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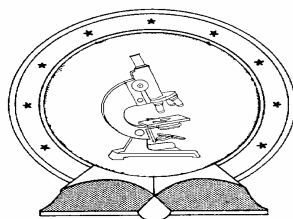**1949**

Individual variation of behaviour in firebugs (*Pyrrhocoris apterus*): causes and consequences

A viselkedés egyedi változatossága a verőköltő bodobácsnál (*Pyrrhocoris apterus*): okok és következmények

Egyetemi doktori (PhD) értekezés

Gyuris Enikő

Témavezető:
Prof. Barta Zoltán

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Értekezés a doktori (Ph.D.) fokozat megszerzése érdekében
a biológia tudományágban

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Készült a Debreceni Egyetem Juhász-Nagy Pál doktori iskolája
(Biodiverzitás programja) keretében

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Chapter I.

A viselkedés egyedi változatossága a verőköltő bodobácsnál

(*Pyrrhocoris apterus*): okok és következmények

I. 1. Bevezetés

Az állati viselkedés tanulmányozása az utóbbi évtizedben egy jelentős változáson ment keresztül. A viselkedésben fellépő egyedi különbségek jelensége, melyet régebben „zajnak", az egyedfejlődés során fellépő „hibák" következményének tekintettek, ma már a viselkedésökológiai kutatások egyik központi kérdése lett (Réale és mtsai 2010). Ezeket a viselkedésben megjelenő egyedei különbségeket, melyek időn és szituációkon keresztül állandóak, és gyakran egymással összefüggnek szokták viselkedési szindrómának, vérmérsékletnek (temperamentumnak), viselkedési típusnak illetve, állati személyiségnek is definiálni (Sih és mtsai 2004, Réale és mtsai 2007, Sih és Bell 2008). Egy nemrég megjelent tanulmány szerint azonban ezeket az eddig egymás szinonimájaként használt fogalmakat az alábbiak szerint pontosíthatjuk (Herczeg és Garamszegi 2012):

Vérmérséklet: Egy egyedre jellemző hipotetikus jelleg, mely különböző élethelyzetben jelenik meg különböző viselkedésekként (pl. kockázat vállaló viselkedés szintje predációs környezetben).

Állati személyiség: Egyedi viselkedési különbségek, mely kontextusokon és időn keresztül konzisztensek. Leggyakrabban vizsgált személyiség jellegek a bátorság, felfedezőképesség, aktivitás, szociabilitás és agresszivitás (Réale és mtsai 2007).

Viselkedési típus: Egy egyedre jellemző személyiség jelleg.

Viselkedési szindróma: Csoport szinten (pl. populáció) értelmezhető legalább két személyiség jelleg között megjelenő rang-sorrenden alapuló korreláció (Bell 2007).

Az, hogy az emberek rendelkeznek stabil egyedi viselkedésbeli különbséggel már egy régóta köztudott tény (Eysenck 1953), azonban viselkedésökológusok nemrég felfigyeltek arra a jelenségre, hogy ezek a különbségek leegyszerűsödve, de nagyon hasonlóképpen megjelenhetnek állatfajok számunkra teljesen azonosnak tűnő egyedeinél is.

Riechert és Hedrik (1990) a személyiség kutatás kezdeti szakaszán végzett vizsgálata arra a kérdésre kereste a választ, hogy a környezeti hatások hogyan hatnak a korrelált viselkedési minták evolúciójára. Az észak-amerikai sivatagi „füves" pók (*Agelenopsis aperta*) előfordul mind száraz, füves élőhelyeken, mind pedig páradús, folyó menti habitaton is. A száraz élőhelyen kevesebb a préda és kisebb a predációs kockázat, ugyanakkor nagyobb a kompetíció a területért. Ezzel szemben a folyó melletti habitaton a pókok több predátorral

találkozhatnak, de magasabb a táplálék ellátottság is és így kisebb a kompetíció. Megfigyelték, hogy a vízi élőhelyen előforduló pókok félénkebbek, sok időt töltenek el a ragadozó elöli bujkálással, ugyanis az ebből származó előny nagyobb, mint az adott esetben elszalasztott táplálékból származó hátrány, hiszen nagy a táplálék ellátottság. Ezzel szemben a füves élőhelyeken élő pókoknak a territórium fenntartásáért előnyös agresszívabbként viselkedniük. Ezen természetben megfigyelt két személyiség jelleget (bátorság, agresszivitás) kísérleti úton is tesztelték, és azt tapasztalták, hogy a pókok viselkedése a helyi környezethez való adaptációnak tekinthető, azaz a természetes szelekció a vizes élőhelyen a félénkebb, kevésbé agresszívebb egyedeket, míg a száraz élőhelyeken a bátrabb, agresszívebb egyedeket részesíti előnyben (Riechert és Hall 2000).

A viselkedésben megjelenő egyedi különbségek evolúciós alapjainak megértéséhez egy másik érdekes jelenség a viselkedési „túlfolyás (*spillover*)", mely azon eseteket írja le, amikor egy jellegre ható pozitív szelekció egy adott helyzetben maladaptív viselkedést eredményez egy másik helyzetben a jellegek közötti kapcsoltság miatt. (Sih és mtsai 2004). Egy észak-amerikai halászpók fajnál (*Dolomedes triton*) azt találták, hogy egyes nőstény pókok gyakran a párzás előtt felfalják a nekik udvarló hímeket (Johnson és Sih 2005). Ez a „prekopulációs kannibalizmus" valószínűleg annak az eredménye, hogy a természetes szelekció azokat a juvenilis nőstényeket részesíti előnyben, akik a táplálékhiány miatt agresszíven viselkedtek. Megfigyelték, hogy az agresszivitás felnőttkorban is stabilan megmarad és korrelál a fekunditással, ugyanakkor egyes esetekben a nőstények a túlzott agressziónak súlyos árát fizetik, azaz nem szaporodnak.

A viselkedési és fiziológiai jellegek sokszor nem függetlenek egymástól és együtt változhatnak, ami miatt egy ún. „viselkedés-fiziológiai szindróma" alakulhat ki (Mather és Logue 2013). Kortet és mtsai (2007) a viselkedésben megjelenő egyedi különbségek és az azt alátámasztó fiziológiai háttér közötti korrelációt tanulmányozták. Három populációból - melyek különböztek a predációs kockázat és parazitáltság tekintetében - gyűjtöttek hím tücsköket (*Gryllus integer*), és vizsgálták, hogy az aktivitásuk (látencia idő), valamint bátorságuk (búvóhelyről való előbújást) hogyan függ össze az immunválaszukkal. Az erősen predált és parazitált terültről gyűjtött tücskök erősebb immunválaszt mutattak, mint a kevésbé veszélyeztetett területről gyűjtöttek. Ugyanakkor a fertőzésre adott „betokozódási" válasz (immunválasz) pozitívan korrelált az aktívvá válás látenciájával és a búvóhelyről való kibújási idővel a magas predációs nyomású populációban. Ez a vizsgálat egy jó példa arra, hogy a ragadozás és az élősködés növelheti a tücskök parazita rezisztenciába való befektetését, a ragadozók elleni viselkedés potenciális költségeinek ellenére.

A személyiség kutatás egyik központi kérdése, hogy milyen evolúciós okokra vezethető vissza a konzisztens egyedi különbségek megléte. Milyen faktorok idézik elő a személyiség evolúcióját? Hogyan alakítják ezek a faktorok a viselkedés struktúráját és a személyiség egyedfejlődésének stabilitását? Proximális szinten elmondhatjuk, hogy a személyiség jellegek korrelációit genetikai (Mackay 2004), hormonális (Ketterson és Nolan 1999), illetve kognitív (Rolls 2000) mechanizmusok okozzák. Néhány esetben ugyanakkor az _állapot_ban megjelenő egyedi különbségekkel (McNamara és Houston 1996) –pl. morfológiai (Ehlinger és Wilson 1988), fiziológiai (Koolhaas és mtsai 1999), kognitív (Howard és mtsai 1992) – magyarázhatjuk a viselkedési variabilitást. Vannak állapot különbségek, melyek jól megfigyelhetőek, pl. a méretbeli különbségek, nemi különbségek, dominanciában való különbségek: míg más állapotbeli különbségek kevésbé látványosak; pl. stressz válasz, tapasztalat. Ezen egyszerűnek tűnő magyarázat ellenére, számos tanulmány egyedi különbségeket ír le azoknál az állatoknál is, amelyek nem különböznek azon állapotukban, melyek fontosak lehetnek a megfigyelt viselkedési jellegeknél (Dingemanse és mtsai 2002, Bell 2007). Emellett felmerül az a kérdés is, hogy miért kellene egy bátor egyednek agresszívebbnek lennie, mint a félénk fajtársaiknak, és miért kellene egy bátor egyednek bátornak maradnia az egyedfejlődés során? Ez a sok esetben tapasztalt limitált rugalmasság azért meglepő, mert a viselkedést, szemben pl. több morfológiai jelleggel, sokáig igen flexibilisnek hitték.

Wolf és mtsai (2013) összegyűjtötték azokat a mechanizmusokat, melyek előidézhetik az állati személyiség evolúcióját. Ezek a mechanizmusok két fő kérdés köré csoportosulnak: (1) mely faktorok idézik elő az adaptív viselkedésbeli változatosságok együttélését egy populáción belül; (2) mely faktoroknak köszönhetően alakultak ki az adaptív korrelációk a viselkedési jellegek között időn és helyzeteken keresztül.

(1) Adaptív _viselkedési változatosság_ kialakulásának okai lehetnek:

    (a) állapotban megjelenő különbségek

    (b) frekvencia-függő szelekció

    (c) tér-időbeli változatosság

    (d) nem egyensúlyi dinamikák

(a) Az állapotban lévő különbségeket könnyen megfigyelhetjük. Ha pl. egy populációból kiemelünk két egyedet, akkor jó eséllyel találunk köztük morfológiai vagy fiziológiai

különbségeket. De mégis miért kellene az egyedeknek, akik pl. egyedfejlődésük során nem különböztek különbözniük később az állapotukban? Ezek az eltérések annak köszönhetőek, hogy az egyedek állapotára random faktorok különbözőképpen hathatnak, például az egyik egyed gazdag környezetben nő fel, míg a másik szegény környezetben, vagy az egyik egyed megfertőződik, míg a másik nem.

(b) A keresgélő-potyázó játszma során például attól függ az egyed nyeresége, hogy a populációban milyen gyakorisággal van jelen az adott típus; tehát például minél több a keresgélő stratégiát folytató egyed, annál kevésbé lesz előnyös keresgélőnek lenni, ez esetben a szelekció a ritka fenotípusnak fog kedvezni (negatív gyakoriság függő szelekció) (Barta és Giraldeau 1998). A ritkaság előnye eredményezi, hogy a két fenotípus együtt fordul elő adott frekvenciával, stabil egyedi különbségeket kialakítva így az adott populációban. A denzitás-függő forrás-kompetíció szintén elősegítheti azon egyedek stabil együttélését egy populáció belül, akik különbözőképpen aknázzák ki a forrásokat (Wilson 1998).

