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ORIGINAL ARTICLE

Impacts of ionization radiation on the cuticular hydrocarbon profile and mating success of male house crickets (*Acheta domesticus*)

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ABSTRACT

Purpose: Ionizing radiation is well known to have drastic impacts on major life history features including survivorship, growth, fertility, and longevity. What is much less appreciated is how radiation stress can cause changes to more subtle traits, such as those associated with sexual signaling, an underappreciated but vital aspect of insect reproduction. In the House Cricket (*Acheta domesticus)* cuticular hydrocarbons are vital for sex and species recognition, as well as a possible indicator of stress, making them crucial for successful mating and reproduction.

Materials and methods: Here, we analyze the impacts of ionizing radiation on the cuticular hydrocarbons of male crickets and its subsequent impacts on mating success. We exposed juvenile (14-day, 4th instar) male crickets to a broad range of radiation doses (2 Gy − 2 Gy).

Results: We detected significant changes in individual cuticular hydrocarbons across a broad range of doses in mature male crickets using gas-liquid chromatography. Specifically, dose was identified as a significant contributing factor to hydrocarbon increases $p < .0001$. Mating success was significantly reduced in 12 Gy ($p < .0001$), 10 Gy (0.0001), and 7 Gy (0.0060) groups compared to non-irradiated controls.

Conclusion: Insect chemical communication can be species specific, and functionally specialized. Here, we show that radiation can alter the chemical signals used to attract mates in a large bodied insect and this may be a contributing factor to the described reduction in male mating success. Further research should be conducted to further analyze the various modes of communication employed by male crickets to attract mates i.e. acoustic signaling, and how this may also contribute to the reduction in mating success seen in irradiated males.

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Cuticle; volatile hydrocarbons; Crickets; reproduction; mating behavior; ionizing radiation

IntroductionRadiation can inflict damage through the direct ionization of biological molecules, including DNA, or indirectly through excess free radical production associated with the ionization of cellular water (Einor et al. 2016). A large amount of research has been conducted on radiation impacts to insect reproduction as it pertains to sterilization. This knowledge is largely associated with the use of the sterile insect technique (SIT), a method which uses radiation to sterilize males and reduce insect populations (Dyck et al. 2005). However, much less research has focused on the more subtle radiation impacts such as to sexual signaling, which may have a large effect on mating success and reproduction as a whole (Dyck et al. 2005).

In *Acheta*, copulation requires females to mount males to accept spermatophores (Balakrishnan and Pollack 1997). Thus, males cannot coerce females into copulation, making their ability to elicit mounting through sexual signaling vital (Balakrishnan and Pollack 1997). In most insects, species-specific chemical communication is highly developed (Botha et al. 2017). For *A. domesticus* and many other insects, key male chemical signals include cuticular hydrocarbons (Tregenza and Wedell 1997; Thomas and Simmons 2010; Pavković-Lučić et al. 2012; Botha et al. 2017). Hydrocarbons and to a lesser extent lipids are the predominant components of insect cuticular extracts and have been documented in over 100 species (Assis et al. 2017). Hydrocarbon compounds however, unlike lipids are (Tregenza and Wedell 1997). These compounds are synthesized in the epidermal cells associated with the cuticle and have been shown to have a sex specific hydrocarbon profile in *Acheta* (Warthen and Uebel 1980; Assis et al. 2017). Other then playing a role in sex and species recognition, stress induced alterations to male sexual traits may be employed by females to detect males of lower fitness. Indeed, females can avoid 'damaged' males in a variety of species, including flies, spiders, rats, deer, and birds if one or more secondary sexual characteristics are altered (Kotiaho et al. 1996; Kavaliers et al. 2004; Mays and Hill 2004; Surinov 2007; Velando et al. 2008).

