettorre et al., 2006; d'Ettorre et al., 2002),
255 acting for example as a recognition signal of their own nest for the social wasp *Polistes metricus* Say
256 (1981) (Singer and Espelie, 1996; Espelie et al., 1990). Moreover, 2meC_{24}, that we only detected in PF
257 CHC profiles, has been shown to serve as a contact pheromone in peach twig borers *Anarsia lineatella*
258 (Schlamp, 2005). As puffin burrows are often deep, and densely distributed (Harris and Wanless,
259 2011), the production of these cuticular hydrocarbons in *I. uriae* may enable ticks to find conspecifics
260 in the host nesting environment. The use of this particular blend of CHCs may also help ticks to find

261 individuals that smell similar, favoring assortative mating (van Zweden and d'Ettorre, 2010). The
262 production of a specific CHC blend may not be necessary for CG ticks because guillemots breed in
263 extremely dense numbers on cliff ledges with no constructed nest; ticks tend to aggregate under and
264 around rocks on the cliff ledge such that finding a mate from the same host type may be easier
265 compared to ticks exploiting puffin hosts. More generally, the presence of complex compounds in the
266 CHC pattern of *I. uriae* suggest that chemical communication may be important in this tick species,
267 potentially enabling ticks to find a suitable mating partner that would enable them to maintain host-
268 adapted gene complexes (Sonenshine and Roe, 2014).

269 **Alternative hypotheses to explain the origin of CHC patterns**

270 As expected, chemical analyses revealed that each tick population had a distinct CHC profile, but that
271 specific CHCs were also associated with different host types. In particular, *n*-C_{33}, 2meC_{24} and *n*-C_{29}
272 were most frequently or exclusively detected in PF populations. The quantitative variability among
273 detected hydrocarbons could be related to different factors.

274 First, aging and development have been demonstrated to impact cuticular hydrocarbon patterns in
275 different taxa (Desena et al., 1999; Ichinose and Lenoir, 2009). For example, aging favors the
276 production of longer hydrocarbon chains and decreases sexual attractiveness in *Drosophila*
277 *melanogaster* (Kuo et al., 2012). The high quantities of long-chain hydrocarbons (*n*-C_{27}, *n*-C_{29}, *n*-C_{31})
278 observed in the puffin tick samples could be a consequence of age variability between host-associated
279 tick samples. Samples used in the present study were collected in the field and the relative age of the
280 specimens could not be determined. However, as tick activity is relatively synchronous with seabird
281 breeding, we did not expect the overall timing in adult female activity to differ in a systematic way
282 between ticks exploiting the different host species, nor among distinct colony locations within
283 Iceland.

284 Second, climatic conditions can also shape CHC composition. Differences in cuticular hydrocarbon
285 composition were observed in geographically distant tick populations of *Amblyomma variegatum*
286 (Estrada-Peña et al., 1994) and some extreme climatic parameters were shown to be correlated with
287 methyled-alkanes in *Rhipicephalus sanguineus* (Estrada-Peña, 1993). These results suggest a potential
288 link between variation in CHC compounds and adaptation to environmental temperatures. The
289 different types of off-host environments used by *I. uriae* (rock or burrow) may display significant
290 variation in terms of temperature and relative humidity due to differential exposure to climatic
291 factors such as sun, rain and/or snow (Buckley and Buckley, 1980). These selective factors can impact
292 tick survival and could lead to the quantitative variation in cuticular components observed in this
293 study. Howard et al (1978) argued that the effectiveness of CHCs in preventing desiccation depends
294 on the quantity of CHCs and that saturated CHCs are more effective components in protecting against
295 water loss. By positioning temperature and humidity captors during one year in the off-host
296 environment in a heterospecific seabird breeding colony in northern Norway (70°22' N, 31°10' E), we
297 observed that the average temperature and relative humidity (HR) ranged respectively from -7.5 to
298 18°C and from 0 to 110% HR in breeding sites of Common guillemots, and from -7.5 to 10°C and from
299 80 to 105% HR in those occupied by puffins (data not shown). The micro-habitat used by CG ticks may
300 therefore be more exposed to temperature and humidity variation than the more stable deep
301 burrows used by PF ticks. However, the presence and abundance of saturated CHCs, such as $9meC_{24}$
302 and $2meC_{24}$, were not more frequent in CG samples compared to PF samples. More detailed
303 environmental data from each location and more sampled locations are therefore necessary to more
304 fully evaluate this hypothesis.