(c) Környezeti feltételek térben és időben változnak mely variabilitás a szelekciós nyomás eltéréseiben is megjelenik. Szituációtól függ (Moran 1992, Leimar 2005), hogy vajon a populáció a tér és időbeli változatossággal hogyan birkózik meg, és az egyedek hogyan tudnak a helyi környezethez alkalmazkodni. Azokban az esetekben, amikor a különböző környezetek más-más állapotoknak kedveznek, a térbeli változatosság jellemezheti a viselkedési típusok együttélését. A környezet időbeli variabilitásával is gyakran értelmezhetjük a viselkedési típusok együttélését. Jó példa erre Dingemanse és mtsai (2004) vizsgálata, melyben a környezet időbeli fluktuációja segíti a bátor és félénk egyedek együttélését; azaz a környezet egyszer a bátor egyedeket részesíti előnyben, majd máskor pedig a félénkeket.

(d) A fentebb említett példák azt az elképzelést támogatják, hogy a természetes szelekció az egyensúly elérését részesíti előnyben, ahol adott stratégiák léteznek együtt stabil gyakorisággal. Számos esetben azonban nem-egyensúlyi dinamikát is kialakíthatnak változatos faktorok, mint pl. forrás kompetíció (pl. Huisman és Weissing 1999), frekvencia-függő szelekció (pl. Weissing 1991) vagy szexuális szelekció (pl. Van Doorn és Weissing 2006). Jó példa erre a sok fajnál megfigyelhető „kolonizáció típus" - mely gyakran jobb terjedési képességgel is rendelkezik - és az „otthon-ülő stratégia" együtt élése (Duckworth és Badyaev 2007). Ezeknél az egyedeknél néhányan kolonizálnak, míg mások otthon maradnak

(ők viszont jobb kompetítorok); a terjedők általában új területeket is el tudnak foglalni, viszont ez a kolonizációs tulajdonság hátrányos egy zsúfolt környezetben (pl. Duckworth és Kruuk 2009), ezért e két stratégia aránya dinamikusan változik.

Az időn és helyzeteken keresztüli adaptív *korrelációk* (2) kialakulásáért a következő tényezők lehetnek felelősek (Wolf és mtsai 2013):

(a) különbségek a stabil állapotokban

(b) különbségek a „változékony" állapotokban

(c) „társadalmi" minták

(a) Ha egy egyed állapota stabil az időn keresztül, akkor az adaptív állapotfüggő viselkedés is konzisztens marad az időn keresztül. Vannak olyan állapotok, mint például a nem, vagy a különböző kasztok a szociális rovarok között, melynek irreverzibilis tulajdonsága miatt állandó, konzisztens különbségeket eredményez a viselkedésben. Ezek az ún. „velejáró" állapotok (morfológiai, fiziológiai, vagy neurobiológiai tulajdonságok) gyakran egy nagyon komplex és időigényes fejlődési folyamatokon keresztül alakulnak ki, ezért ezek megváltoztatása sok esetben lehetetlen vagy igen költséges. Például a nemi különbségekkel együtt járó viselkedések hasonlóképpen jelenhetnek meg különböző kontextusokban (pl. szülői gondozás vagy párválasztás) korrelált viselkedési jelleg-együtteseket kialakítva így.

(b) Ezzel szemben a „változékony" állapotok nem ennyire merevek, könnyedén tudnak váltani ezért időben igen variábilisak. Ilyen például a hormon összetétel, az energia tartalék, a vérnyomás, mely állapotok különböző faktorok hatására (pl. viselkedés) könnyedén megváltozhatnak. Néhány esetben azonban a viselkedés és az állapot közötti pozitív visszacsatolás segítheti az időbeli konzisztencia kialakulását. Például az egyed annál „optimálisabban" viselkedik egy adott helyzetben minél több korábbi tapasztalata van (Rosenzweig és Bennett 1996). Jó példa erre a ragadozó biztos felismerése, azaz, ha megtanulta az állat azonosítani a veszélyt, csökkentheti az azonosítás költségét, ami megerősítheti így a kockázatos élettér gyakoribb látogatását (Griffin 2004). Amikor egy adott helyzetben összegyűjtött információk hatással vannak egy másik helyzetben megjelenő viselkedés költség-haszon arányára, ezek a visszacsatolások magyarázhatják a korrelált viselkedések stabil különbségeit.

(c) A „társadalmi minták" hatása is stabilizálhatja az idő és kontextuson keresztüli korrelációt, azzal, hogy egy egyed a viselkedését a többi egyeddel való korábbi interakciója révén állítja be (Nowak és Sigmund 1998, Leimar és Hammerstein 2001). Jó példa erre a győztes-vesztes effektus, melyet számos állatfajnál leírtak már (Chase és mstai 1994). Eszerint azok az egyedek, akik egy korábbi harcban győztesként kerültek ki, a következő mérkőzésben is jó eséllyel nyerni fognak, míg azok, akik vesztettek nagy eséllyel újra veszíteni fognak. Egy lehetséges magyarázat erre, hogy az egyed korábbi „sikerét" egy „random múltbeli aszimmetriaként" használja az adott szituációban (Parker 1974, Maynard Smith és Parker 1976, Van Doorn és mtsai 2003a, b).

Viselkedési szindrómának a legalább két személyiség jelleg között megjelenő rang-sorrenden alapuló korrelációt nevezzük, melynek jelenléte vagy hiánya egy csoportra jellemző tulajdonság (Bell 2007). Herczeg és Garamszegi (2012) a viselkedési szindrómát egy új megközelítésbe helyezi, azaz a jelenséget egyedi szinten és egy folytonos skálán határozza meg a populációs szintű értelmezés helyett. Feltételezik, hogyha a populációs szintű szindrómák a természetes szelekció eredményének tekinthetők, akkor a stabil viselkedési jelleg együttesnek örökölhetőnek kellene lennie és egyedi szinten fitnesz előnyöket kellene eredményeznie. Bevezettek egy olyan mérőszámot, mely az egyedi eltérést méri a szindróma által predikált tökéletes korrelációtól. Ez azért hasznos, mert így lehetőség nyílhat olyan evolúciós mechanizmusok tanulmányozására melyek a viselkedési korrelációkért felelősek (pl. bátorság és agresszió között). Ezt az indexet úgy határozhatjuk meg, hogy először az egyes viselkedési jellegek rangokat kapnak, majd az egyes egyedek értékét kiszámoljuk a két viselkedés rangjai közötti különbségeinek abszolút értékeit véve. Dingemanse és mtsai (2012) ezzel szemben a viselkedési szindrómát nem egyszerűen csak egyedeken belüli fenotipikus korrelációnak tekintik, hanem egyedek közötti korrelációnak (mely kizárólag az egyedek közötti hatásoknak köszönhető – mint pl. additív genetikai, állandó környezeti korrelációknak). Az egyedek közötti variancia azt méri, hogy az egyedek mennyire különböznek egymástól az „átlagos fenotípusukban", míg az egyeden belüli variancia azt méri, hogy az ismételt válaszok mennyire különböznek egymástól ugyanazon egyeden belül. Ha például az állatokkal bátorság és agresszió tesztet is végzünk, és ezt megismételjük, akkor tudjuk mérni mind az egyeden belüli mind pedig az egyedek közötti korrelációt. Dingemanse és mstai (2012) szerint ahelyett, hogy azt tanulmányoznánk, hogy az individuumok mennyire különböznek a tökéletes korrelációtól (Herczeg és Garamszegi 2012), azt kellene vizsgálni, hogy az egyedek mennyire különböznek a megfigyelt egyedek közötti korrelációtól. Az

egyedek közötti adott korrelációból eredő eltérésnek több biológiai értelme van Dingemanse és mtsai (2012) szerint, ugyanis például a viselkedési konzisztencia relatív szintje, mint egyfajta fitnesz indikátor a szexuális szelekció tárgyát képezheti (Dall és mtsai 2004, Schuett és mtsai 2010). Garamszegi és Herczeg (2012) szerint azonban elengedhetetlenül fontos a fenotípusos korrelációk egyedek közötti és egyeden belüli változatainak elkülönítése, és az empirikus vizsgálatok során mindkét mérőszámot érdemes figyelembe venni. Mindezek tükrében úgy gondolom, hogy mind az egyedek közötti és az egyeden belüli korreláció tanulmányozása megalapozott, és fontos lehet az állati személyiségek vizsgálatában, azonban hogy melyik megközelítés bizonyul tudományosan hasznosabbnak a későbbi empirikus vizsgálatok során derül ki.

Milyen ökológiai és evolúciós következményei lehetnek a személyiségbeli különbségeknek és milyen fontosabb alkalmazási területei (Wolf és Weissing 2012)?

(1) Életmenet és demográfia: a viselkedési különbségek fontos hatással lehetnek a különböző életmenet jellegekre és demográfiai változásokra, mely variabilitás hatással van a fitneszre és a populáció növekedési rátájára (pl. az egyedek a forrásokat és a környezetüket különbözőképpen használják).

(2) Populáció denzitás és produktivitás: a különbségek felerősíthetik a populáció eltartóképességét, és produktivitását (pl. kompetíció elkerülése révén, Huges és mtsai 2008).

(3) Terjedés, kolonizáció és invázió: az új habitatok megtalálásánál fontos lehet, ha különböző viselkedési típussal rendelkeznek az egyedek, mely később a populáció stabilitását és „szívósságát" növeli (Chapple és mtsai 2012)

(4) Szociális evolúció: a különbségek megváltoztathatják a szociális evolúció irányát és kimenetelét (pl.: kölcsönhatás a szociális válaszkészség és konzisztencia között; partnerválasztás, hátrányelv, McNamara és Leimar 2010)

(5) „Átviteli dinamika": különbségek figyelhetőek meg a betegségek iránti fogékonyságban, és fertőzőképességben, valamint az információterjedés sebességét is nagyban befolyásolhatja az egyedi variabilitás (Barber és Dingemanse 2010)

(6) Fajképződés: a viselkedési különbségek hozzájárulhatnak a kezdeti fajok divergenciájához, azzal, hogy megfelelő körülményeket teremtenek a kompetitív fajképződéshez (Duckworth 2009)

(7) Evolúció sebessége és adaptációs lehetőségek: a különbségek felgyorsíthatják az evolúciót, a környezeti változásokra adott gyors alkalmazkodással (Barrett és Schluter 2008)

8

I. 2. Célkitűzések

Jól látható, hogy a személyiség kutatás egy igen fiatal és dinamikusan fejlődő tudományterület, mely során sok elméleti hipotézis született arról (Wolf és Weissing 2010), hogy mi tartja fent az egyedi varianciát, viszont ezek tesztelése és értelmezése napjaink egyik fontos feladata. A fentiek alapján disszertációm egyik célja kidolgozni egy rendszert, mely a megfelelő modell állattal lehetővé teszi, hogy labor körülmények között jól mérhetőek és vizsgálhatóak legyenek a viselkedésben megjelenő egyedi különbségek.

Módszerek

Európa egyik legközönségesebb poloskafajával a **verőköltő bodobáccsal** (*Pyrrhocoris apterus*) szinte mindenhol találkozhatunk, kedvelt előfordulási helye a hársfák környéke. Mivel jól határozható, tömeges előfordulása miatt könnyen begyűjthető, laboratóriumi körülmények között gond nélkül tenyészthető és igen széles szakirodalom foglalkozik velük, ezért ideális alanyai vizsgálatainknak. Két közismert megjelenési formája a szárnyas és a szárnyatlan formák fiziológiájuk és viselkedésüket tekintve is különbözőek (Socha 1993), mely tulajdonsága miatt alkalmas modell állat a harmadik fejezetben leírt kérdések megválaszolásához.

