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Original article

Reproductive traits and mandibular gland pheromone of anarchistic honey bee workers *Apis mellifera* occurring in China

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Abstract – I h e bee c l ie , ke i a ic la f "a a chi ic" li eage, ca ac i a e hei a ie a d la egg , e e i he e e ce f he ee . We ide ified h ee ee igh c l ie h i g ical ig f ke e d c i . T cha ac e i e hi e li eage, e e ac ed he a dib la gla d a d a al ed i i g ga ch a g a h . The al a f he fi e ai c e f he a dib la gla d, a el e h l - h d be a e (HOB), 9- -2(E)-dece ic acid (9-ODA), (S)-9-h d -(E)-2-dece ic acid (9-HDA), 10-HDA, a d 10-h d de-ca ic acid (10-HDAA) e e ig ifica l highe i he a dib la gla d file f ke i h ac i a ed a ie (AW , 8.88 1.71 μg) c a ed ke i h i ac i a ed a ie (IAW , 4.00 2.09 μg). F he e, he che ical file f IAW e e d i a ed b he " ke b a ce" 10-HDA (34.64 8.19 %) a d i ec 10-HDAA (22.88 4.95 %), hile he che ical file i AW e e d i a ed b he ec f he ee b a ce 9-HDA (40.04 7.55 %). The a i f ec b a ce 10-HDAA/9-HDA f IAW e e e ke like (>1.0) he ea AW e e e ee like (≤1.0). The e e l gge ha he a dib la he e f a a chi ic ke e ble a e ee -like e d c i e ac i e file a d ha he e ke a e e a e e i a e ba al e d c i e h e.

Apis mellifera / anarchistic colony / ovary activation / egg production / worker policing / worker mandibular gland pheromone

1. INTRODUCTION

Like a e cial i ec , he h e bee A m L. i cha ac e i ed b e e e e d c-i e di i i f lab be ee he ee a d ke (Miche e 1974). U de al c di-i , he ee i all he le fe ale e -d c i e ac i e i di id al i a c l , hile ke efai f e d ci g de i e ha i g f c i al a ie a d i g ge e al, ca la l ha l id ale egg (a he k) (Wi 1987; He b a d Radl ff 1998; H e e al. 2003; Sle e al. 2005). I ild- e c l ie f E - ea b ecie , a i a el 0.01 % f ke la 7 % f all ale egg , f hich l e egg i 1000 i ea ed a d he he a e e-ed b he ke ; he -called ke

Electronic supplementary material The li e e i f hi a icle (d i:10.1007/s13592-015-0396-4) c ai le e a a e ial, hich i a ailable a h i ed e .

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Ma c i edi : Da id Ta

lici g (Ra iek 1993; Vi che 1996). H e -
e , effec i e ke lici g i e e i a a e
ai f *Am* “a a chi ic” c l ie , i
hich a la ge be f ke -laid egg a e

beca e 9-ODA ha i d ced i eg la c l ie b a f c i al ee ha bee h i hibi a ac i a i a d e he d c i f a ee -like he e ig al i he ke (C e e 1988; M i e al. 2000, 2004, 2008; Die e a e al. 2007). Th he a i f 9-ODA/(9-ODA + 9-HDA + 10-HDA + 10-HDAA) a d 10-HDAA/9-HDA ha e bee ed a g i dica f i di id al fec di (Ple e e al. 1993; M i e al. 2004; H e e al. 2005a; Sch fe e al. 2006).