Understanding the impacts of radiation stress on cuticular hydrocarbon profiles is of relevance to the economically important sterile insect technique (SIT). The SIT refers to the release of radiation sterilized males into the breeding population, resulting in a reduction of female fertility and thus the target population as a whole (Dyck et al. 2005). However, the SIT functions under the paradigm that males are exposed to doses of radiation that sterilize them but

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allow them to remain competitive amongst their non-irradiated counterparts (Dyck et al. 2005). As female insects have been shown to have preference for a particular cuticular profile in males, any subtle changes to the profile can result in devastating impacts on male competitiveness (Peschke 1987; Kortet and Hedrick 2005; Thomas and Simmons, 2009). Several studies have indicated that other stressors such as dietary condition can alter the cuticle profile and alter conspecific responses (Henneken et al. 2017). Other studies have shown stress responses to the cuticular profile alterations are stress specific. A study conducted by Engl et al. (2018) described alterations to male Tsetse fly cuticular hydrocarbon profiles when exposed to antibiotic treatment but not to ionizing radiation (Engl et al. 2018).

Here we aimed to analyze the impact of ionizing radiation on the cuticular hydrocarbon profile of our model, the House Cricket *(Acheta domesticus)*. Furthermore, we aimed to assess the impact of ionizing radiation on mating success on irradiated male crickets paired with normal females.

Methods

Breeding colony

Acheta domesticus were generated in a large breeding colony housed in an acrylic terrarium (93 × 64.2 × 46.6 cm), insulated with 1.5 cm thick Durofoam insulation. Fans provided air circulation. The colony was maintained at 29° ± 2° C on a 12 h day-12h night photoperiod. Food consisted of *ad libitum* chick feed (Country Range MultiFowl Grower®, 17% protein) and *ad libitum* distilled water (soaked cellulose sponges) replaced daily. Crickets were provided with egg-carton shelters, and paper towels sprayed daily with distilled water and replaced weekly. The colony was provided with oviposition medium (Vigoro Organic Garden Soil®) in small plastic containers (7 × 7 × 7 cm). These were collected after 24 h and incubated at 29° ± 2° C until hatching, providing cohorts of nymphs of known age.

Experimental groups

Experimental animals were generated from the breeding colony by leaving an oviposition container filled with Vigoro Organic Garden Soil®. To ensure experimental animals were of the same age, the oviposition container was removed from the breeding colony after 24 h and incubated at 29° ± 2° C . After individuals hatched from the oviposition containers (after 14 days), approximately 1000 nymphs were separated after 24 h of hatching, to again ensure the same aged individuals were used. Experimental individuals were housed in the same conditions as the breeding colony. At 14 days of age (4th instar nymphs), approximately 600 individuals (100 per group) were randomly selected, separated, and irradiated for specific durations using a Cs-137 source at a dose rate of 0.25 Gy/min totaling (0 Gy, 2 Gy, 4 Gy 7 Gy, 10 Gy, 12 Gy) at the Taylor Radiobiology Source at McMaster University. A maximum dose of 12 Gy was chosen as previous work has shown sterilization to occur around this dose. All individuals from each experimental group were irradiated during a single exposure. 100 individuals were chosen to ensure enough individuals survived to maturity for later analysis. All groups were then immediately brought to McMaster's Life Sciences Building (LSB) where they were maintained for life. Adult males are known to fight other males for access to females, often causing bodily damage, so at approximately 30 days of age, before maturation, females were removed from all experimental groups. Prior to this males and females are not distinguishable, therefore it was not until later life stages, when females develop an ovipositor, that females were removed. All experimental individuals used for cuticular hydrocarbon analysis were males.

Cuticular hydrocarbon isolation

Cuticular hydrocarbons were collected from randomly selected unmated/virgin male crickets from each experimental group 0 Gy ($n = 6$), 2 Gy ($n = 6$), 4 Gy ($n = 5$), 7 Gy ($n = 5$), 10 Gy ($n = 6$), and 12 Gy ($n = 6$). Individuals one-week post-maturation (50 days of age) were removed and immobilized with CO_2. They were then weighed and swirled in hexane (dissolving the cuticular hydrocarbons) for 5 min at a concentration of 5 ml per 0.5 g of cricket mass (to control for cricket size) in a sterilized glass container. After 5 min in hexane, crickets were removed and disposed of. Glass containers with the collected hexane and cuticular hydrocarbons were then sealed with an airtight lid and wrapped in elastic tape to ensure no outside contamination. Samples were stored at 4 °C until processing.