Állati személyiség mérésére az alábbi módszert használtuk (Gyuris és mtsai 2011, 2012): egy 55 cm átmérőjű kivilágított arénában futtattuk az egyedeket, mely arénában 4 gumidugót helyeztünk el, mint ismeretlen tárgyat. Minden egyedet két szituációban teszteltünk, egyrészt egy ún. bátorság teszttel mértük azt, hogy milyen hamar bújik elő az állat a búvóhelyéről, majd pedig az ún. „nyitott aréna" (*open field*) teszttel az bodobácsok útvonal koordinátái alapján mértük, hogy mennyire alaposan fedezi fel az egyed a környezetét, illetve mennyire aktívan viselkedik. A módszer validálása során a bodobácsokkal négyszer végeztük el a teszteket, így megmutatva, hogy a mért jellegek ismételhetőek. A módszer segítségével jól tudjuk mérni a szakirodalomban leggyakrabban vizsgált személyiség jellegek közül a bátorságot, aktivitást és felfedező képességet.

Disszertációm további céljai e módszer segítségével egyrészt vizsgálni azt, hogy vajon mérhető-e stabil egyedi különbség a verőköltő bodobács egyedeinél, valamint az életmenetbeli különbségek magyarázzák-e a személyiségben megjelenő stabil különbségeket egy adott populációban (3. fejezet). Másrészt mennyire marad állandó, illetve milyen tengelyek mentén változik a személyiség a bodobácsok egyedfejlődése során (4. fejezet). Harmadrészt arra a kérdésre keresem a választ, hogy hogyan befolyásolja egy parazitafertőzés (5. fejezet) az adott személyiségbeli különbségeket (6. fejezet).

I. 2. 1. Konzisztens egyedi különbségek a viselkedésben

Wolf és munkatársainak (2007) tanulmánya egy adaptív magyarázattal szolgál arra a kérdésre, hogy miért léteznek stabilan egyidejűleg különböző típusú személyiségek egy populációban. Az elméleti modell az életmenet teórián alapszik, mely szerint a várható jövőbeli szaporodási érték különbségei a kockázatvállaló viselkedésben is különbségeket kellene, hogy eredményezzenek. Azoknak, akiknek jók a jövőbeni esélyeik, azaz sok veszítenivalójuk van, kockázatkerülőbben kellene viselkedniük, mint azoknak, akiknek rosszabbak a jövőbeni esélyeik. Mivel az egyes viselkedési jegyek kapcsoltak, ezért a kockázatvállaló viselkedés összefügghet pl. az agresszióval, aktivitással és mindez az állatok személyiségének evolúcióját eredményezi. Disszertációm e fejezetében célom megvizsgálni azt, hogy alátámasztható-e a fenti elmélet, azaz azok az egyedek, akik különböző életmenet stratégiával, és így eltérő jövőbeli szaporodási értékkel rendelkeznek különböző személyiségűek-e. A kérdés tesztelésére a verőköltő bodobács kiváló modell állat, hiszen a két, morfológiailag eltérő megjelenési formája különböző életmenet stratégiával rendelkezik. A szárnyas bodobácsokról tudjuk, hogy jobban terjednek, annak ellenére, hogy nem tudnak repülni, míg a szárnyatlan formák korábban kezdenek el szaporodni (Socha és Zemek 2003, Socha és Zemek 2004). Feltételezzük tehát, hogy mivel a szárnyas bodobácsoknak kisebb a reziduális reproduktív értéke (mivel felnőtté válás után előbb terjed, ami kockázatos, és csak azután kezd szaporodni), mint a szárnyatlannak, ezért nekik bátrabbnak és felfedezőbbnek kellene lenniük.

I. 2. 2. Személyiségjegyek stabilitása és változásai az egyedfejlődés során

Azok a korai körülmények, melyeket az egyed életének kezdeti szakaszában tapasztal, fontos hatással lehetnek életének későbbi periódusaira (Lumma és Brock 2002). Labor patkányoknál (*Rattus norvegicus*) például azt találták, hogy a korai fejlődés megváltoztathatja a személyiség fejlődését; akik nagyobb súllyal születtek bátrabbak és felfedezőbbek voltak (Rödel és Meyer 2011). Egy egyed az élete során meghatározott élet-szakaszokon megy keresztül (pl. gyerekkor, pubertás, felnőttkor). Az egyes életszakaszokon belül az egyedeknek eltérő kihívásokkal kell szembenéznie (pl. juvenilis korban elsődleges cél a növekedés, míg felnőttként a szaporodás), és a szelekciós erők is különbözőképpen hathatnak rá (McNamara és mtsai 2009), így az adott szakaszban más-más tulajdonságok lesznek előnyösek. Ezek alapján feltételezzük, hogy az egyedek ugyanarra a szituációra másként fognak reagálni a különböző életszakaszokban. Ezért azt várhatjuk, hogy e fontosabb életszakasz átmenetek során (pl. felnőtté válás, szexuális érés), amikor a fejlődés az egyik szakaszból a másikba lép, a személyiség is megváltozik. Kimutatták például, hogy a texasi tücsök (*Gryllus integer*) lárvakorban a predációs kockázat ellenére is az intenzív táplálkozásra szelektálódott azért, hogy minél nagyobbra nőjön, mivel ezzel jelentős előnyhöz juthat felnőttként (Hedrick és Kortet 2012). Ugyanakkor egy szexuálisan érett egyednek érdemes kockázatkerülőbbnek lennie, mivel már korábban sikeresen összegyűjtötte azokat a forrásokat, melyeket a szaporodásba fektetnek (Niemelä és mtsai 2012). Ez a példa is illusztrálja, hogy életmenet evolúciós megfontolások alapján várható, hogy a korai életszakaszokon az egyedek arra adaptálódtak, hogy maximalizálják a növekedésüket, túlélésüket és terjedésüket, míg a felnőttkorban arra, hogy maximalizálják a szaporodási rátájukat (McNamara 1996, Roff 2002). Disszertációmat alkotó második cikkben (harmadik rész) arra a kérdésre keresem a választ, hogy a személyiség hogyan változik az életmenet jellegek tükrében egy nagyobb életszakasz váltáson keresztül. Stamps és Groothuis (2010) tanulmánya alapján, két szinten vizsgáljuk az egyedfejlődés során bekövetkező változásokat verőköltő bodobácsoknál (*Pyrrhocoris apterus*). Egyedi konzisztenciát mérve azt teszteljük, hogy egy egyed mennyire hasonlóan viselkedik ugyanabban a szituációban különböző időkben. Csoportos szinten egyrészt teszteljük azt, hogy az adott viselkedési különbségek mennyire maradnak stabilak az egyedfejlődés során (*rang konzisztencia*), másrészt vizsgáljuk azt is, hogy a szexuális érettség előtt és után lévő bodobácsok viselkedése mennyire különbözik (*csoportátlag konzisztenciája*). Harmadrészt pedig azt tanulmányozzuk, hogy a viselkedési jellegek

egymáshoz viszonyított helyzete mennyire hasonló a két életszakaszban (*strukturális konzisztencia*). A kérdés megválaszolására a fentebb leírt személyiségtesztet alkalmazzuk.

I. 2. 3. A *Hemipteroseius adleri* atka megjelenése hazánkban

A *Hemipteroseius adleri* (Costa 1968) atka az Otopheidomenidae családba tartozik, mely családba lévők rovarokat parazitáló életmódot folytatnak (Lindquist és mtsai 2009). A *Hemipteroseius* genusból csak ez a faj ismert Európából (Lengyelországból és Litvániából) valamit Izraelből (Lewandowski és Szafranek (2005), Costa 1968) és a verőköltő bodobácsokon (*Pyrrhocoris apterus*) él. Feltételezhető volt, hogy ahol verőköltő bodobács él, mindenhol előfordul, azonban Magyarországi megjelenését mi írtuk le először. Disszertációm ötödik fejezete a *H.adleri* hazai előfordulását leíró cikkből áll.

I. 2. 4. A verőköltő bodobácsok (*Pyrrhocoris apterus*) személyiségjegyeinek és a *Hemipteroseius adleri* atkának kapcsolata

A bátor állatoknál a halálozás fő oka általában a ragadozás, melynek fontos szerepe van az olyan jellegek evolúciójában, mint például az aktivitás, vakmerőség, felfedezőkedv (Dingemanse 2007). A kockázatvállalás adaptív jelentősége annak relatív költség-haszon arányától függ: ha a ragadozás esélye kicsi, akkor a bátor egyedek fitneszelőnybe kerülnek, viszont ha a ragadozás nagy, akkor a félénk egyedeknek lesz magasabb a fitneszük (Sih és mtsai 2004). A parazitizmus a ragadozáshoz hasonló fitneszköltségeket jelenthet, mivel a paraziták jelentős mortalitási tényezők de halált nem okozó fitneszköltségek forrásai is lehetnek (Raffel és mtsai 2008, Rohr és mtsai 2009). E hatás miatt és mivel bizonyos személyiségjellegek befolyásolhatják a parazitáltságot vagy parazitákkal szembeni rezisztencia valószínűségét (Wilson és mtsai 1993, Hart 1997), feltételezhetjük, hogy a paraziták befolyásolják a személyiség kialakulásának evolúcióját. Az egyik tendencia szerint a paraziták szelektív hatást gyakorolnak a személyiség és viselkedési jegyekre, melynek oka az, hogy az egyed viselkedés típusa befolyásolhatja a gazdaszervezetté válást. A második irányvonal szerint a paraziták maguk idézik elő egy adott gazda-viselkedéstípus egyedi különbségeit a helyi fertőzött populációkban, azaz a parazitafertőzés következményének

tekinthető a gazda állapota és így a személyisége is (Barber és Dingemanse 2010). Disszertációm e fejezetében célom megvizsgálni, hogyan hat a *Hemipteroseius adleri* ektoparazita atka a verőköltő bodobács viselkedésére. Ennek során természetes populációkból begyűjtött fertőzött és nem fertőzött egyedek személyiségét mértük, és a tesztek során a fentebb leírt két irányvonalat teszteltük statisztikailag, azaz vajon hogyan hat a fertőzöttség mértéke a bodobácsok viselkedésére, illetve vajon az egyed viselkedési típusa hogyan befolyásolja a gazdaszervezetté válást. További célom a vizsgálattal egy nemrég leírt jelenség igazolása, mely szerint a bodobácsok azért, hogy elkerüljék, a *H.adleri* atkát, megváltoztatják élőhelyüket, azaz egyes egyedek legalább 1 méter magasra másznak a fán. Kimutatták, hogy az avarból gyűjtött bodobácsok fertőzöttebbek voltak, mint a fáról gyűjtöttek (Zemek és Socha 2009). A gyűjtés során regisztráltuk, hogy mely habitatból gyűjtöttük a bodobácsot, és ennek segítségével tesztelni tudjuk, hogy vajon a különböző helyről gyűjtött egyedek különböznek-e a személyiségükben.