A a chi a a ecial ca e f ke e d c i ide a e e i al e ce f i e iga i g he i a e echa i de l i g he ke e d c i i ild- e c l ie. H e e a a ch i a c le d e, hich i i fl e ced b he e ke lici g, ee a d ke ge e ic c e , a d he fac . The ai i f e ea ch f he a a chi ic ai i ba ed he elec i el b ed li e ai ai ed b he U i e i f S d e , hich eliabl h highe le el f a a chi ic he e (Old d e al. 1999; Old d a d O b e 1999). I 2012, e fi a d e egg a d la ae a ea ed ab e he ee e cl de i e e al ee igh Am L. c l ie i Sha i i ce, Chi a. I de c fi hei a a chi ic ai e i e iga ed he f ll i g: (1) he e ce age f ke i h age 4–5 ac i a ed a ie (He 1942; Pi k e al. 2010) (2) a d if ke -laid egg a e able e ca e ke lic i g. I de f he de a d he le f he ke a dib la gla d ec e i i he ac i i i f e d c i e a a d i he i a e echa i de l i g he a a chi ic d e, (3) e i e iga ed he c i i f a dib la gla d file f ke i h i ac i a ed a ie (IAW) a d ke i h ac i a ed a ie (AW) a led i h ee c l ie i h ical a a chi ic ai a d de e i ed if AW d ce ee -like b a ce i hei a dib la gla d ec e i .

2. MATERIALS AND METHODS

Egg a d la ae e e f d ab e he ee e cl d e i e ee igh Am L. c l ie i he a ia f Sha i i ce, Chi a, f hich h ee e e ed Ha g h a d he U i e i ' a ia . All f he e e ec ed f bei g "a a chi ic" c l ie . F he e, h ee c l ie h i g a fea e f a a chi ic ac i i ie e e ed a di c i i a c l ie .

2.1. Experiment 1. Ovary activation analysis

H e bee abd e e e di ec ed acc di g Dade (1977) a d a ig ed a bei g i ac i a ed (a ie h ead-like a d lacki g defi ed a, age 1–3) f ll ac i a ed (clea l defi ed a, age 4, a lea e egg e e i a i le , age 5) (He 1942; Pi k e al. 2010). Si ke e a a chi ic c l (=3) e e b ai ed f d e c b ab e he ee e cl de , a d he ced e a e lica ed i 3-da i e al f f i e i J e 2012, e l i g i 720 ke bei g di ec ed a d c ed.

2.2. Experiment 2. Egg-laying behavior analysis

Each a a chi ic c l (=3) a li i hal e (ee igh half: he a ea bel ee e cl de , a d ee -e cl ded half: he a ea ab e ee e cl d e) i g a ee e cl de , hich all a age f eel f ke b f he ee . I de ea e he e d c i e f he ee a d ke i e f d e egg d ced i hi c l ie , e d e c b a i each half. Af e 8 h, d e c b e e e ed f he c l ie a d he egg i each half e e c ed.

T c a e he be f ke -laid egg be ee he hal e a d e al a e he ial c ib i f ke he egg laid i he ee igh half, e laced e d e c b each i a la ic ee e cl de b e ab e a d bel he ee e cl de . Agai , he be f ke -laid egg a c ed i each half af e 8 h, a d hi a e lica ed h ee f i e i hi 1 eek. A al i f a i ical diffe e ce f he egg d c i be ee ee igh half a d ee -e cl ded half a e f ed i g S de ' e . Da a a e e e ed a ea a d a da d de ia i .

2.3. Experiment 3. Worker policing analysis

2.3.1. Sources of eggs

Th ee ild- e ee igh c l ie (WT1, WT2, WT3) a e he ce f ild- e ee -laid egg (WTQE), h ee ild- e ee -le c l ie (WTL1, WTL2, WTL3) a he ce f ild- e ke-laid egg (WTWE), h ee a a chi ic e igh c l ie (AC1, AC2, AC3) a he ce f a a chi ic e -laid egg (ACQE), a d a a chi ic ke-laid egg (ACWE). The e c l ie (=9) e e di ided i h ee g ; he fi g WT1, WTL1, AC1; he ec d g WT2, WTL2, AC2; a d he hi d g WT3, WTL3, AC3. Each g ided f diffe e e f egg , i cl di g WTQE, WTWE, ACQE, a d ACWE.

2.3.2. Discriminator colonies

T a a he e al a e f egg f ai ce , e ed h ee ild- e c l ie (WT1, WT2, WT3) a d h ee a a chi ic c l ie (AC1, AC2, AC3) a di c i i a c l ie . Each hi e a e a a ed i a b a ee e cl de , i hich he ee a c fi ed he b , ieldi g ee -e cl ded a ea ab e he ee e cl de a d ee igh a ea bel .