305 Third, diet also appears to be an important factor shaping cuticular hydrocarbon profiles. In the
306 Argentine ant *Linepithema humile*, colonies eating different prey items present particular
307 hydrocarbon profiles that include components coming directly from the prey (Liang and Silverman,

308 2000). In the same way, Geiselhardt et al., (2012) showed that males of the phytophagous mustard
309 leaf beetle *Phaedon cochleariae* preferred to mate with females reared on the same host plant
310 compared to females from a different host plant, even though they originated from the same
311 laboratory stock population. Studies have also shown that the ectoparasite *Varroa destructor* can
312 mimic its host's cuticular hydrocarbons, enabling the parasite to escape the hygienic behavior of the
313 host honeybee (Le Conte et al., 2015; Nazzi and Le Conte, 2016). In ticks, it was demonstrated that
314 the cuticular fatty acid profiles of *Rhipicephalus* spp. presented significant differences in abundance
315 according to host use (Shimshoni et al., 2013). In our system, avian erythrocyte membrane lipids
316 might provide a direct pathway for the tick to synthesize cuticular hydrocarbons from pre-existing
317 shorter-chain fatty acids and could result in the acquisition of specific hydrocarbon mixtures. This
318 type of acquisition could explain both the variation among ticks from different host species, and
319 variation among colony locations, if seabird diets shift among locations. Futures studies could
320 therefore be expanded to look for correlations between avian erythrocyte membrane lipid
321 composition and tick cuticular signatures by comparing ticks and host blood samples. In addition,
322 looking at patterns in tick cuticular lipids, such as fatty acids and steroids, which have been reported
323 as pheromones in metastriate ticks (Sonenshine, 2004; Sonenshine et al, 1985), would also be of
324 particular interest.

325 Fourth, CHCs can be altered by infection with different micro-organisms. For example, both the corn
326 borer (*Ostrinia nubilalis*) and the common cockchafer (Melolontha melolontha) show altered CHC
327 profiles when infected by fungi of the genus Beauveria (Lecuona et al, 1991). Moreover, Yoder and
328 Domingus (2003) demonstrated that production of the CHCs *n*-C_{20} and *n*-C_{24} by *Dermacentor variabilis*
329 ticks could protect against predatory behavior by ants. The abundances of *n*-C_{20}, *n*-C_{21}, *n*-C_{23} and *n*-
330 C_{24} in the puffin tick pools of the present study may represent different infection statuses and/or that

puffin burrows provide a less protective environment against predators, such as ants or spiders, than stones in common guillemot colonies.

In general, making inferences on environmental versus host effects will require the examination of ticks from additional sites and host types. However, regardless of the origin of host-associated differences in CHC profiles of *I. uriae*, what is important to now determine is whether these differences reinforce assortative mating patterns, favoring the divergence of sympatric populations and the rapid formation of local host races. Future analyses should focus on the characterization and isolation of the main components of the cuticular mixture from ticks of each seabird host type to test for their biological activity and potential role in tick mating behavior.

Acknowledgements

We would like to thank Yann Kolbeinsson from Northeast Iceland Nature Research Centre, Iceland for sampling help. We thank “Tiques et Maladies à Tiques” Working Group of the Societé Française d'Ecologie et d'Evolution (SFE2) for stimulating discussions and support.

Funding

Funding for this study was provided by the ANR grant ESPEVEC (ANR-13-BSV7-0018-01) to KDM. MD was supported by a fellowship from the French Ministry for National Education and Research at University of Montpellier.

Conflict of interest disclosure

The authors declare they have no conflict of interest relating to the content of this article.

Supplementary data

Table S1: Relative abundance of the CHC extracts of each population replicate after log centered ratio transformation (also available on Zenodo at https://doi.org/10.5281/zenodo.5889077).