I. 3. Az értekezés új tudományos eredményei

I. 3. 1. Konzisztens egyedi különbségek a viselkedésben

Gyuris, E., Feró, O., Tartally, A., Barta, Z. *Individual behaviour in firebugs (Pyrrhocoris apterus).* **Proceedings of the Royal Society B: Biological Sciences,** *2011,* **278** *(1705) 628-633.*

Sikerült megmutatnunk, hogy mind a szárnyas és szárnyatlan bodobácsoknál jól mérhetőek személyiségbeli különbségek, azaz különböző egyedek különböző szituációkban hasonlóan viselkedtek. Eredményeink jól alátámasztják a Wolf és mtsai (2007) által kidolgozott modellt, mely szerint a különböző szaporodási érték „elvárásokkal" rendelkező egyedek várhatóan különböznek a személyiségükben. Szárnyas és szárnyatlan verőköltő bodobácsok személyiségét mérve azt kaptuk, hogy a szárnyas nőstények bátrabban és felfedezőbben viselkednek, mint a szárnyatlanok. Ez a különbség támogatja a fent említett hipotézist, ugyanis korábban kimutatták, hogy a két morfológiai forma különböző életmenet stratégiával rendelkezik. Mivel a nőstények többet fektetnek a szaporodásba a nagy és értékes petecsomó révén, mint a hímek, ezért feltételezzük, hogy rájuk jobban hatnak az életmenetbeli

különbségek, és ezért nem találtunk különbségeket a szárnyas és szárnyatlan hímek viselkedésében.

I. 3. 2. Személyiségjegyek stabilitása és változásai az egyedfejlődés során

Gyuris, E., Feró, O., Barta, Z. Personality traits across ontogeny in firebugs (Pyrrhocoris apterus), **Animal behaviour***, 2012,* **84***, 103-109.*

Kutatásunk során azt találtuk, hogy a verőköltő bodobács konzisztens viselkedést mutat azon fontos élet-szakasz átmeneten keresztül, mely során eléri a szexuális érettséget, valamint a viselkedési változók egymáshoz viszonyított helyzete, azaz a korrelációs struktúrája sem változik ezen átmenet során, melyhez hasonló eredményt talált Rödel és Meyer (2011) laboratóriumi patkányoknál. Eredményeink alapján elmondható továbbá, hogy a viselkedés leginkább felnőttkorban konzisztens, ami azért érdekes, mert humán tanulmányok is azt igazolják, hogy a korral egyre kevésbé változik a személyiség (Roberts és mtsai 2001). A viselkedési jellegek abszolút értékeinek változásait vizsgálva azt kaptuk, hogy a lárvák és a felnőtt egyedek alapvetően másképp viselkednek. A lárvák hamarabb kezdik el felderíteni az új környezetüket, azaz bátrabban viselkednek, mint a felnőtt bodobácsok, több ismeretlen tárgyat látogatnak, alaposabban felfedezve a környezetüket, illetve aktívabbak is voltak. Ezek a különbségek magyarázhatóak azzal is, hogy a különböző életszakaszokban az egyedek különböző életmenet kilátásokkal rendelkeznek (Wolf és mtsai 2007, McNamara és mtsai 2009). Feltételezzük, hogy a lárváknak az elsődleges céljuk a táplálkozás, míg a felnőtt egyedeknek a szaporodás (Roff 2002), ezért a lárvák magasabb predációs veszélyt is elviselnek. Más-más életszakaszokban ezért a különböző viselkedések vagy ugyanannak a viselkedésnek a különböző szintjei lesznek előnyösek (Wolf és mtsai 2007), mely hipotézist eredményeink is alátámasztanak.

I. 3. 3. A *Hemipteroseius adleri* atka megjelenése hazánkban

> *Kontschán, J., Gyuris, E. - Hemipteroseius adleri Costa, 1968 collected on red firebug: the first record of the family Otopheidomenidae Treat, 1955 (Acari: Mesostigmata) in Hungary.* **Opusc. Zool. Budapest,** *2010,* **41** *(2), 241-243.*

Disszertációm ötödik fejezetében egy a hazai faunára új atkafaj leírását mutatom be.

I. 3. 4. A verőköltő bodobácsok (*Pyrrhocoris apterus*) személyiségjegyeinek és a *Hemipteroseius adleri* atkának kapcsolata

> *Gyuris, E., Hankó, J. F., Feró, O., Barta Z. Ectoparasitic mites (Hemipteroseius adleri) and firebugs' (Pyrrhocoris apterus) personality traits (kézirat)*

Célunk a vizsgálattal az volt, hogy megnézzük van-e kapcsolat a verőköltő bodobácsok személyisége és a rajtuk található ektoparazita atka (*H.adleri*) okozta fertőzés között. A természetes élőhelyükről begyűjtött *H. adlerivel* fertőzött és nem fertőzött bodobácsok viselkedésének összehasonlítása során azt kaptuk, hogy mind a fertőzött és nem fertőzött egyedeknél is mérhetőek személyiségbeli különbségek (bátorság, felfedező képesség, aktivitás), illetve a viselkedési változók egymáshoz viszonyított helyzete is hasonló. A verőköltő bodobácsoknál megfigyelhető egy a parazita fertőzés elkerülésére szolgáló élőhely váltó viselkedés (Zemek és Socha 2009) azaz a bodobácsok azért, hogy elkerüljék az atkákat magasabbra másznak a fára. E jelenség alapján vizsgáltuk a különböző habitatról gyűjtött bodobácsok személyiségét és fertőzöttségét. Habár a vizsgált populációnkban nem találtunk szignifikáns különbséget a különböző helyekről gyűjtött bodobácsokon lévő atkák prevalencia értékei között, azonban eredményeink alapján elmondható, hogy a három habitat közül a fatörzs alján a legkisebb a fertőzés súlyossága. Mivel természetben megfigyelt populációt vizsgáltunk, és kísérletes vizsgálat nem történt, ezért nem tudjuk biztosan, hogy vajon a mutatott viselkedés a fertőzés következménye, vagy azért lettek atkások az egyedek, mert egy adott módon viselkedtek (Barber és Dingemanse 2010). Kutatásunk során ezért statisztikailag megnéztük mindkét irányt, és azt találtuk, hogy a viselkedésre egy enyhe hatása van a fertőzés mértékének, ami szerint az alapvetően hímekhez képes félénkebben viselkedő nőstények

bátrabbak lesznek. Megvizsgáltuk továbbá azt is, hogy vajon a mért viselkedési változók hogyan hatnak az atkaszámra, és azt találtuk, hogy a bátrabb nőstények nagyobb eséllyel fertőződtek meg, mint a félénkek. Ezen eredmények pontosabb alátámasztására azonban további labor vizsgálatok folynak, mely során fertőzést modellezünk, és így tudjuk majd vizsgálni a fertőzés előtti és utáni viselkedést. Morfológiai méréseket is végeztük a begyűjtött bodobácsokkal, többek között szimmetriát is mértünk, és eredményeink azt mutatják, hogy a kevésbé szimmetrikusabb egyedeken több atka fordul elő. Ezek alapján valószínűsíthetjük, hogy egyfajta minőség szignál lehet a szimmetria utalva az egyed fejlődési rendellenségeire.

I. 4. Összefoglalás és jövőbeni tervek

A viselkedésben megjelenő konzisztens egyedi variabilitás megléte egy igen komplex, összetett jelenség, melyet állati személyiségnek, viselkedési szindrómának, illetve vérmérsékletnek definiál a szakirodalom (Bell 2007, Réale és mtsai 2007); és melynek okai és következményei a viselkedésbiológia egy fiatal, dinamikusan fejlődő tudományterületének aktuális kérdései közé tartozik. Munkám során egyik fő célom volt beállítani egy rendszert, mellyel egyszerűen, világosan tudjuk mérni ezeket a viselkedésben megjelenő stabil egyedi különbségeket (3. fejezet).

Jelenleg az ízeltlábúak alkotják Földünk élőlényfajainak több mint kétharmadát, ezért tanulmányozásuk során a viselkedésekben megjelenő különbségek egy széles skáláját ismerhetjük meg. A fentebb említett kérdések megválaszolására irányuló vizsgálatok nagy részét mégis gerinceseken végzik, annak ellenére, hogy több okból is érdemes modell állatnak ízeltlábút választani. Viszonylag kis testméretűek, nagy mennyiségben tarthatóak laborban; általában rövid életciklusúak, így akár egy egyed teljes életútját is végigkövethetjük és etikai engedélyek nélkül is végezhetünk velük kísérleteket. Ezen előnyöket kihasználva választottuk modell állatnak a verőköltő bodobácsot (*Pyrrhocoris apterus*), mely állat további előnye, hogy rendkívül közönséges, jól határozható, tömegesen előforduló rovar. Jelen disszertációmban bemutatott módszer alkalmas a leggyakrabban mért személyiség jellegek közül a bátorság, felfedezőképesség és aktivitás mérésére. A vizsgálatok elvégzése és a tesztek kiépítése egyszerű és a bemutatott statisztikai eljárások is jól alkalmazhatóak akár más állatfajok esetében is.

A viselkedésben megjelenő stabil egyedi variancia kialakulásának magyarázatára az utóbbi néhány évben számos elméleti hipotézis született (Wolf és Weissing 2010), azonban ezek igazolására empirikus vizsgálatok szükségesek. Dolgozatom harmadik fejezetében egy ilyen hiányt pótlok, és egy elméleti modellt (Wolf 2007) tesztelek, mely feltételezi, hogy ezek a különbségek annak köszönhetőek, hogy az egyedek az aktuális és későbbi szaporodási értékük optimalizálása miatt különböző életmenet stratégiát használnak. A verőköltő bodobács két megjelenési formája alkalmasnak tűnt e kérdés megválaszolására, és eredményeink alapján az a következtetés vonható le, hogy az eltérő életmenet stratégiák megléte (esetünkben ez stabil állapot különbségeket is jelent, azaz szárnyas és szárnyatlan egyedekkel dolgozunk) eltérő személyiséget is jelent (Gyuris és mtsai 2011). Ezen különbségek viszont csak a nőstény egyedeknél jelentek meg, melyet feltételezünk, hogy azért lehet, mert a nemek eltérő energiát fektetnek az aktuális szaporodási értékükbe. Ezen eredmények további kérdéseket vetnek fel, mint például mennyire segíti elő egy populáció stabilizálását (Chapple és mtsai 2012) a különböző morfológiai formák aránya, mennyire stabil vagy épp nem-egyensúlyi dinamikát (Van Doorn és Weissing 2006) követ e formák együtt létezése egy populáción belül.

Dolgozatom negyedik fejezetében egy fontos életszakasz átmeneten keresztüli személyiség változást vizsgálok (Gyuris és mtsai 2012). A verőköltő bodobács utolsó vedlése során eléri a szexuális érettséget és kifejlett rovarrá fejlődik. Eredményeink szerint ezen átmeneten keresztül is konzisztens marad a személyiség, azonban az utolsó vedlés előtt lévő lárvák másképp viselkednek, mint a felnőtt egyedek. Feltételezzük, hogy mindez annak köszönhető, hogy adott életszakaszok alatt eltérő életmenet kilátásokkal rendelkeznek az egyedek (McNamara és mtsai 2009). Ebben a vizsgálatban a Stamps és Groothuis (2010) által az állati személyiség mérésére bevezetett indexeket alkalmaztuk, mely során egyedi és csoportos szinten is mértük a személyiség változását. Ezzel a tanulmánnyal rávilágítottunk arra, hogy fontos és hasznos ezen indexek használata, hiszem más-más szempontból mérve a személyiséget különböző kérdésekre kaphatunk választ. Disszertációm e fejezetének egy további fontos eredménye szerint a személyiség leginkább felnőtt korban marad konzisztens, mely eredmény jól egybecseng humán tanulmányoknál találtakkal (Roberts és mtsai 2001). Olyan további kérdések megválaszolásához adhat alapot a tanulmányunk, mint például mely fontosabb életszakasz átmenetek során változik a személyiség és milyen tengelyek mentén.