Cuticular hydrocarbon analysis

Samples were analyzed at McMaster's regional center for mass spectrometry. Samples were first vortexed and then evaporated using nitrogen gas to remove the hexane solvent. Once evaporated, samples were reconstituted in 40ul of pure hexane and 10ul of internal standard (Napthalene-d8), making each sample volume a total of 50ul. Samples were then processed using an Agilent 5973/6890 for gas chromatography and mass spectrometry analysis. Output was analyzed with Bruker Compass DataAnalysis 4.0.®. Significant peaks were identified using the DataAnalysis program and the area/concentration under each peak was recorded. Each significant peak was shown to have a very similar 'staircase' like mass/charge pattern, indicating its hydrocarbon composition. Peaks which were not identified as hydrocarbons were excluded from analysis. The average intensity of each peak in the control group was then compared to average intensity in each irradiated group.

Mating success

At midlife, approximately 56–67 days post-hatching, experimental adult males from each group Control ($n = 55$), 2 Gy ($n = 60$), 4 Gy ($n = 59$), 7 Gy ($n = 53$), 10 Gy ($n = 30$), 12 Gy ($n = 43$) were individually paired with a non irradiated

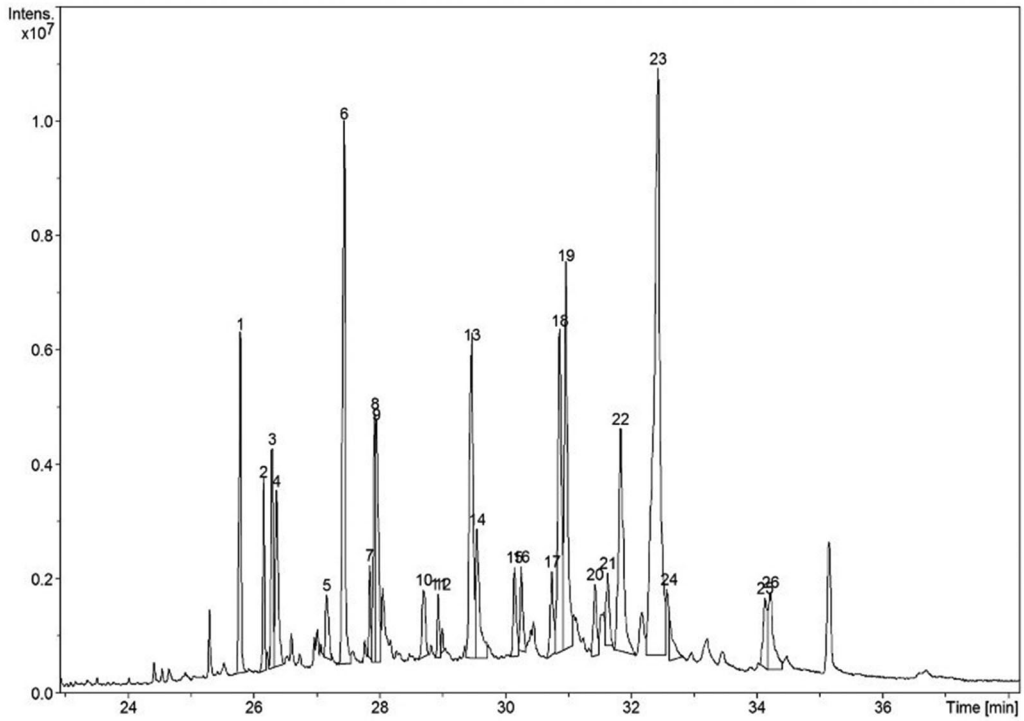

Figure 1. A typical total ion chromatogram of a control male *Acheta domesticus* extracted using a hexane solvent at 1 week post maturation (~ 50 days). All individuals were immobilized with CO_2 and swirled in hexane for 5 min at a concentration of 5 ml per 0.5 g of cricket mass. Samples were analyzed at McMaster's regional center for mass spectrometry using an Agilent 5973/6890 gas chromatography instrument and Bruker Compass DataAnalysis 4.0.® software for analysis. All 26 hydrocarbon peaks anaylzed are labeled. Each peak corresponds to a specific hydrocarbon compound.