	C17	meC17	C18	C20	C21.1	C21
CHC_GPF1	1,258262	-1,675478	-1,225611	-1,358771	-0,456587	-1,093444
CHC_GPF2	-0,983004	-0,983004	-0,783199	-1,164937	-1,056892	-0,184697
CHC_GPF3	4,151361	3,580785	4,724183	4,617548	3,807260	3,540713
CHC_GPF4	3,597384	3,540178	2,810370	-5,405227	2,969631	3,222111
CHC_LIPF1	1,518413	-6,017122	1,043470	-1,007387	0,183513	-1,120153
CHC_LIPF2	0,687396	-0,588309	-0,053014	-0,504584	0,166784	-1,747215
CHC_LIPF3	2,953938	1,854215	2,570707	-4,252033	-4,252033	2,319610
CHC_LIPF4	3,334867	2,899295	1,532183	2,736876	-4,685930	2,599998
CHC_GCG1	4,385533	1,306893	1,157818	0,389237	1,944246	0,212800
CHC_GCG2	1,730616	1,703967	1,991403	1,042497	2,791342	0,217889
CHC_GCG3	5,149559	5,171603	4,695299	-4,141914	-4,141914	-4,141914
CHC_GCG4	6,607656	6,507890	-2,764376	-2,764376	-2,764376	6,667177
CHC_LCG1	4,213065	2,588977	1,956074	2,221551	-5,462891	1,390069
CHC_LCG2	1,933896	1,561455	1,352674	1,168282	2,599910	1,493046
CHC_LCG3	5,173815	-3,295400	-3,295400	-3,295400	-3,295400	5,004318
CHC_LCG4	-2,395630	-2,395630	-2,395630	-2,395630	-2,395630	6,592884

	C22.1	C22	meC22	C23	C24	9meC24
CHC_GPF1	1,50623611	-0,50555381	-1,70555949	0,12096462	-0,42768644	-1,2206834
CHC_GPF2	1,18425441	-0,49071836	-0,98066082	0,94030298	-0,28189781	-1,02914483
CHC_GPF3	4,32918786	4,60171239	4,02667532	-4,77602802	-4,77602802	-4,77602802
CHC_GPF4	2,85991037	2,24131129	3,95590755	3,57761114	-5,4052267	2,55126443
CHC_LIPF1	2,6847376	0,88062159	-6,01712163	0,22189045	0,56501804	-0,13693536
CHC_LIPF2	2,96343585	0,37650416	-5,92683159	0,07138213	0,62140857	-0,18069582
CHC_LIPF3	-4,25203345	-4,25203345	-4,25203345	2,48114139	2,91217821	-4,25203345
CHC_LIPF4	-4,68592953	2,30293014	-4,68592953	2,17284599	2,95775455	-4,68592953
CHC_GCG1	4,72183226	2,16796305	-5,97456355	0,50141786	1,61476737	1,69619514
CHC_GCG2	4,63765818	1,96470376	-6,27678757	0,9386865	1,89458577	1,80575829
CHC_GCG3	-4,14191373	-4,14191373	4,50899999	4,55481651	5,23921344	4,3019409
CHC_GCG4	-2,76437623	-2,76437623	-2,76437623	6,56677188	-2,76437623	-2,76437623
CHC_LCG1	5,14840786	2,88187094	-5,46289066	2,15974193	2,64600173	1,30457536
CHC_LCG2	5,19919581	2,44288367	-5,83634374	0,96429749	1,55031557	1,00827119
CHC_LCG3	-3,2954001	-3,2954001	-3,2954001	4,10398495	5,06658076	-3,2954001
CHC_LCG4	-2,39563008	-2,39563008	-2,39563008	6,38876341	-2,39563008	-2,39563008