Disszertációm ötödik fejezete egy a hazai faunára új atkafaj *(Hemipteroseius adleri)* leírását tartalmazó leíró cikkből áll (Kontschán és Gyuris 2010), mely ektoparazita atka a verőköltő bodobácsok szárnya alatt található. A viselkedésben megjelenő egyedi

különbségekért felelős ökológiai faktorok közül a parazitizmus is egy potenciálian fontos tényező lehet, viszont e hatások irányáról és következményeiről kevés információnk van (Barber és Dingemanse 2010). Dolgozatom utolsó részében célom megvizsgálni e parazita atka és a verőköltő bodobács személyiségjegyeinek kapcsolatát. A kutatás során összehasonlítottuk a természetből begyűjtött fertőzött és nem fertőzött egyedek személyiség jegyeit, valamint statisztikailag megnéztük azt is, hogy a fertőzés mértékének milyen hatása van a viselkedésre, és fordítva a viselkedésnek milyen hatás van a fertőzésre, egy általános képet kapva így a rendszerről. Erre a vizsgálatra építve, jelenleg további kutatások folynak annak kiderítésére, hogy vajon az egyed immunrendszerének válasz reakciója milyen kapcsolatban van a fertőzés mértékével; lehet-e kísérleti úton modellezni azt.

A fentebb említett stabil viselkedésbeli változatosságok kialakulásának okai és következményei nem egyértelműek, számos kérdés megválaszolásra vár még. A verőköltő bodobács nem euszociális rovar, viszont a szakirodalom a szociális viselkedés egy kezdeti formájába, a preszociális viselkedésű állatokhoz sorolja (Socha 1993). Megfigyelhetjük, hogy főleg ősszel és tavasz elején csoportokba tömörülnek, viszont nem tudjuk, hogy vajon mindez egy passzív aggregálódás vagy az egyedek társas hajlama miatt alakul ki. Jelenleg futó vizsgálatunkban a társas viselkedés mérésére kialakított teszttel mérjük, hogy kimutatható-e egyedi variancia az egyedek szociális viselkedésében, illetve mindez milyen összefüggésben van az állati személyiséggel.

I. 5. Köszönetnyilvánítás

I. 6. Irodalomjegyzék

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Chapter II.

Individual variation of behaviour in firebugs (*Pyrrhocoris apterus*): causes and consequences

II. 1. Introduction

Studying animal behaviour has gone thought a remarkable change in the last decade. The phenomenon of individual differences in behaviour - previously considered as consequences of random effects during an individual's ontogeny – have became a central research question of behavioural ecology and evolutionary biology (Réale *et al.* 2010). Differences in behaviour that are consistent across time and situation and often correlate with each other can be referred to as behavioural syndrome, temperament, behavioural type or animal personality (Sih *et al.* 2004, Réale *et al.* 2007, Sih and Bell 2008). According to Herczeg and Garamszegi (2012) these definitions that have been used as synonyms of each other can now be classified as follows:

Temperament: A hypothetical trait of an individual that is expressed in different biological contexts as different behaviours (e.g. as a level of risk-taking behaviour in a predation risk context).

Animal personality: Individual differences in behaviour which are consistent across context and time. The most frequently measured personality traits: boldness, exploration, activity, sociability and aggression (Réale *et al.* 2007).

Behavioural type: Individual configuration of the personality traits.

Behavioural syndrome: Correlation between rank-order differences between individuals' personality traits which can be studied with reference to a group of individuals (e.g. population) (Bell 2007).

It has been known for a long time that humans have personality (Eysenck 1953). Recently behavioural ecologists have also recognized that the phenomenon of these consistent differences in seemingly identical individuals of the same animal species can be related to human personality.

A study of Riechert and Hedrick (1990) was published in the early years of personality research and furnished an answer to the question of how environmental factors affect the evolution of correlated behaviour patterns.

A North American grass spider (*Agelenopsis aperta*) occurs in both dry grassland and also in moist riparian habitats. Predation risk and prey availability is low in a grassland habitat,

whereas competition for suitable places of webs is high. In contrast, spiders in riparian habitats have to face more predators, but food availability is also high hence competition is low. Riechert and Hedrick (1990) found that riparian spiders are shier and spend more time hiding from predators, because the benefit of this is higher than the cost of failing to catch a prey, since food is abundant. Contrarily, grassland spiders have been found to be more aggressive to maintain their territory. These two personality traits (braveness and aggressiveness) - observed in the wild - have been tested further under laboratory conditions and it was found that spiders' behaviour can be considered as an adaptation to local environment, that is natural selection favours shier and less aggressive individuals in a riparian habitat, while braver and more aggressive ones in a grassland habitat (Riechert and Hall 2000).

Another remarkable phenomenon for understanding the evolution of individual differences is the behavioural spillover, which describes cases when positive selection acting on one trait in a given context results in a maladaptive behaviour in another context because of the correlation of traits (Sih *et al.* 2004). Johnson and Sih (2005) found in a North American fishing spider (*Dolomedes triton*) that females sometimes eat the courting males before mating. This "precopulatory cannibalism" is a result of the phenomenon that natural selection favours juvenile females who behave more aggressively because of the shortage of food. They observed that aggressiveness remain stable in adulthood and correlate with fecundity but at the same time some females pay a lot for high aggressiveness, that is, they will not mate.

Behavioural and physiological traits are often non-independent of each other and they change together hence a co-called behavioural-physiological syndrome can evolve (Mather and Logue 2013). Kortet *et al.* (2007) investigated the correlation of individual differences in behaviour and the underpinning physiological background. Male crickets (*Gryllus integer*) were collected from three populations which differed in the level of predation and parasitism and they investigated crickets' latencies to become active (freezing time) and emerge from a shelter (hiding time) correlated with their immune response. Crickets from habitat of high level of predation and parasitism showed stronger immune response than the ones from habitat of low level predation and parasitism. At the same time, encapsulation response (immune response) to infection correlated positively with the latency time of becoming active and emergence time from a shelter in the population of high level predation. This study is a good example of that predation and parasitism can increase cricket's investment into resistance against parasitism despite the potential cost of anti-predator behaviour.

A major question of animal personality research is what the evolutionary causes of consistent individual differences are. What factors give rise to the evolution of personality? How these factors can shape the structure of behaviour and the stability of development of personality? On a proximate level correlations of personality traits are caused by genetic (Mackay 2004), hormonal (Ketterson and Nolan 1999) and cognitive (Rolls 2000) mechanisms. At the same time, in some cases individual differences in – e.g. morphological (Ehlinger and Wilson 1988), physiological (Koolhaas *et al.* 1999), and cognitive (Howard *et al.* 1992) – state can explain behavioural variation between individuals (McNamara and Houston 1996). Some of the state differences e.g. differences in size, sex or dominance are well-observable, while others, like stress response, experience, are less). In spite of this seemingly simple explanation, several studies describe individual differences in animals that do not differ in those states that could be relevant in the observed behavioural traits (Dingemanse *et al.* 2002, Bell 2007). So why a brave individual should be more aggressive than its shy conspecifics and why a brave individual should remain brave during ontogeny? This limited flexibility experienced in many cases is surprising because behaviour has been known as the most flexible trait for a long time.

Wolf *et al.* (2013) collected the mechanisms that can promote the evolution of animal personality. These mechanisms gather around two main questions: (1) which factors promote the coexistence of adaptive behavioural variabilities within a population; (2) due to which factors do adaptive correlations develop between behavioural traits across time and context?

 (1) Causes of adaptive behavioural variation:
   (a) State differences
   (b) Frequency-dependent selection
   (c) Spatio-temporal variation
   (d) Non-equilibrium dynamics

(a) *State differences* are well-observable in many times. For example, if we choose two individuals from a population there is a good chance to find morphological or physiological differences between them. But why should individuals – who, for example, did not differ across ontogeny - differ later in their states? These differences can be due to fact that inevitable random factors affect individuals' state in a different way, e.g. an individual may

grow up in a rich or in a poor environment, or one individual may become infected, while the other one may not.

(b) *Frequency dependent selection*. For example, in the case of "producer-scrounger" situation, the benefits of an individual depend on the frequency of the phenotypes in a population; that is the more producers there are, the less beneficial it will be to be a producer and vice versa – so, in this case, selection favours the rarer phenotype (strong negative frequency-dependent selection) (Barta and Giraldeau 1998). The benefit of rarity results in that two phenotypes coexist with a given frequency shaping individual differences in a given population. Density-dependent resource competition also promotes the stable coexistence of those individuals within a population who use their source in different way (Wolf et al 2007).

(c) *Spatio-temporal variation*. Environmental conditions usually change in space and time, which variability could translate to variation in selection pressure. The coping of a population with variability of space and time depends on the situation (Moran 1992, Leimar 2005) and on how individuals can adapt to their local environment. In those cases when different environments favour different states, the variability of space can characterize the coexistence of behavioural types. Similarly, we can interpret the coexistence of phenotypes with the variability of the environment in time. The study of Dingemanse *at el.* (2004) is a good example for that the fluctuation of the environment in time favours the coexistence of brave and shy individuals, that is environment one time favours the brave individuals while at other time the shier ones.

(d) *Non-equilibrium dynamics*. The above mentioned examples support the idea that natural selection favours equilibria when given strategies coexist at stable frequencies. However, in several cases various factors can develop non-equilibrium mechanisms; for example resource competition (e. g. Huisman and Weissing 1999), frequency-dependent selection (e. g. Weissing 1991) or sexual selection (e. g. Van Doorn and Weissing 2006). An illustrative example for that is the coexistence of the colonizer type detectable in a plenty of, e.g., insect species – that often possess better dispersal ability - and the settler type (Duckworth and Badyaev 2007). Some of those individuals colonize while others settle (who are better competitors); colonizers can usually occupy new spaces, but this feature is less beneficial in a crowded environment (e. g. Duckworth and Kruuk 2009), which means that the proportion of

these two strategies alter dynamically especially if it is coupled with unpredictable and drastic environmental changes.

Causes of (2) adaptive behavioural correlations across contexts and time can be (Wolf *et al.* 2013):
(a) State affecting behaviour in multiple contexts
(b) Inherently stable states
(c) Social conventions

(a) *State affecting behaviour in multiple contexts*. If an individual's state remains stable across time and contexts, then its adaptive state dependent behaviour will be consistent across time. There are states, like sex or different casts in eusocial insects, whose irreversible features result in consistent differences in behaviour. These so called "attendant" states (morphological, physiological or neurobiological features) often develop along quite complex and time-consuming processes; therefore in many cases changing them are either impossible or very costly. For example, behaviours associated with differences in sexes manifest themselves very similarly in different contexts (e.g. parental care or courtship behaviour) developing suites of correlated behavioural traits.

(b) *Inherently unstable states*. In contrast, labile states are not so strict, which means that they are very variable and could change easily in time. For instance, hormone content, energy reserve, blood pressure, which states can easily alter as an impact of different factors (e.g. behaviour). In some cases, however, positive feedback between behaviour and state can help the development of time consistency. For example, an individual will behave in a more optimal way in a given context if it has more previous experience (Rosenzweig and Bennett 1996). A good example is the sure predator recognition that is if an animal could learn to identify the danger, it will reduce the cost of identification, which can increase the frequency of visiting the risky habitat (Griffin 2004). If the information collected from a given situation has an effect on the rate of cost and benefit of behaviour expressed in another context, they can explain the stable differences of correlated behaviours.