Table 1. Two-way ANOVA results representing the relative impact of error, dose, and peak on Acheta domesticus cuticular hydrocarbon analysis.

	SS	DF	MS	F (DFn, DFd)	*p* Value
Interaction	2.405e + 016	125	1.924e + 014	F (125, 728) = 1.552	$p = .003$
Peak	4.238e + 017	25	1.924e + 014	F (25, 728) = 136.8	$p < .0001$
Dose	5.053e + 015	5	1.011e + 015	F (5, 728) = 8.153	$p < .0001$
Residual	9.024e + 016	728	1.240e + 014		

female for a 15 min period to assess mating succes. During this period each pair had access to food and distilled water. Mating was considered successful if females mounted a male for more then 5 s. This period was chosen as males occasionally force themselves underneath females, in which females, if rejecting the male will jump off. All males were given a second 15 min trial with a new female to ensure that female inability to mate was not the cause of a failed mating trial.

Statistics

A two-way ANOVA followed by a Dunnett's multiple comparisons test was employed to determine significant differences in the average intensity of individual peaks in each irradiated group compared to the control group. The impact of dose on sample variation was also analyzed. For mating success significant differences were analyzed using a one-way ANOVA followed by a Dunnett's multiple comparisons test to distinguish differences between groups compared to controls. All statistical analyses were carried out using Prism Graph Pad 8.

Results

Cuticular hydrocarbons

The typical ion chromatogram for control male crickets revealed 26 significant peaks/hydrocarbons used for our analysis (Figure 1). Results of the two-way ANOVA indicated significant contributions of dose on total variance ($F_{(5,728)} = 8.153$, $p < .0001$). Results of the two-way ANOVA are summarized in Table 1. A Dunnett's multiple comparisons test indicated significant differences in peak 22; 2 Gy ($p = .0014$), 4 Gy ($p = .008$), 7 Gy ($p < .0001$), 12 Gy ($p = .0124$) and peak 23; 2 Gy ($p < .0001$), 4 Gy ($p < .0001$), 7 Gy ($p < .0001$), 10 Gy ($p = .0303$) and 12 Gy ($p < .0001$) compared to controls (Figure 2). Increased concentrations of hydrocarbons, although not significant, were evident in most irradiated groups. Specifically, doses between 2-12Gy showed increased concentration compared to controls in 16 of the peaks

analyzed. Percent differences between controls and all irradiated groups are summarized in Table 2. Likely hydrocarbon candidates for each identified peak are summarized in Table 3.

Mating success

Male mating success were recorded as successful when females mounted the male for more then 5 s. A observable linear decline in mating success with increase dose was observed (Figure 3). A one-way ANOVA indicated significant differences between groups ($F_{(5,294)} = 2.386$, $p < .0001$). A Dunnett's multiple comparisons test indicated significant differences in mating success in 12 Gy ($p < .0001$), 10 Gy (0.0001), and 7 Gy (0.0060) groups compared to non-irradiated controls.