	2meC24	C25.1	C25	I1	C26	I2
CHC_GPF1	-1,49255919	0,710483	1,09996476	0,56276083	-0,17627985	0,07387322
CHC_GPF2	-0,85129625	0,41550683	1,72274199	0,15326967	-0,25663413	-0,00255114
CHC_GPF3	3,04100103	-4,77602802	-4,77602802	3,46602618	3,89103385	-4,77602802
CHC_GPF4	2,74237448	-5,4052267	4,27702093	3,00740146	-5,4052267	3,29174679
CHC_LIPF1	-6,01712163	-0,1488945	1,29293382	1,12637653	0,69030705	-6,01712163
CHC_LIPF2	-5,92683159	-0,64688596	1,31627079	0,90987066	0,41085836	-5,92683159
CHC_LIPF3	-4,25203345	-4,25203345	4,71776728	3,3029661	2,56104558	-4,25203345
CHC_LIPF4	-4,68592953	-4,68592953	4,6771672	-4,68592953	2,68595365	-4,68592953
CHC_GCG1	-5,97456355	-0,42396916	1,22349549	1,72540467	1,38243536	-1,39612756
CHC_GCG2	-6,27678757	-0,2065063	1,72213495	1,06728457	1,33585569	-0,21747187
CHC_GCG3	-4,14191373	-4,14191373	5,71433159	-4,14191373	4,75085336	-4,14191373
CHC_GCG4	-2,76437623	-2,76437623	7,51121475	7,01077959	-2,76437623	-2,76437623
CHC_LCG1	-5,46289066	-5,46289066	3,01341895	2,82230157	2,69452068	-5,46289066
CHC_LCG2	-5,83634374	2,0586822	1,72477962	2,25712355	1,39064679	-5,83634374
CHC_LCG3	-3,2954001	-3,2954001	7,60591058	5,62063417	5,2526945	-3,2954001
CHC_LCG4	-2,39563008	-2,39563008	7,96176069	-2,39563008	7,19765085	-2,39563008

	C27.1	C27	C28	C29	C31	C33
CHC_GPF1	-0,00016215	1,30711449	0,33827026	2,04171998	1,59307887	0,72564782
CHC_GPF2	-0,19069859	1,69885837	-0,1473274	1,99452145	1,07445349	0,20275287
CHC_GPF3	-4,77602802	-4,77602802	4,75882151	-4,77602802	-4,77602802	-4,77602802
CHC_GPF4	4,00281861	-5,4052267	-5,4052267	-5,4052267	-5,4052267	-5,4052267
CHC_LIPF1	1,02468304	2,57346606	1,2522136	4,63157554	4,23145935	2,56117937
CHC_LIPF2	-1,29244538	2,91653471	0,74631061	4,80493688	4,29222175	2,5097294
CHC_LIPF3	4,42572948	-4,25203345	-4,25203345	6,29373406	6,22187233	4,15746354
CHC_LIPF4	3,97386234	-4,68592953	-4,68592953	5,79395404	5,57504998	3,61655868
CHC_GCG1	-2,31093524	1,17815423	0,96870906	1,45238521	-5,97456355	-5,97456355
CHC_GCG2	-2,63802842	1,37672655	1,18012447	0,76792459	-6,27678757	-6,27678757
CHC_GCG3	4,78876251	-4,14191373	-4,14191373	-4,14191373	4,9694991	-4,14191373
CHC_GCG4	6,12290594	-2,76437623	-2,76437623	-2,76437623	-2,76437623	-2,76437623
CHC_LCG1	-5,46289066	3,03426816	2,96262862	2,66565265	-5,46289066	-5,46289066
CHC_LCG2	-5,83634374	1,89920237	2,48119674	1,9322039	-5,83634374	-5,83634374
CHC_LCG3	6,05677419	-3,2954001	-3,2954001	-3,2954001	5,54628953	-3,2954001
CHC_LCG4	7,47336812	-2,39563008	-2,39563008	-2,39563008	7,50691468	-2,39563008

References

Andersen, S.O., 1979. Biochemistry of Insect Cuticle. Annu. Rev. Entomol. 24, 29–59. https://doi.org/10.1146/annurev.en.24.010179.000333

Bagnères, A.-G., Killian, A., Clement, J.-L., Lange, C., 1991. Interspecific recognition among termites of the genusReticulitermes: Evidence for a role for the cuticular hydrocarbons. J. Chem. Ecol. 17, 2397–2420. https://doi.org/10.1007/BF00994590

Bartelt, R.J., Armold, M.T., Schaner, A.M., Jackson, L.L., 1986. Comparative analysis of cuticular hydrocarbons in the Drosophila virilis species group. Comp. Biochem. Physiol. Part B Comp. Biochem. 83, 731–742. https://doi.org/10.1016/0305-0491(86)90138-0

Bartelt, R.J., Jackson, L.L., 1984. Hydrocarbon Component of the Drosophila virilis (Diptera: Drosophilidae) Aggregation Pheromone: (Z)-10-Heneicosene. Ann. Entomol. Soc. Am. 77, 364–371. https://doi.org/10.1093/aesa/77.4.364

Bartelt, R.J., Schaner, A.M., Jackson, L.L., 1988. Aggregation pheromones inDrosophila borealis andDrosophila littoralis. J. Chem. Ecol. 14, 1319–1327.