(c) The effect of *social conventions* can stabilize the correlation across time and contexts, that is individuals adjust their behaviour based on their previous interactions with others (Nowak and Sigmund 1998, Leimar and Hammerstein 2001). It can be well depicted by the winner-

loser effect that has already been described in several animal species (Chase *et al.* 1994). According to this effect, individuals who have won a previous contest have a higher chance winning the subsequent ones, while those who have lost will probably lose again. A possible explanation is that the individual uses its previous success as a "random past-assymetry" in a given situation (Parker 1974, Maynard Smith and Parker 1976, Van Doorn *et al.* 2003a, b).

Behavioural syndrome can be defined as correlation between rank-order differences between individuals (Bell 2007). Herczeg and Garamszegi (2012) approach behavioural syndromes from a new perspective, namely determine this phenomenon at an individual level and in a continuous scale instead of interpreting at a population level. They hypothesised that if syndromes at a population level could be considered as a consequence of natural selection, then stable suites of correlated behavioural traits should be heritable and should result in fitness benefits at an individual level. They suggested a variable that describes the individual deviation from the hypothetical perfect correlation predicted by the syndrome. This is useful because it can provide an opportunity to study the evolutionary mechanisms responsible for correlations between behaviours (e.g. between braveness and aggression). Contrarily, Dingemanse *et al.* (2012) considered behavioural syndromes not only phenotypic correlations within individuals but also correlations between individuals (which are due to between-individual effects such as e.g. additive genetic or permanent environment conditions). Between individual variation measures how individuals differ from each other in their "average phenotype", while within individual variation measures how repeated responses differ from each other within the same individual. If we carry out boldness and aggressiveness tests on animals and repeat these procedures, then we can measure within and between individual variance. According to Dingemanse *et al.* (2012) we should study how individuals differ from observed between individual correlation instead of studying how individuals differ from a perfect correlation (Herczeg and Garamszegi 2012). Deviation deriving from correlation between individuals is more meaningful biologically (Dingemanse *et al.* 2012) because the relative level of behavioural consistency partly constitutes the subject of sexual selection as a fitness indicator (Dall *et al.* 2004, Schuett *et al.* 2010). According to Garamszegi and Herczeg (2012) it is essentially important to separate the correlation between individuals and within individuals and empirical studies should consider both metrics.

In the light of all this, I believe, it is just as established to study correlations of differences between as within individuals, what can have a considerable effect on the research

of animal personality, however, it is yet to be revealed by future experimental studies scientifically which proves more useful.

What are the main evolutionary and ecological consequences of differences in personality traits and what are their main implications (Wolf and Weissing 2012)?

(1) Life history and demography: Behavioural differences might have an important effect on different life-history traits and demographical variation, which variability has an impact on fitness and population growth rate (e.g. individuals use their resources and environment in different ways).

(2) Population density and productivity: differences can enhance the carrying capacity and productivity of a population (e.g. via competition avoidance, Huges *et al.* 2008).

(3) Dispersal, colonization and invasion: it can be important at the establishment of a new habitat that individuals have different behavioural types, which is to increase the stability and persistence of the population (Chapple *et al*. 2012).

(4) Social evolution: differences can change the direction and outcome of social evolution (e.g. interaction between social responsiveness and consistency; partner choice; handicap principle, McNamara and Leimar 2010).

(5) "Transmission dynamics": behavioural differences can be observed in the susceptibility of infections, virulence and can have a significant effect on the direction and speed of spreading information (Barber and Dingemanse 2010).

(6) Speciation: behavioural differences can contribute to the divergence of incipient species by generating environment to competitive speciation (Duckworth 2009).

(7) Speed of evolution and adaptive potential: differences can speed up evolution allowing a rapid adaptation to environmental changes (Bartett and Schluter 2008).

II. 2. Aims

It can be seen that the research of animal personality is a quite young and dynamically developing area, in the course of which many hypothetical theories (Wolf and Weissing 2010) were published to explain what maintains individual variability, but testing and interpreting them are one of our major challenge nowadays. Based on the above mentioned one of the

aims of my dissertation is to work out a model system that allows us to measure individual differences in behaviour properly under laboratory conditions on a suitable species.

Methods

Firebug (*Pyrrhocoris apterus*) is one of the most common true bug in Europe and can be found nearly everywhere but mainly around linden trees the seeds of which provide its food. As it can be well identified, can be collected easily - due to its mass occurrence, in addition, it is a well breeding species under laboratory conditions and has a quite detailed literature, it seemed to be an ideal model species. They have two known morphological forms, i.e. winged and un-winged ones, which differ in their physiological and behavioural traits (Socha 1993) and thanks to these features it is an appropriate model species to answer the questions raised in the third chapter.

We used the following methods for **measuring animal personality** (Gyuris *et al.* 2011, 2012): individuals were tested in an arena 55 cm in diameter where we placed four plugs as novel objects. We tested all individuals in two tests; the first one was the "braveness test" where we measured how quickly the bugs came from their refuge, while in the second test, i.e. the "open field test" we measured - based on the their trajectories – how thoroughly the bugs explore their environment and how active they are. While validating of this method, we carried out these tests four times in order to demonstrate that these traits are repeatable. Out of the most frequently tested personality traits in literatures we can measure braveness, activity and exploration well.

A further aim of my dissertation is to investigate - with the help of this method - whether any consistent individual differences can be measured in firebugs and whether life-history differences can explain stable differences in behaviour in a given population (Chapter 3). On the other hand to explore what extent of personality traits remains stable and along what axes personality changes across ontogeny (Chapter 4). Thirdly, I examine whether a parasite infection (Chapter 5) has any effect on differences in personality traits (Chapter 6).

II. 2. 1. Consistent individual differences in behaviour

A study of Wolf *et al.* (2007) provides an adaptive explanation for the question why different personality types coexist in a stable way within a population. The hypothetical model is based on life-history theory, and it states that differences in future reproductive expectations should result in differences in risk taking behaviour. Those who have higher future expectations, i.e. who have much to lose, should behave in a more risk-avers way compared to those who have lower future expectations. Since each behavioural trait is correlated, therefore risk-taking behaviour can associate with aggression and activity, and these result in the evolution of animal personalities. In this Chapter of my dissertation my aim is to examine whether the above mentioned theory can be supported empirically, that is whether individuals who have different life-history strategies and different future expectations have different personalities as well. Firebug is an excellent model species to test this question because it has two different morphological forms that possess different life-history strategies. We have known that its winged form can disperse better despite its flightlessness, while its un-winged form starts to reproduce sooner (Socha and Zemek 2003, Socha and Zemek 2004). We assume that since winged firebugs have lower residual reproductive value (since first they disperse, which is riskier, and only after that they start to reproduce) than un-winged ones, therefore they should be brave and more explorative.

II. 2. 2. Stability and changes of personality traits across ontogeny

Circumstances that an individual experiences in its early life stage can have an important impact on its succeeding life periods (Lumma and Brock 2002). For instance, Rödel and Meyer (2011) found in laboratory rats (*Rattus norvegicus*) that early development can change the ontogeny of personality, namely who were born heavier those were braver and more explorative later. An individual goes though determinate life-stages (e.g. childhood, pubescence, adulthood) along its life. Individuals have to cope with different challenges in different life-stages (e.g. juveniles' primary "aim" is growth, while in adulthood it is reproduction) and selection forces can act on them differently (McNamara *et al.* 2009) in this way in given stages different trait can be beneficial. Based on these we suppose that individuals will respond to the same situation in different ways in different life-stages. One can expect that along the important life-stage transitions during which individuals go through

from one stage to another (e.g. becoming an adult, or reaching sexual maturity), their personalities will also change. Hedrick and Kortet (2012) showed that juvenile field crickets (*Gryllus integer*) were selected for intensive feeding to grow larger in spite of high predation risk, because they can later gain significant fecundity benefit as adult. At the same time, sexually mature individuals should be risk-averse because they have already collected the resources that can be invested into reproduction (Niemelä *et al.* 2012). These examples illustrate well that based on the theory of life-histories one can expect that individuals in their early stages are selected for maximizing their grow rate, survival and dispersal, while in adulthood to maximize their reproductive rate (McNamara 1996, Roff 2002). In the second paper constituting Chapter 4 of my dissertation I set out to furnish an answer to the question that how personality changes in association with life-history traits across a major life-stage transition. In accordance with a study of Stamps and Groothius (2010), we examined the changes across ontogeny on two levels in firebugs (*Pyrrhocoris apterus*). By measuring *individual consistency* we tested how similarly an individual behaves in the same situation at different times. At group level, we measured first how stable behavioural differences remain across ontogeny (*differential consistency*), second how firebugs' behaviour differ before and after sexual maturity (*mean-level consistency*). Third, we examined how correlations of behavioural traits differ between these two life-stages (*structural consistency*). To answer to this question we used the above mentioned personality test.

II. 2. 3. Occurrence of *Hemipteroseius adleri* ectoparasitic mites in Hungary

Hemipteroseius adleri (Costa 1968) belongs to the family of Otopheidomenidae most members of which are parasites of insects (Lindquist *et al.* 2009). Belonging to *Hemipteroseius* genus only this species is known from Europe (Poland and Lithuania, Lewandowski and Szafranek 2005) and from Israel (Costa 1968), which lives on firebugs (*Pyrrhocoris apterus*). Presumably, they live everywhere where firebugs do but it was us that described its occurrence in Hungary for the first time. Chapter five of my dissertation consists of a descriptive paper about the occurrence of *H.adleri* in Hungary.

II. 2. 4. Ectoparasitic mites (*Hemipteroseius adleri*) and firebugs' (*Pyrrhocoris apterus*) personality traits

One of the main causes of mortality of brave individuals is predation, which can exert an important effect on the evolution of personality traits such as activity, braveness and exploration (Dingemanse 2007). The adaptive significance of risk-taking depends on their relative rate of cost and benefit: if predation is low, brave individuals have higher fitness benefits, while if predation is high, then shy individuals have higher fitness benefits (Sih *et al.* 2004). Parasitism may cause fitness costs very similar to that of predation, because parasites are significant mortality factors but can also be a source of non-lethal fitness costs (Raffel *et al.* 2008, Rohr *et al.* 2009). Because of this effect and as some personality traits affect the probability of being infected or the resistance against parasitism (Wilson *et al.* 1993, Hart 1997), one can assume that parasites can have an effect on the evolution of personality. One of the ideas suggests that parasites act as a selective agent on personality and behavioural traits, the causes of which are that an individual's behavioural type can influence the chance of being parasitized. The other direction suggests that parasites themselves induce the individual differences in host behaviour in local populations, that is host behaviour can be considered as a consequence of infections (Barber and Dingemanse 2010). In this chapter of my dissertation my aim is to examine how the ectoparasitic mite *Hemipteroseius adleri* act on firebugs' behaviour. In this study we measured the infected and non-infected firebugs' personality traits and tested statistically the above mentioned two ideas, namely how the extent of infection affects behavioural traits and on the other hand how behavioural types influence the chance of becoming a host. Further aim of this study is to test a recently described phenomenon which suggests that firebugs change their habitats, i.e. climb up to trees, in order to avoid *H.adleri* mites. Zemek and Socha (2009) showed that firebugs collected from the ground were more infected than firebugs collected from trees. We registered the habitat types (from which they were collected) and with the help of this we could test whether individuals collected from different habitats differ in their personality traits.