2.3.3. Egg removal bioassays

T e f he a a , e a fe ed 20 egg f each ce f egg ; he f diffe e ce (WTQE, WTWE, ACQE a d ACWE) i d e cell f he a e e c b ha ha bee lef e igh i hei c e di g di c i i a c l ie . All f he e e egg e e c llec ed f hei igi al d e cell b i g e i ed h ick. A e h ick a ed f each . Af e a fe i g, he e c b i h 80 egg a a d iched be ee b d c b ha e i l laced i he ce e f he e cha be f each di c i i a c l (Pi k e al. 2002). Egg e e i d ced i hei c l f igi a id a i e-fe e ce f e a e ec g i i (Pi k e al. 2007). D e c b i h f e f egg e e laced i he di c i i a c l ie e i g ha c b a d egg e e igi a i g f he c l ie ha he di c i i-a c l ie . The be f e ai i g egg a c ed 1, 2, 4, a d 6 h af e i d c i , a d i a e ea ed f i e e a a e da .

2.3.4. Statistical analysis

S i al da a f (WTQE, WTWE, ACQE, a d ACWE) e e a alz ed i g a C eg e i i al a al i (C lle 1994) a i le e ed i SPSS. F hi a al i , egg e ed a 1, 2, 4, 6 h e e c le e da a i he ea e ai i g egg af e 6 h e e ea ed a ce ed da a. Egg ce, da , a d di c i i a e e ed a a iable i he C eg e - i i al del, a d e ed i calc la e he likelih d a i f he i al a e f he diffe e egg ce af e addi g he fac f da a d di c i - i a . The i al f c i a deled i h ("N ll") a d h i h (e all) ce f egg , da , a d di c i i a c l (e all) a fac , a d he i e e f he abili f he del de c ibe he da a e ed i h a χ^2 e . The del h e ed he effec f addi g ce f egg , da , di c i i a a fac . La l , e e e ed a ai i e c ai be ee he i al egg f f diffe e ce . We e e ed he da a g a hicall a he ea - i (a da d de ia i) f egg e ai i g a each i e e i d.

2.4. Experiment 4. Workers' mandibular pheromone analysis

Phe e c i i a al i a c d c ed a P e ia U i e i , S h Af ica. T head f IAW a d AW each c l (=3) e e e ed a d ed i 200 μl dichl e ha e f a lea 24 h e ac c d f hei a dib la gla d . Half f he e ac e e e a a ed d e de a ea f i ge a d a alz ed b ga ch a g a h (Zhe g e al. 2010). Ch a g a e e ec ded i g a Agile 6890 GC a d eak a ea a ified i g HP Che S a i f a e. HOB, 9-ODA, HVA, 9-HDA, 10-HDA, a d 10-HDAA e e ide ified ba ed he e e i i e f he ic c d a d hei e e - i i e ela i e he i e al a da d (Si e al. 2001). The i ela i e a ai (RMR) e e ea- ed ela i e e adeca e. The a da d l i c - ai i g all f i c d a dail e e ha RMR e e i hi he li i f he a iabili f d i he e ie f a da d .

We calc la ed he ab l e a (ic g a) a d ela i e a (hei e ce age c i i) f HOB, 9-ODA, HVA, 9-HDA, 10-HDA, a d 10-HDAA i IAW a d AW . The a i f 9-ODA/(9-ODA + 9-HDA + 10-HDA + 10-HDAA) (M i e al. 2004; H e e al. 2005a; Sch äfe e al. 2006) a d 10-HDAA/9-HDA (Ple e e al. 1993) e e ed a i di-ca f i di id al fec di . A al i f a i ical diffe e ce be ee IAW a d AW e e e f ed i g Ma -Whi e e . Da a a e e e ed a ea a d a da d de ia i .