Blomquist, G.J., Bagnères, A.-G., 2010. Insect Hydrocarbons: Biology, Biochemistry, and Chemical Ecology. Cambridge University Press.

Buckley, F.G., Buckley, P.A., 1980. Habitat Selection and Marine Birds, in: Behavior of Marine Animals. Springer, Boston, MA, pp. 69–112. https://doi.org/10.1007/978-1-4684-2988-6_3

Desena, M.L., Edman, J.D., Clark, J.M., Symington, S.B., Scott, T.W., 1999. Aedes aegypti (Diptera: Culicidae) Age Determination by Cuticular Hydrocarbon Analysis of Female Legs. J. Med. Entomol. 36, 824–830. https://doi.org/10.1093/jmedent/36.6.824

D'Ettorre, P., Mondy, N., Lenoir, A., Errard, C., 2002. Blending in with the crowd: social parasites integrate into their host colonies using a flexible chemical signature. Proc. R. Soc. Lond. B Biol. Sci. 269, 1911–1918. https://doi.org/10.1098/rspb.2002.2110

D'Ettorre, P., Wenseleers, T., Dawson, J., Hutchinson, S., Boswell, T., Ratnieks, F.L.W., 2006. Wax combs mediate nestmate recognition by guard honeybees. Anim. Behav. 71, 773–779. https://doi.org/10.1016/j.anbehav.2005.05.014

Dietrich, M., Beati, L., Elguero, E., Boulinier, T., McCoy, K.D., 2013. Body size and shape evolution in host races of the tick Ixodes uriae. Biol. J. Linn. Soc. 108, 323–334. https://doi.org/10.1111/j.1095-8312.2012.02021.x

Dietrich, M., Gómez-Díaz, E., McCoy, K.D., 2011. Worldwide Distribution and Diversity of Seabird Ticks: Implications for the Ecology and Epidemiology of Tick-Borne Pathogens. Vector-Borne Zoonotic Dis. 11, 453–470. https://doi.org/10.1089/vbz.2010.0009

Dietrich, M., Lobato, E., Boulinier, T., McCoy, K.D., 2014. An experimental test of host specialization in a ubiquitous polar ectoparasite: a role for adaptation? J. Anim. Ecol. 83, 576–587. https://doi.org/10.1111/1365-2656.12170

Espelie, K.E., Wenzel, J.W., Chang, G., 1990. Surface lipids of social waspPolistes melricus say and its nest and nest pedicel and their relation to nestmate recognition. J. Chem. Ecol. 16, 2229–2241. https://doi.org/10.1007/BF01026933

Estrada-Peña, A., 1993. Climate and cuticular hydrocarbon variation inRhipicephalus sanguineus ticks (Acari: Ixodidae). Parasitol. Res. 79, 512–516. https://doi.org/10.1007/BF00931594

Estrada-Peña, A., CASTELLÁ, J., MOREL, P.C., 1994. Cuticular Hydrocarbon Composition, Phenotypic Variability, and Geographic Relationships in Allopatric Populations of Amblyomma variegatum (Acari: Ixodidae) from Africa and the Caribbean. J. Med. Entomol. 31, 534–544.