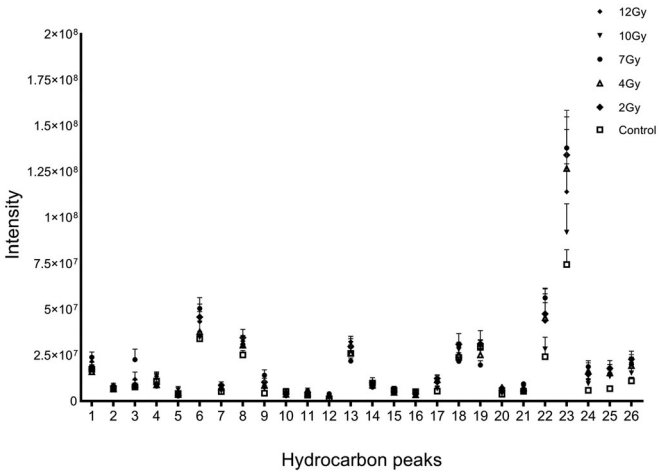

Figure 2. Dose-response effects of early life radiation on cuticular hydrocarbons, specifically the effect on each of the 26 significant hydrocarbon peaks identified using gas-liquid chromatography. All individuals were irradiated at 14 days of age at 0.25 Gy/min with hydrocarbon extraction occurring 1-week post maturation. Values are shown as the mean area under each peak/concentration at each dose +/− SEM; 0 Gy ($n = 6$), 2 Gy ($n = 6$), 4 Gy ($n = 5$), 7 Gy ($n = 5$), 10 Gy ($n = 6$), and 12 Gy ($n = 6$). Significant impacts were identified for peak 22; 2 Gy ($p = .0014$), 4 Gy ($p = .0080$), 7 Gy ($p < .0001$), and 12 Gy ($p = .0124$) and peak 23; 2 Gy ($p < .0001$), 4 Gy ($p < .0001$), 7 Gy ($p < .0001$), 10 Gy ($p = .0303$) and 12 Gy ($p < .0001$) compared to control values. All significant differences were analyzed compared to control values using a 2-way ANOVA followed by Dunnett's multiple comparison test. Mass of the cricket was control for when extracting hydrocarbons.

Discussion

The importance of male cuticular hydrocarbons in insect sex and species recognition, as well as mating behavior has been well studied in literature. von Hörmann-Heck (2010) was one of the first researchers to show that male crickets required contact with the female cuticle to differentiate between sexes. Later, Tregenza and Wedell (1997) showing that without these female chemical's males would not display mating behavior. Further studies using *Acheta domesticus* showed that males touched with the antenna of another male will display aggressive behavior but when touched with a female antenna would produce mating behavior i.e. courtship songs (Tregenza and Wedell 1997). Further studies have indicated that males touched with specifically the cuticle extract from a male cricket they showed aggressive and avoidance behavior and with female extract showed mating behavior (Iwasaki and Katagiri 2008). In regard to mating, there are several studies, many in cockroaches, which indicate that chemical signals allow females to detect aspects of male fitness, including male dominance, immunocompetence, status, and genetic relatability (Moore et al. 1995; Moore et al. 1997; Rantala and Kortet 2003; Thomas and Simmons 2009; Thomas and Simmons 2011).

In our study, we focused on chemo-signaling, as they are vital to communication in the vast majority of species

Table 2. Summary of GC results for cuticular hydrocarbon peaks. Concentration for Control males, calculated as area under each peak, with % change from control (2-12Gy).

Peak #	Control (Peak Area)	2Gy	4Gy	7Gy	10Gy	12Gy
1	17409157.5	0.21	−7.96	37.51	7.63	24.24
2	6698274.5	24.37	−1.91	13.50	−8.75	8.32
3	7716919	5.08	14.91	193.25	13.69	55.18
4	10946526.3	−16.14	−18.96	−24.92	24.63	23.59
5	4219188.33	−20.69	−15.71	−32.85	46.81	18.07
6	34076790.7	34.64	10.91	48.39	1.75	27.14
7	5214956	66.70	45.23	61.29	4.23	48.56
8	25207099.5	37.57	20.89	22.47	18.48	29.99
9	4336674.5	138.65	97.12	225.87	59.36	100.78
10	5276627.67	−29.75	−29.07	−42.84	9.56	−5.33
11	3303594.17	47.67	27.77	69.15	11.53	53.69
12	1298574.67	98.53	129.77	212.14	38.94	119.50
13	26059292.2	14.32	0.27	−15.97	20.48	24.23
14	9826848.33	4.31	−12.39	−22.15	0.23	−4.09
15	5900219.17	−13.12	−18.49	−25.03	14.43	15.18
16	5189231	−20.47	−33.20	−38.82	−0.41	−24.72
17	5501772.33	125.30	111.63	93.97	22.21	79.37
18	23853652.5	30.01	6.23	−8.85	17.67	25.76
19	29395787.7	6.47	−14.30	−32.85	0.74	−3.77
20	3789247.33	87.39	96.08	75.38	6.63	68.59
21	5358352.83	2.22	34.43	76.41	36.71	34.30
22	24211545.2	96.79**	87.53*	132.81****	17.17	79.84*
23	74548407.7	79.90****	69.97****	85.05****	23.33*	53.06****
24	5917652.17	149.49	175.96	218.35	61.62	99.56
25	6846318	161.47	124.19	118.86	95.44	163.73
26	11032329.3	107.51	75.631	81.94	39.25	92.05

Table 3. Summary of GC/MS results for male cuticle profile with likely compound candidates using a pooled sample including individuals from 0–12Gy.