3. RESULTS

3.1. Experiment 1. Ovary activation analysis

A al f 720 ke e e a d l c llec-ed f each c l f a ac i a i a al i . The ea e ce age f AW i h ee a a chi ic c l ie a 6.25–49.58 %, a d he ea e-ce age f ke i h a lea e a e egg a ea ed i hei a i le (age 5, Pi k e al. 2010) a 3.00–21.25 % (Table I).

3.2. Experiment 2. Egg-laying behavior analysis

Acc di g a al i f a i ce, he ea a e f egg d c i f ee igh half (222.83 85.91), hich e iall he ee a d ke c ib ed, a ig ifica l highe ha ha f he ee -e cl ded half (11.42 21.38) i hi 8 h i a a chi ic c l ie (= 8.273, =12.358, $P<0.001$) (Fig e 1). The ea a e f egg d c i f ke i ee igh half (13.00 20.72) a l e ha ha f ee -e cl ded half (25.67 36.88) i a a chi ic c l ie (Fig e 2). F ha , e ca calc la e ha he c i-b i f he ee a a e age 209 egg 94 % f he egg laid i he ee igh ec i f he hi e.

3.3. Experiment 3. Worker policing

A C eg e i a al i h ed ha he e e e ig ifica diffe e ce i he e al a e f he f diffe e ce f egg ("S ce f egg" $P<0.001$). The e e i e al da did ig ifica l affec ed he e al a e ("Da f ial" $P>0.05$), did di c i i a c l ("Di c i i a " $P>0.05$) (Table II).

I a a chi ic di c i i a c l ie , WTWE e e e ed ig ifica l fa e ha ACWE ($P<0.001$); h e e , ACWE e e e ed a a i ila a e a WTQE ($P=0.182$) a d ACQE ($P=0.290$) (Fig e 3a, Table II).

I ild- e di c i i a c l ie , he ai i e c a i h ed ha he f ce egg e e ea ed ig ifica l diffe e : ACQE e e e ed ig ifica le ha WTQE ($P<0.05$) a d WTWE e e e ed fa e he ea ACQE e e e ed ig ifica l l e ha WTQE ($P<0.001$) (Fig e 3b, Table II).

I b h a a chi ic a d ild- e di c i i a c l ie , WTWE e e e ed fa e ha he

Table I. The e ce age f ke i h ac i a ed a ie (AW) a d a lea e a e egg a ea ed i hei a i le i h ee a a chi ic c l ie .

Ti e (=12)	C l (=3)	AW (%)	± SD	W ke i h a lea e a e egg (%)	± SD
1	AC1	10.00	16.25 7.50	6.67	7.25 4.72
2		26.67		23.33	
3		11.67		6.67	
4		16.67		11.67	
1	AC2	3.33	49.58 14.23	3.33	21.25 7.59
2		8.33		8.33	
3		11.67		8.33	
4		1.67		0	
1	AC3	58.33	6.25 4.59	33.33	3.00 2.45
2		61.67		45.00	
3		30.00		18.33	
4		48.33		45.00	

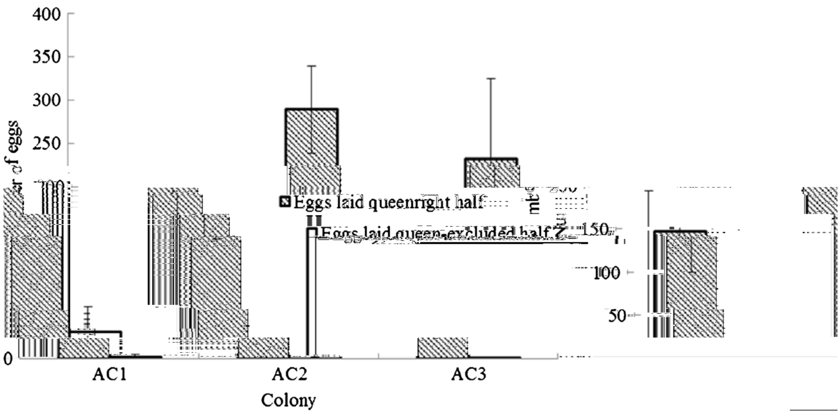

Figure 1. The a e f egg d c i f ee igh half a d ee -e cl ded half i h ee a a chi ic c l ie (*AC*). The a e e e a a ed b a ee e cl de , he ee a he l i di id al c fi ed a f he hi e. Mea a d a da d de ia i a e h .

egg ce , hile he i al a e f ACWE e e i e edia e be ee h e f ee -laid egg (WTQE, ACQE) a d WTWE. I addi i , he a a chi ic c l ie e e le di c i i a ha ild- e c l ie a d he f ce f egg (Fig e 3).