Estrada-Peña, A., Estrada-Peña, R., Peiró, J.M., 1992. Differentiation of Rhipicephalus Ticks (Acari: Ixodidae) by Gas Chromatography of Cuticular Hydrocarbons. J. Parasitol. 78, 982. https://doi.org/10.2307/3283217

Estrada-Peña, A., Gray, J.S., Kahl, O., 1996. Variability in cuticular hydrocarbons and phenotypic discrimination of Ixodes ricinus populations (Acarina: Ixodidae) from Europe. Exp. Appl. Acarol. 20, 457–466. https://doi.org/10.1007/BF00053309

Estrada-Peña, A., Guglielmone, A.A., Mangold, A.J., Castellá, J., 1993. Patterns of cuticular hydrocarbon variation and genetic similarity between natural populations of Amblyomma cajennense (Acari: Ixodidae). Acta Trop. 55, 61–78. https://doi.org/10.1016/0001-706X(93)90049-H

Filshie, B.K., 1982. Fine Structure of the Cuticle of Insects and Other Arthropods, in: Insect Ultrastructure. Springer, Boston, MA, pp. 281–312. https://doi.org/10.1007/978-1-4615-7266-4_10

Geiselhardt, S., Otte, T., Hilker, M., 2012. Looking for a similar partner: host plants shape mating preferences of herbivorous insects by altering their contact pheromones. Ecol. Lett. 15, 971–977. https://doi.org/10.1111/j.1461-0248.2012.01816.x

Gibbs, A., Mousseau, T.A., Crowe, J.H., 1991. Genetic and acclimatory variation in biophysical properties of insect cuticle lipids. Proc. Natl. Acad. Sci. 88, 7257–7260. https://doi.org/10.1073/pnas.88.16.7257

Harris, M.P., Wanless, S., 2011. The Puffin. Bloomsbury Publishing.

Hervé, M., 2014. Aide-mémoire de statistique appliquée à la biologie. Constr Son Étude Anal Résultats À Aide Logiciel R Version 5.

Holze, H., Schrader, L., Buellesbach, J., 2021. Advances in deciphering the genetic basis of insect cuticular hydrocarbon biosynthesis and variation. Heredity 126, 219–234. https://doi.org/10.1038/s41437-020-00380-y

Howard, R.W., Blomquist, G.J., 2005. Ecological, Behavioral, and Biochemical Aspects of Insect Hydrocarbons. Annu. Rev. Entomol. 50, 371–393. https://doi.org/10.1146/annurev.ento.50.071803.130359

Howard, R.W., McDaniel, C.A., Blomquist, G.J., 1978. Cuticular hydrocarbons of the eastern subterranean termite,Reticulitermes flavipes (Kollar) (Isoptera: Rhinotermitidae). J. Chem. Ecol. 4, 233–245. https://doi.org/10.1007/BF00988058

Hunt, L.M., 1986. Differentiation between three species of Amblyomma ticks (Acari: Ixodidae) by analysis of cuticular hydrocarbons. Ann. Trop. Med. Parasitol. 80, 245–249.

Ichinose, K., Lenoir, A., 2009. Ontogeny of hydrocarbon profiles in the ant Aphaenogaster senilis and effects of social isolation. C. R. Biol. 332, 697–703. https://doi.org/10.1016/j.crvi.2009.04.002

Jallon, J.-M., David, J.R., 1987. Variation in Cuticular Hydrocarbons Among the Eight Species of the Drosophila melanogaster Subgroup. Evolution 41, 294–302. https://doi.org/10.2307/2409139

KRUGER, E.L., PAPPAS, C.D., HOWARD, R.W., 1991. Cuticular Hydrocarbon Geographic Variation Among Seven North American Populations of Aedes albopictus (Diptera: Culicidae). J. Med. Entomol. 28, 859–864.

Kuo, T.-H., Yew, J.Y., Fedina, T.Y., Dreisewerd, K., Dierick, H.A., Pletcher, S.D., 2012. Aging modulates cuticular hydrocarbons and sexual attractiveness in Drosophila melanogaster. J. Exp. Biol. 215, 814–821. https://doi.org/10.1242/jeb.064980

Le Conte, Y, Huang, Y. Z., Roux, M., Zeng, Z.-J., Christidès, J.-P., Bagnères, A.-G., 2015. Varroa destructor changes its cuticular hydrocarbons to mimic new hosts. Biol. Lett. 11, 20150233. https://doi.org/10.1098/rsbl.2015.0233

Lecuona, R., Riba, G., Cassier, P., Clement, J.L., 1991. Alterations of insect epicuticular hydrocarbons during infection with Beauveria bassiana or B. brongniartii. Journal of Invertebrate Pathology 58, 10–18. https://doi.org/10.1016/0022-2011(91)90156-K