Peak #	RT (min)	Hydrocarbon	Compound	Match	Mol. Weight	Branched
1	25.857	$C_{34:0}$	Hexacosane, 9-octyl	855	478	Y
2	26.217	$C_{29:0}$	Nonacosane	922	408	N
3	26.355	$C_{29:1}$	Z-14-Nonacosane	852	406	N
4	26.427	$C_{30:0}$	11-Methylnonacosane	855	422	Y
5	27.213		Unresolved			
6	27.55	$C_{36:o}$	Hexatriacontane	855	506	N
7	28.00	$C_{35:1}$	Tetratriacontane	745	490	N
8	28.03	$C_{34:0}$	13-Methylnonacosane	747	478	Y
9	28.13		Unresolved			
10	28.77	$C_{36:0}$	Hexatriacontane	811	506	N
11	29.01	$C_{34:0}$	Tetratriacontane	710	478	N
12	29.06	$C_{35:1}$	17-Pentatriacontene	626	490	N
13	29.55	$C_{39:0}$	11,15-Dimethylheptatriacontane	722	548	Y
14	29.62	$C_{43:0}$	Tritetracontane	734	604	N
15	30.21	$C_{40:0}$	Tetracontane	792	562	N
16	30.32	$C_{44:0}$	Tetratetracontane	685	618	N
17	30.8	$C_{35:1}$	17-Pentatriacontene	833	490	N
18	30.94	$C_{40:0}$	Tetracontane	768	562	N
19	31.05	$C_{37:0}$	15,19-Dimethylpentatriacontane	857	520	Y
20	31.49	$C_{35:1}$	17-Pentatriacontene	755	490	N
21	31.68	$C_{38:2}$	1,37-Octatriacontadiene	693	530	N
22	31.97	$C_{35:1}$	17-Pentatriacontene	821	490	N
23	32.61	$C_{38:2}$	1,37-Octatriacontadiene	736	530	N
24	32.74		Unresolved			
25	34.36	$C_{38:2}$	1,37-Octatriacontadiene	760	530	N
26	34.45	$C_{38:2}$	1,37-Octatriacontadiene	660	530	N

Potential candidates were identified using NIST library. Match probability, and compound characteristics are shown.
$C_{n:x}$ where n is the number of carbons and x is the number of double bonds.

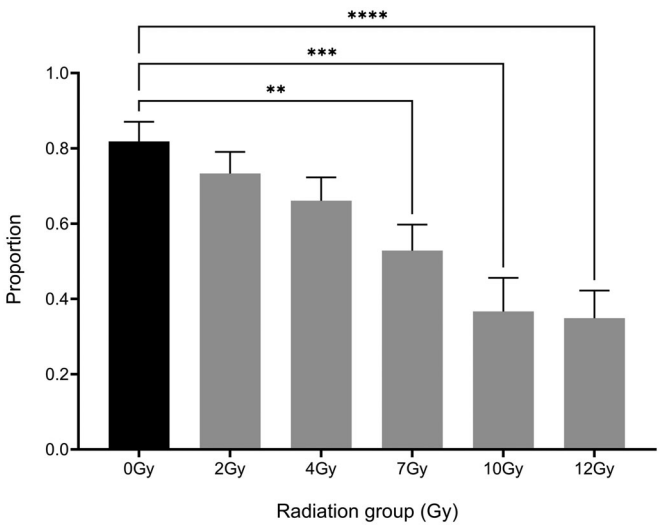

Figure 3. Effects of early life radiation on male *Acheta domesticus* mating success. Males were irradiated at 14 days of age (0–12Gy) at a dose rate of 0.25 Gy/min and paired with normal unirradiated females 2–3 weeks post maturation. Success was indicated as female mounting of males. A one-way ANOVA indicated significant differences between groups ($F_{(5,294)} = 2.386$, $p < .0001$). A Dunnett's multiple comparisons test indicated significant differences in mating success in 12 Gy ($p < .0001$), 10 Gy (0.0001), and 7 Gy (0.0060) groups compared to non-irradiated controls.