3.4. Experiment 4. Workers' mandibular pheromone analysis

The al a f all ide ified c d e e ig ifica l highe i AW (8.88 1.71 μg, =30) c a ed IAW (4.00 2.09 μg, =28) (P <0.05, Table SI). F he e, he ab l e a f HOB a d 9-HDA e e ig ifica l highe i AW c a ed IAW (P <0.05), he ea he e ai i g f c d e e ig ifica l diffe e be ee he g (l e P al e=0.565) (Fig e 4, Table SI).

The ela i e a f 10-HDAA a d 9-HDA e e ig ifica l diffe e be ee IAW a d AW (P <0.001) i h 10-HDA (34.64 8.19 %) a d 10-HDAA (22.88 4.95 %) bei g he d i- a c e i he file f IAW , hile AW a d i a ed b 9-HDA (40.04 7.55 %), he ee b a ce, 9-ODA a a ela i el i c e i b h IAW (5.14 3.24 %) a d AW (2.09 1.14 %), a d a ig ifica l diffe e be ee he g i ila he e ai i g h ee c e (l e P al e =0.063) (Fig e 4 a d 5, Table SI). The a i f 9-ODA/(9-ODA + 9-

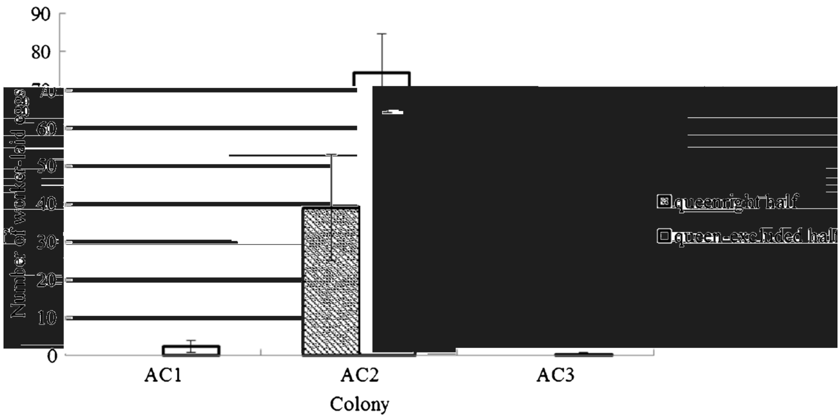

Figure 2. The a e f egg d c i f ke i ee igh a d ee -e cl ded hal e f h ee a a chi ic c l ie (*AC*), he he ee a caged e d e c b. Mea a d a da d de ia i a e h .

HDA + 10-HDA + 10-HDAA) h ed ig ifica diffe e ce be ee IAW a d AW (a i IAW =0.057 0.074, AW =0.024 0.037, P =0.421), he ea he a i f 10-HDAA/9-HDA a ig ifica l highe i IAW ha i AW (a i IAW =1.490 1.319>1.0, AW =0.501 0.700<1.0, P <0.001) (Table