Léger, E., Vourc'h, G., Vial, L., Chevillon, C., McCoy, K.D., 2013. Changing distributions of ticks: causes and consequences. Exp. Appl. Acarol. 59, 219–244. https://doi.org/10.1007/s10493-012-9615-0

Leonovich, S.A., 2004. Phenol and lactone receptors in the distal sensilla of the Haller's organ in Ixodes ricinus ticks and their possible role in host perception. Exp. Appl. Acarol. 32, 89–102. https://doi.org/10.1023/B:APPA.0000018200.24760.78

Liang, D., Silverman, J., 2000. "You are what you eat": Diet modifies cuticular hydrocarbons and nestmate recognition in the Argentine ant, Linepithema humile. Naturwissenschaften 87, 412–416. https://doi.org/10.1007/s001140050752

Lockey, K.H., 1988. Lipids of the insect cuticle: origin, composition and function. Comp. Biochem. Physiol. Part B Comp. Biochem. 89, 595–645.

McCoy, K.D., Boulanger, N. (Eds.), 2015. Tiques et maladies à tiques : biologie, écologie évolutive, épidémiologie, Didactiques. IRD, Marseille.

McCoy, K.D., Boulinier, T., Tirard, C., Michalakis, Y., 2001. Host specificity of a generalist parasite: genetic evidence of sympatric host races in the seabird tick Ixodes uriae. J. Evol. Biol. 14, 395–405. https://doi.org/10.1046/j.1420-9101.2001.00290.x

McCoy, K.D., Chapuis, E., Tirard, C., Boulinier, T., Michalakis, Y., Bohec, C.L., Maho, Y.L., Gauthier-Clerc, M., 2005. Recurrent evolution of host-specialized races in a globally distributed parasite. Proc. R. Soc. B Biol. Sci. 272, 2389–2395. https://doi.org/10.1098/rspb.2005.3230

McCoy, K.D., Léger, E., Dietrich, M., 2013. Host specialization in ticks and transmission of tick-borne diseases: a review. Front. Cell. Infect. Microbiol. 3. https://doi.org/10.3389/fcimb.2013.00057

McCoy, K.D., Tirard, C., 2002. Reproductive Strategies of the Seabird Tick Ixodes uriae (Acari: Ixodidae). J. Parasitol. 88, 813–816. https://doi.org/10.1645/0022-3395(2002)088[0813:RSOTST]2.0.CO;2

McCoy, K.D., Tirard, C., Michalakis, Y., 2003. Spatial genetic structure of the ectoparasite Ixodes uriae within breeding cliffs of its colonial seabird host. Heredity 91, 422–429. https://doi.org/10.1038/sj.hdy.6800339

Nazzi, F., Le Conte, Y., 2016. Ecology of *Varroa destructor*, the Major Ectoparasite of the Western Honey Bee, *Apis mellifera*. Annu. Rev. Entomol. 61, 417–432. https://doi.org/10.1146/annurev-ento-010715-023731

Paulmier, I., Bagnères, A.-G., Afonso, C.M., Dusticier, G., Rivière, G., Clément, J.-L., 1999. Alkenes as a sexual pheromone in the alfalfa leaf-cutter bee Megachile rotundata. J. Chem. Ecol. 25, 471–490.

Peschke, K., Metzler, M., 1987. Cuticular hydrocarbons and female sex pheromones of the rove beetle, Aleochara curtula (Goeze) (Coleoptera:Staphylinidae). Insect Biochem. 17, 167–178. https://doi.org/10.1016/0020-1790(87)90157-0

Randolph, S.E., 1998. Ticks are not Insects: Consequences of Contrasting Vector Biology for Transmission Potential. Parasitol. Today 14, 186–192. https://doi.org/10.1016/S0169-4758(98)01224-1

Randolph, S.E., Storey, K., 1999. Impact of Microclimate on Immature Tick-Rodent Host Interactions (Acari: Ixodidae): Implications for Parasite Transmission. J Med Entomol 36, 741–748. https://doi.org/10.1093/jmedent/36.6.741

Rottler, A.-M., Schulz, S., Ayasse, M., 2013. Wax Lipids Signal Nest Identity in Bumblebee Colonies. J. Chem. Ecol. 39, 67–75. https://doi.org/10.1007/s10886-012-0229-0

Schlamp, K.K., 2005. Contact pheromone components and diel periodicity of sexual communication in peach twig borers, Anarsia lineatella (Lepidoptera: Gelechiidae) (PhD Thesis). Biological Sciences Department-Simon Fraser University.