II. 3. New scientific results of the dissertation

II. 3. 1. Consistent individual differences in behaviour

> *Gyuris, E., Feró, O., Tartally, A., Barta, Z. Individual behaviour in firebugs (Pyrrhocoris apterus). **Proceedings of the Royal Society B: Biological Sciences,** 2011, **278** (1705) 628-633.*

We showed that personality differences can be measured well in winged and un-winged firebugs, i.e. different individuals behaved similarly in different situations. Our result supports the theoretical model published by Wolf *et al.* (2007) that is individuals with different reproductive expectation differ in their personality traits. Measuring personality of winged and un-winged firebugs we found that winged females are braver and more explorative than un-winged conspecifics. These differences support the above mentioned hypothesis, as it has previously been demonstrated that the two morphological forms have different life-history strategies. Since females usually invest more into reproduction through the big and valuable eggs than males we can suggest that differences of life-history traits will affects them more, and this is why we did not detect differences in the behaviour of winged and un-winged males.

II. 3. 2. Stability and changes of personality traits across ontogeny

> *Gyuris, E., Feró, O., Barta, Z. Personality traits across ontogeny in firebugs (Pyrrhocoris apterus), **Animal behaviour**, 2012, **84**, 103-109.*

In this study, we have found that firebugs show consistent behaviour across a major life-stage transition, namely when they reach sexual maturity, besides, the correlation structures of behavioural traits also remain across this transition, which accords well with the findings of Rödel and Meyer (2011) in laboratory rats. We have shown that behaviour is most consistent in adulthood, which is promising because human studies also found the same, that personality will change less with advance of age (Roberts *et al.* 2001). Investigating the alteration of absolute values of behavioural traits we found that larvae behave in a different way than

adults. Larvae started to explore their new environment earlier that is they behaved in a braver way than adult firebugs, visited more novel objects, explored their environment more thoroughly and they were more active. These differences can be explained with that individuals in different life-stages have different life-history expectations (Wolf *et al.* 2007, McNamara *et al.* 2009). We assume that larvae's first "aim" is to feed while for an adult reproduction is more relevant (Roff 2002), this is the reason why larvae can tolerate higher predation risk. Therefore, in different life-stages different behaviours or different levels of the same behaviour will be beneficial (Wolf *et al.* 2007), which hypothesis was supported by our results.

II. 3. 3. Occurrence of ectoparasitic mites (*Hemipteroseius adleri*) in Hungary

Kontschán, J., Gyuris, E. - Hemipteroseius adleri Costa, 1968 collected on red firebug: the first record of the family Otopheidomenidae Treat, 1955 (Acari: Mesostigmata) in Hungary. **Opusc. Zool. Budapest,** *2010,* **41** *(2), 241-243.*

I exhibit a description of a new mite species in Hungary in Chapter 5.

II. 3. 4. Ectoparasitic mites (*Hemipteroseius adleri*) and firebugs' (*Pyrrhocoris apterus*) personality traits

Gyuris, E., Hankó, J. F., Feró, O., Barta Z. Ectoparasitic mites (Hemipteroseius adleri) and firebugs' (Pyrrhocoris apterus) personality traits (manuscript)

Our aim was to investigate whether there are any relations between firebugs' behaviour and their infection caused by their ectoparasitic mites (*H. adleri*). Comparing personality traits of firebugs infected by *H. adleri* with non-infected ones we found that individual differences can be measured (braveness, exploration, activity), and that correlation structures are similar in the two groups. An interesting phenomenon observed in firebugs is the habitat-switching behaviour as an anti-parasite strategy, which means that they climbed up to trees to avoid

mites (Zemek and Socha 2009). Based on this phenomenon we examined the infection and behaviour of firebugs collected from different habitats. Although we did not find any significant differences between the prevalence of mites in firebugs collected from three different habitats, nevertheless our result showed that out of the three habitats the extent of infection is the lowest at the bottom of tree trunks. Since we observed a wild population and we did not carry out experimental study, therefore we do not know exactly whether the observed behavioural difference is the consequence of an infection or individuals will be infected as a consequence of their given behaviour in a given way (Barber and Dingemanse 2010). We tested statistically the two directions and we found that the extent of infections has a slight effect on behaviour that is females who behave in a shier way compared to males will become braver. We also examined how the measured behavioural variables affect the number of mites, and we found that braver females have higher chance to be infected than shier ones. Verifying these results further research is ongoing now in the course of which we model an infection in order to examine behaviour before and after an infection. Morphological measurements were also carried out on firebugs; we measured symmetry indices and found that the less symmetrical individuals are, the more mites they have. Based on these, we assume that symmetry can be a quality signal referring to developmental deviations of the individual.

II. 4. Conclusion and future prospects

Existence of consistent individual variation is a quite complex and structured phenomenon, which can be defined as animal personality, behavioural syndrome and temperament (Bell 2007, Réale *et al.* 2007), and the causes and consequences of which belong to the most current interest of the new, dynamically developing area of behavioural ecology.

One of my aims was to set up a system which provides us an opportunity to measure stable individual differences in behaviour (Chapter 3). Arthropoda constitute more than two thirds of the animal species of the Earth, therefore we can see a wide spectrum of individual differences in behaviour in the course of their study. Observations aiming to answer the above mentioned questions have been mainly carried out on vertebrates in spite of the fact that it is worth several reasons to choose arthropods as model species. They have small body size, so one can keep them in a laboratory in high density and they have short life-cycles so we can

follow individuals' life history, and can carry out experiments without the necessity of ethical permissions. We exploited these advantages and chose firebugs (*Pyrrhocoris apterus*) as a model species, a further advantage of which is that they are very common and well-identifiable insect species. The method introduced in my dissertation is suitable for measuring the most frequently examined personality traits, i.e. braveness, exploration and activity. The construction and completion of the test is simple and the introduced statistical methods can be applied to other animal species. Several theoretical hypotheses were published to explain the existence of stable individual variance (Wolf and Weissing 2010), but only a few empirical studies are there to verify them. In Chapter 3 I covered one of these gaps, and tested a hypothetical model (Wolf 2007) which suggests that these differences are caused by the individuals' optimization between their actual and future reproductive values why they use different strategies. The two morphological forms of firebugs seemed to be suitable to furnish an answer to this question, and our results show that the existence of different life-history strategies (in our case it means stable state differences, that is we used winged and un-winged forms) refer to different personality traits (Gyuris *et al.* 2011). Nevertheless, these differences could only be found in females and we suppose that it is a consequence of the fact that different sexes invest to a different extent into their actual reproductive value. These results raise further questions, for instance, that to what extent does the ratio of different forms promote the stability of a population (Chapple *et al.* 2012), and how stable or non-equilibrium dynamics are followed by the coexistence of these forms within a population (Van Doorn and Weissing 2006). In Chapter 4 I examined personality change across an important life-stage transition (Gyuris *et al.* 2012). Firebugs reach sexual maturity after their final moulting to adult. Our results show that personality remains consistent across this transition but larvae differ from adults in their behaviour. We suppose that this can be explained by that individuals in certain life-stages have different life expectancy (McNamara *et al.* 2009). In this study we used indices for measuring animal personality introduced by Stamps and Groothuis (2010), and we measured the alteration of personality at group and individual levels. In this paper we proposed that using these indices is essentially important and useful because measuring personality from different aspects would answer different questions. Another important result of this Chapter is consonant with human findings, that is personality mostly remains consistent in adulthood (Roberts *et al.* 2001). Our study might provide a basis for further research of fields like during which important transitions of life-stages personality changes and along what axes.

Chapter 5 consists of a description of a new mite species in Hungary (Kontschán and Gyuris 2010). Parasitism might be a crucial factor that is responsible for individual variation in behaviour, but the direction and consequences of these effects are less-known (Barber and Dingemanse 2010). In the last part of my dissertation, I examined the relation of this parasite mite and firebugs' personality traits. In the course of the research, we compared personality traits in infected and non-infected individuals and we tested statistically whether the extent of infection affects behaviour and, vice versa, whether behaviour has any effects on infection to give a general picture about the system. Building on this study, a current research is going on to investigate how individuals' immune responses correlate with the extent of infections and if we can model this system in laboratory conditions.

The causes and consequences of the development of stable behavioural variability are still not entirely clear; there are several questions still to be answered. Firebug is not a eusocial insect but according to the literature (Socha 1993) it is described as a presocial species – which is an initial form of social behaviour. One can observe firebugs aggregating mainly in autumn and early spring, but we still do not know whether it develops as a passive aggregating or because of the social susceptibility of individuals. In our current research we are measuring whether there are any consistent differences in social behaviour and whether it correlates with animal personality.

II. 5. Acknowledgements

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Chapter III.

Study 1: Individual behaviour in firebugs (*Pyrrhocoris apterus*)

Individual behaviour in firebugs (*Pyrrhocoris apterus*)

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The concept of animal personalities has recently become of major interest as researchers began to wonder why animals within a given population show consistent behaviour across situations and contexts, what led to the evolution of such behavioural inflexibility and what mechanisms might underlie the phenomenon. A recent model explains individual differences in a population as the result of trade-off between present and future reproduction. We tested this model on the two wing morphs, i.e. short-winged (brachypterous) and long-winged (macropterous) specimens of the firebug (*Pyrrhocoris apterus*). Since it has been already demonstrated that the two wing morphs differ in their life-history strategies, this species is an ideal subject to test whether the specimens with different life-history strategies have different personalities as well. The results show that individuals behave consistently over time and across contexts, meaning observed bugs do have personalities. We also have found that in females, the two wing morphs have different personalities supporting the theoretical predictions, i.e. winged ones, which are supposed to have lower future reproductive value, are braver and more exploratory. We found no difference between the morphs in males. Differences in reproductive investment might explain this discrepancy between the sexes.

Keywords: animal personality; firebug; wing dimorphism; male–female differences; life history

1. INTRODUCTION

Animals of the same sex and size in the same population usually differ in their behaviour and the underlying physiology even under standard conditions [1–3]. Moreover, the same set of animals shows the same kind of differences in different situations (e.g. in level of predator avoidance at different foraging sites) and contexts (e.g. boldness in foraging and social interactions). For instance, in the field cricket *Gryllus integer* Scudder, 1902 (Orthoptera: Gryllidae), more aggressive males who won more fights had shorter latencies to become active when in a novel environment and shorter latencies to emerge from a safe refuge [4]. Besides being more aggressive, these males are also more active in general, and possibly less cautious towards predation risk [4]. Although individuals could adjust their behaviour depending on situations, nevertheless, consistent differences between individuals usually remain [5]. These are frequently characterized as animal personalities [6], temperament [7], behavioural syndromes [5] or coping styles [8].

The acceptance of the phenomenon that animals have personalities is now widespread, but its evolutionary origin is still a mystery, since a more flexible structure of behaviour should provide a selective advantage [3,9,10]. Recently, Wolf *et al.* [11] have presented a model that offers an adaptive explanation to animal personalities. The model seeks answers to why different personality types (e.g. bold and shy) coexist, why

behaviour is not more flexible for a long time and across situations and why the same traits correlate in different taxa. According to this model, density-dependent selection often leads to dimorphic populations where, because of the trade-offs between present and future reproduction, some of the individuals invest more in their future reproduction than others, resulting in the coexistence of different life-history strategies. As a consequence, the individuals with better future prospects are expected to be risk aversive, while those who have less to lose in the future take greater risks in a situation. As these life-history differences between individuals persists over time and across situations and contexts, one can expect consistent individual differences in behaviour that are correlated across situations and contexts, i.e. the emergence of personalities and behavioural syndromes.