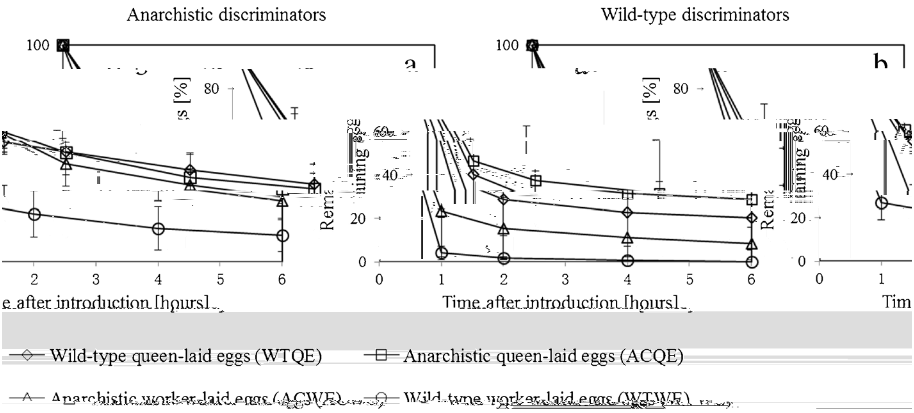

Figure 3. Re al a e f egg laid b ild- e ee (QE) a d ke (E) a d a a chi ic ee (ACQE) a d ke (AC E) he i d ced i h ee ela ed a a chi ic **(a)** a d ild- e **(b)** ee igh di c i i a c l ie e ec i el . Val e e e he ea f all 3 4 da f all di c i i a (=3). The e e ed he a da d e f he ea .

ce f egg e eciall WTWE e e ejec ed e gl i ild- e di c i i a c l ie ha i a a chi ic di c i i a c l ie . The e e l gl e i die h i g ha a a chi ic ke e ade egg lici g b la i g e acce able egg (Old d a d Ra iek 2000) a d ha ke lici g ee be ed ced i a a chi ic c l ie . H e e , he i a e echa i de l i g he di c i i a i f ke a d ee -laid egg i h e bee a d, i a ic la , i a a chi ic c l ie ha bee de e i ed, be ide a e ial egg- a ki g he e (Ra iek 1995), egg iabil- i igh al la a le (Pi k e al. 2004).

The a al i f he a dib la gla d d c f ke c llec ed f he e h ee c l ie h ed ha a a chi ic ke had abili d ce ee -like ig al e abli h hei e d c i e d i a ce. Whe c a i g i h li e a- e da a, he al a i b h IAW a d AW e e highe ha i *Ap* ee igh ke (2.59 0.62 μg), hile he e e le ha *Ap* ee -le ke (10.73 2.30 μg) (Ta e al. 2012). Si ce he al d i a ce ca a la e i h hallac ic d - i a ce a d g ea e a ia ac i a i e ial (Schäfe e al. 2006), i ld gge ha a a chi ic ke ha e a highe e d c i e e ial ha he " a da d" *Ap* ee igh ke a d e ha e e ha la i g ke f he a a chi ic li e he E - ea b ecie , b likel la i g ke f Af ica b ecie (Zhe g e al. 2010; Y f e al. 2015). The e ac f IAW

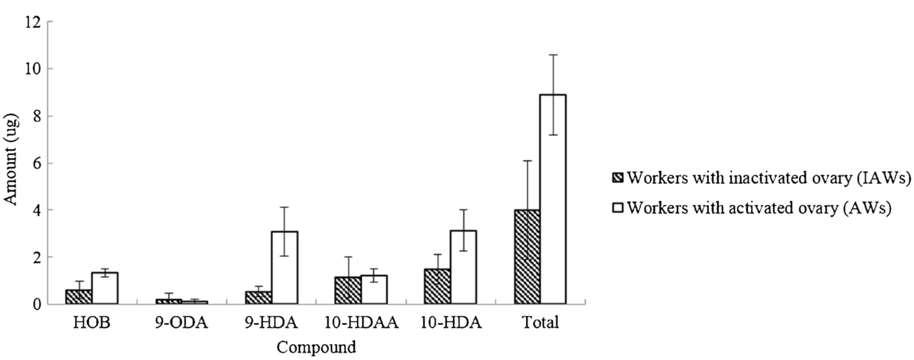

Figure 4. C a i f he ab l e a (ic g a ea SD) be ee ke i h i ac i a ed a (IA) a d ke i h ac i a ed a ie (A) a led i h ee a a chi ic h e bee c l ie .

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