Schöni, R., Hess, E., Blum, W., Ramstein, K., 1984. The aggregation-attachment pheromone of the tropical bont tick Amblyomma variegatum Fabricius (Acari, Ixodidae): Isolation, identification and action of its components. J. Insect Physiol. 30, 613–618. https://doi.org/10.1016/0022-1910(84)90045-3

Shimshoni, J.A., Erster, O., Rot, A., Cuneah, O., Soback, S., Shkap, V., 2013. Cuticular fatty acid profile analysis of three Rhipicephalus tick species (Acari: Ixodidae). Exp. Appl. Acarol. 61, 481–489. https://doi.org/10.1007/s10493-013-9713-7

Simmons, L.W., Thomas, M.L., Gray, B., Zuk, M., 2014. Replicated evolutionary divergence in the cuticular hydrocarbon profile of male crickets associated with the loss of song in the Hawaiian archipelago. J. Evol. Biol. n/a-n/a. https://doi.org/10.1111/jeb.12478

Singer, T.L., Espelie, K.E., 1996. Nest surface hydrocarbons facilitate nestmate recognition for the social wasp,Polistes metricus Say (Hymenoptera: Vespidae). J. Insect Behav. 9, 857–870. https://doi.org/10.1007/BF02208974

Sonenshine, D.E., 2004. Pheromones and other semiochemicals of ticks and their use in tick control. Parasitology 129, S405–S425. https://doi.org/10.1017/S003118200400486X

Sonenshine, D.E., Roe, R.M. (Eds.), 2014. Biology of ticks, 2nd ed. ed. Oxford University Press, New York.

Sonenshine, D.E., Silverstein, R.M., Brossut, R., Davis, E.E., Taylor, D., Carson, K.A., Homsher, P.J., Wang, V.B., 1985. Genital sex pheromones of ixodid ticks: 1. Evidence of occurrence in anterior reproductive tract of American dog tick,Dermacentor variabilis (Say) (Acari: Ixodidae). J Chem Ecol 11, 1669–1694. https://doi.org/10.1007/BF01012120

Tkachev, A.V., Dobrotvorsky, A.K., Vjalkov, A.I., Morozov, S.V., 2000. Chemical composition of lipophylic compounds from the body surface of unfed adult Ixodes persulcatus ticks (Acari: Ixodidae). Exp. Appl. Acarol. 24, 145–158. https://doi.org/10.1023/A:1006430323587

Uebel, E.C., Schwarz, M., Sonnet, P.E., Miller, R.W., Menzer, R.E., 1978. Evaluation of the mating stimulant pheromones of Fannia canicularis, F. pusio, and F. femoralis as attractants. Fla. Entomol. 139–143.

Uebel, E.C., Sonnet, P.E., Bierl, B.A., Miller, R.W., 1975. Sex pheromone of the stable flyl: Isolation and preliminary identification of compounds that induce mating strike behavior. J. Chem. Ecol. 1, 377–385.

van Zweden, J.S., d'Ettorre, P., 2010. Nestmate recognition in social insects and the role of hydrocarbons. Insect Hydrocarb. Biol. Biochem. Chem. Ecol. 11, 222–243.

Wyatt, T.D., 2010. Pheromones and signature mixtures: defining species-wide signals and variable cues for identity in both invertebrates and vertebrates. J. Comp. Physiol. A 196, 685–700. https://doi.org/10.1007/s00359-010-0564-y

Yoder, J.A., Domingus, J.L., 2003. Identification of hydrocarbons that protect ticks (Acari: Ixodidae) against fire ants (Hymenoptera: Formicidae), but not lizards (Squamata: Polychrotidae), in an allomonal defense secretion. International Journal of Acarology 29, 87–91. https://doi.org/10.1080/01647950308684326