(Lockey 1985; Johansson and Jones 2007). The production and radiation alterations of cuticular hydrocarbons were analyzed in both irradiated and control male crickets. Previous studies using cricket species found that volatile hydrocarbon pheromones were distinct between sex's and among species (Warthen and Uebel 1980). Results indicated a species-specific signature associated with male cuticular hydrocarbons. Both irradiated and control *Acheta* males showed identical 26 hydrocarbon peaks in their chromatogram (Figure 1). Although the same 26 peaks were present in all groups and that male size was controlled for, chromatograph 'intensity', which refers to concentration in the sample, was altered between control and irradiated males. Two of the larger peaks (22 and 23), were significantly altered in intensity in almost all males exposed to radiation doses spanning 2-12Gy (Figure 2). In these two peaks intensity was significantly increased, in some cases almost doubling in concentration compared to controls. Furthermore, all irradiated groups tended toward increased concentration in all irradiated groups for many hydrocarbons (16 of 26 peaks) (Table 2).

Our results also indicated an observation dose-dependent decline in mating success as dose increased. Significant differences were evident in the 12 Gy ($p < .0001$), 10 Gy (0.0001), and 7 Gy (0.0060) groups compared to non-irradiated controls. Although this decline may not be entirely due to the cuticular hydrocarbon alterations, we postulate that hydrocarbon alterations are likely a contributing factor. This is due to the plethora of literature on how vital male cuticular profiles are to mating success and recognition. However, we acknowledge that male *Acheta domesticus* produce multiple signal modalities to attract and mate females (including acoustics), it is possible that signals interact or synergize (Wagner and Reiser 2000).

Our results also indicate the importance of further research focusing on the impacts of radiation stress on the sexual signals of insects, particularly in relation to the SIT and in environmental contamination zones. The objective of the SIT is to release sterilized males to compete for mates with normal males resulting in a reduction of the insect populations (Dyck et al. 2005). Understanding

radiation impacts to sexual signals is therefore vital as if males are sterilized but are unable to attract mates the desired outcome of the SIT will be diminished. As well, in areas of contamination sites such as Chernobyl, Fukushima, and waste sites associated with the normal operating procedures of nuclear reactors, determining the impacts to species communication is essential (Imanaka et al. 2015).

Further research should focus more on understanding the subtle impacts of radiation exposure such as to chemical cues but also other modes in which organisms communicate. As well, future experiments to test the specific influence of hydrocarbon alterations, whether the changes to specific peaks correspond to mating success or whether the entire signature is required would be most interesting. As well, the influence of chemical signaling irrespective of other sexual signals would also be intriguing.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

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Notes on contributors

Tamara Fuciarelli is a current PhD candidate at McMaster University, Canada. She focuses on radiation impacts on the reproduction with a focus on generational effects using the House Cricket model. Having completed her M.Sc in 2019 she aims to further the field in radiobiology as it pertains to ecological impacts.

Dr. David Rollo is an environmental physiologist employed at McMaster University, Canada. He is a well known researcher in the study of stress and aging and has published several landmark studies on the subject. His current research focses on the integration and functions of behavior, morphology and physiology in response to environmental stress. He examines adjustments of the above features using ionizing radiation as a precise stressor using a cricket model. A short-lived animal allows for the study of lifetime and trans-generational impacts on life history features, behavior, physiology, and aging. For reproduction, he focuses on sexual signaling (chemical and acoustic) and mating behavior. Trans-generational studies of irradiation focus on life history traits, transmission of stress resistance, fertility, and social recognition. Key aspects of current interest include feeding and thermal choices, cognition, reproduction, growth, immunology, avoidance of death cues, aging and longevity.

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