To test the model by Wolf *et al.* [11], one needs a dimorphic population where individuals with different life-history strategies can be readily recognized and then the personality of the different types assessed. Populations of common firebugs (*Pyrrhocoris apterus* (Linnaeus, 1758) (Heteroptera: Pyrrhocoridae)) offer a good opportunity for such investigations. This bug is one of the most common species of Pyrrhocoridae in Europe, and has two wing morphs: macropterous (long-winged) and brachypterous (short-winged) ones. These morphs coexist in the same population, and several studies have shown that the macropterous individuals have a better ability to disperse, despite their flightlessness, and they delay reproduction, whereas the brachypterous

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individuals start to reproduce much earlier [12,13]. Consequently, these two forms seem to follow different life-history strategies: they can be considered as two alternative solutions to the dilemma of dispersing or staying [14,15]. The coexistence of disperser and phylopatric morphs in the same populations is rather common in insect species living in a metapopulation structure [16–18], where local catastrophes eradicating local populations make dispersing to be essential for long-term persistence [19]. In order that the two morphs have different personalities, the model by Wolf *et al.* [11] requires that the individuals belonging to the different morphs should have different residual reproductive values.

To show this, we consider a metapopulation where the two morphs coexist and where a female can produce both morphs. For simplicity, we assume that the two morphs differ only in their migratory tendency: the brachypters never migrate from a patch while the macropters always do so. From their similarity, it follows that their reproductive values just before egg laying (the number of adult descendants gained in the next generation) are the same, W_1, if they are in the same patch, i.e. if the macropters have immigrated into an already occupied patch. On the other hand, when a macropter colonizes an empty patch, it gains W_0 adult descendants in the next generation. We assume that $W_0 > W_1$ because of density-dependent effects. The probability of reaching an empty patch is given by the proportion of empty patches, p (i.e. the macropters choose patches at random), and the probability of surviving migration, q. Then, the reproductive value of brachypters is $W_B = W_1$, while that of the macropters *before* migration, W_M, is as follows:

$$W_M = [pW_0 + (1 - p)W_1]q.$$

For $W_M < W_B$, the following condition must be fulfilled:

$$q < \frac{1}{1 + p(W_0/W_1 + 1)}.$$

An acceptable estimate of p can be 0.01, meaning that a patch exists for 100 years on average, which is reasonable for linden trees, the main habitats for common firebugs [13]. As a brachypter female can have around 150 hatched larvae under ideal laboratory conditions [20], a reasonable value for $W_0/W_1 + 1$ would be 50. With these values, $W_M < W_B$ holds for $q < 0.67$. Given that brachypters are more fecund than macropters in many cases [18], which contradicts our no-difference assumption above, the condition of $W_M < W_B$ can hold for even larger values of q. Therefore, we may conclude that macropters have lower residual reproductive value than brachypters. Consequently, based on the model by Wolf *et al.* [11], one would predict that macropterous morhps would be braver and more exploratory than the brachypterous morphs. Furthermore, as several differences were found between males and females in firebugs (e.g. macropterous females have lower sexual activity [13]) and females invest more in reproduction, we expect that different life-history strategies would have a larger effect on females.

In this paper, we first investigate whether firebug individuals behave consistently over time and across contexts, i.e. whether they have personality. Second, we test the

following predictions: (i) macropters are braver and more exploratory than brachypters and (ii) these differences are more expressed in females than in males.

2. MATERIAL AND METHODS
(a) *Experimental animals*
The experimental animals were collected in four batches (to obtain enough of the rarer macropterous forms) from wild populations in Debrecen (47.52° N, 21.62° E; 130 m a.s.l.; subcontinental climate), northeast Hungary, in 2008 and 2010. Each bug was accommodated for a maximum of 8 days in the laboratory before the behavioural observations. The bugs were kept and the behavioural tests were performed in an air-conditioned laboratory that provided buffered conditions (mean air temperature: 23.25°C, range 23.0–24.0°C). Food (sunflower and lime tree seeds) and water were provided ad libitum.

One group of 60 brachypterous female bugs was used to test the consistency of behaviour over time. During these investigations, the firebugs were tested (see below) four times over a period of 5 days (the first two tests were separated by a 1 day break from the second two tests because of logistical reasons). These bugs were kept separately in jars between tests. In the other three groups (84 bugs (macropters: 7♀, 35♂; brachypters: 8♀, 34♂), 80 bugs (macropters: 13♀, 27♂; brachypters: 13♀, 27♂) and 100 bugs (macropters: 30♀, 20♂; brachypters: 30♀, 20♂) collected in the spring, summer and autumn, respectively), we tested our predictions.

(b) *Behavioural test and walking path analysis*
The tests were carried out in a circular arena of 55 cm in diameter with black wall (46 cm high), where four coloured plugs (made of gum, 0.75 cm high, 1.83 cm in diameter) as novel objects were placed on the floor. The floor of the arena was covered with white filter paper. This paper and the plugs touched by bugs were replaced after each run (they were used only once to avoid uncontrolled olfactory cues). The experimental arena was lit by two 18 W fluorescent-type MASSIVE tubes during the tests.

In the first part of the test, we measured fear responses (emerging from a refuge), while in the second part, we performed an open field test (responses to startling stimulus after arrival to a new environment). At the beginning of the test, the experimental animal was put into the arena in a brown semi-transparent vial (length: 9 cm, diameter: 2.56 cm). The bug was kept in the vial covered with paper (to prevent it from leaving) for a minute to get used to the environment. After the minute had passed, the vial was flicked as a startling stimulus (also to ensure that all bugs were at the end of the vial), laid on its side and the paper removed so that the bug could leave the refuge. Then we waited for the bug to leave the vial for a maximum of 10 min. Both the time when the antennae appeared first and the time when the bug actually came out were registered, but later we only used the time of the first appearance of the antennae (referred to as *emergence* hereafter) because many bugs (115 out of 264) did not emerge at all from the vial. We consider emergence as a measure of boldness.

The bugs leaving within 10 min were put back into the vial, while bugs remaining in the vial were left in it. In both cases, i.e. when (i) the bug left the vial itself and then was put back or (ii) remained in the vial, the vial was then flicked

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again (to be in the end of the vial) and the bug was kept in it for another minute, which was followed by yet another flick (to detach the bug from the wall of the vial), after which the bug was placed into the arena by shaking it out from the vial preferably into the centre of the arena. The time when the bug started to move after its placement into the arena (*walking latency*, another measure of boldness) and the time when it reached the wall (*wall time*, a measure of exploration) were registered and an observation lasted 10 min. We also recorded how many novel objects were visited (*number of novel objects*, measuring explorativeness).

A Quickcam S5500 webcam was used to record the movement of the bug at 1 s intervals, until it reached the wall for a maximum of 10 min. From the pictures taken, we reconstructed the path of each bug as a list of *x*-, *y*-coordinates. These lists were then used to derive the following variables for each bug: (i) the mean and (ii) the variance of step sizes (the distance between two consecutive positions), and (iii) the mean and (iv) variance of turning angles [21–24].

(c) Statistical analyses

To test the consistency of the behaviour over time, we measured the behavioural variables (see above) four times for each individual in a group of 60 brachypterous females. Then we calculated Kendall's W coefficient of concordance for each measured variable. Values of W significantly differing from random expectation mean that the individuals' rankings based on a given behavioural variable are in agreement among the different times of measurement [25], i.e. the individuals behave consistently over time [26]. We used permutation tests to infer levels of significance [25]. As we did not vary the situations over the tests (i.e. the level of risk was the same across all four repetitions), this procedure is unable to detect behaviour plasticity.

We have also investigated whether the behaviour of firebugs is consistent across contexts by calculating Kendall's W involving all measured behavioural variables. This analysis was performed on the combined dataset of the three larger groups of bugs (see above). To account for the possible effects of grouping, we subtracted the appropriate group median from each individual measurement for those variables where a Kruskal–Wallis test indicated significant difference among the groups (we used median because of the highly skewed distribution of many of the variables). To identify possible associations among the behavioural variables, i.e. possible personality axes, we followed the procedure outlined in [25]. In short, we computed a Spearman rank-correlation matrix among the variables and performed an agglomerative clustering ('agnes' function of the R statistical environment with Ward's clustering method) using one minus the absolute value of correlation coefficients as dissimilarity measures. Groups of correlated variables were identified by inspecting the mean overall silhouette values for the given number of groups (M. Maechler, P. Rousseeuw, A. Struyf & M. Hubert 2005, unpublished data; http://cran.r-project.org/web/packages/cluster/citation.html). To assess the robustness of this partition of the variables, we calculated consensus partition from 1000 random permutations of the original data frame [27]. A random permutation is obtained by randomly permutating a randomly chosen column of the original data frame. To test for significant associations, we submit each group of variables to a separate test of concordance. To characterize the bugs with these personality 'axes', we

calculated a composite rank variable for each group of variables. This composite variable is simply the sum of the individuals' ranks for the variables in the given group [25].

To test the effect of wing morphology and sex on personality traits, we performed general linear model analyses on the composite variables. In these models, the given composite variable was entered as response and the wing morphology (two levels: macropterous and brachypterous) and sex (male, female) were entered as explanatory variables. We also analysed the individual behavioural and path variables. As most of the behavioural variables were highly skewed and often truncated, we dichotomized these variables (using the medians as cut points) and used generalized linear models with binomial error distribution and logit link function (i.e. logistic regressions). Here, the categorized behavioural variable (e.g. 'slow' and 'fast' emergence) was the dependent variable while wing morphology and sex were entered as explanatory variables.

All statistical analyses were carried out in the R interactive statistical environment [28] with irr [29], cluster (M. Maechler, P. Rousseeuw, A. Struyf & M. Hubert 2005, unpublished data), boot [30,31] and vegan [32] packages.

3. RESULTS

(a) Consistency of behaviour over time

We found that firebugs behave consistently over time as all but two W calculated for the behavioural and path variables were significantly different from random expectation (emergence: $W = 0.386$, $p = 0.003$; walking latency: $W = 0.481$, $p < 0.001$; wall time: $W = 0.402$, $p < 0.001$; number of novel objects: $W = 0.283$, $p = 0.236$; mean turning angle: $W = 0.271$, $p = 0.322$; variance of turning angle: $W = 0.394$, $p = 0.002$; mean step size: $W = 0.443$, $p < 0.001$; variance of step size: $W = 0.495$, $p < 0.001$).

(b) Consistency of behaviour across contexts

Firebugs responded similarly in the different contexts as shown by the significant Kendall's coefficient of concordance ($W = 0.198$, $p < 0.001$). This means that the bugs were similarly ranked by all variables.

On the basis of the Spearman correlation matrix and the cluster analysis, our variables can be divided into the following groups (figure 1). The first group consists of emergence and walking latency, so it might be considered as a kind of shy–bold axis of personality. Kendall's W calculated for this group of variables is highly significant ($W = 0.625$, $p = 0.003$). The second group identified can be considered as the exploratory axis of bugs' personality since it contains the variables of wall time, variance of turning angle and number of novel objects visited. Kendall's W calculated for this group is also high and significant ($W = 0.594$, $p = 0.003$). The third group consists of mean step size and variance of step size (Kendall's $W = 0.920$, $p = 0.003$). Finally, mean turning angle appears not to correlate with any of the other variables. The interpretation of these last variables is less clear. The three composite variables and the mean turning angle are not significantly consistent (Kendall's $W = 0.254$, $p = 0.429$). The separate analyses of the composite rank variables show that macropterous female bugs are bolder (they have a lower rank) than the rest of the population (sex × wing morph
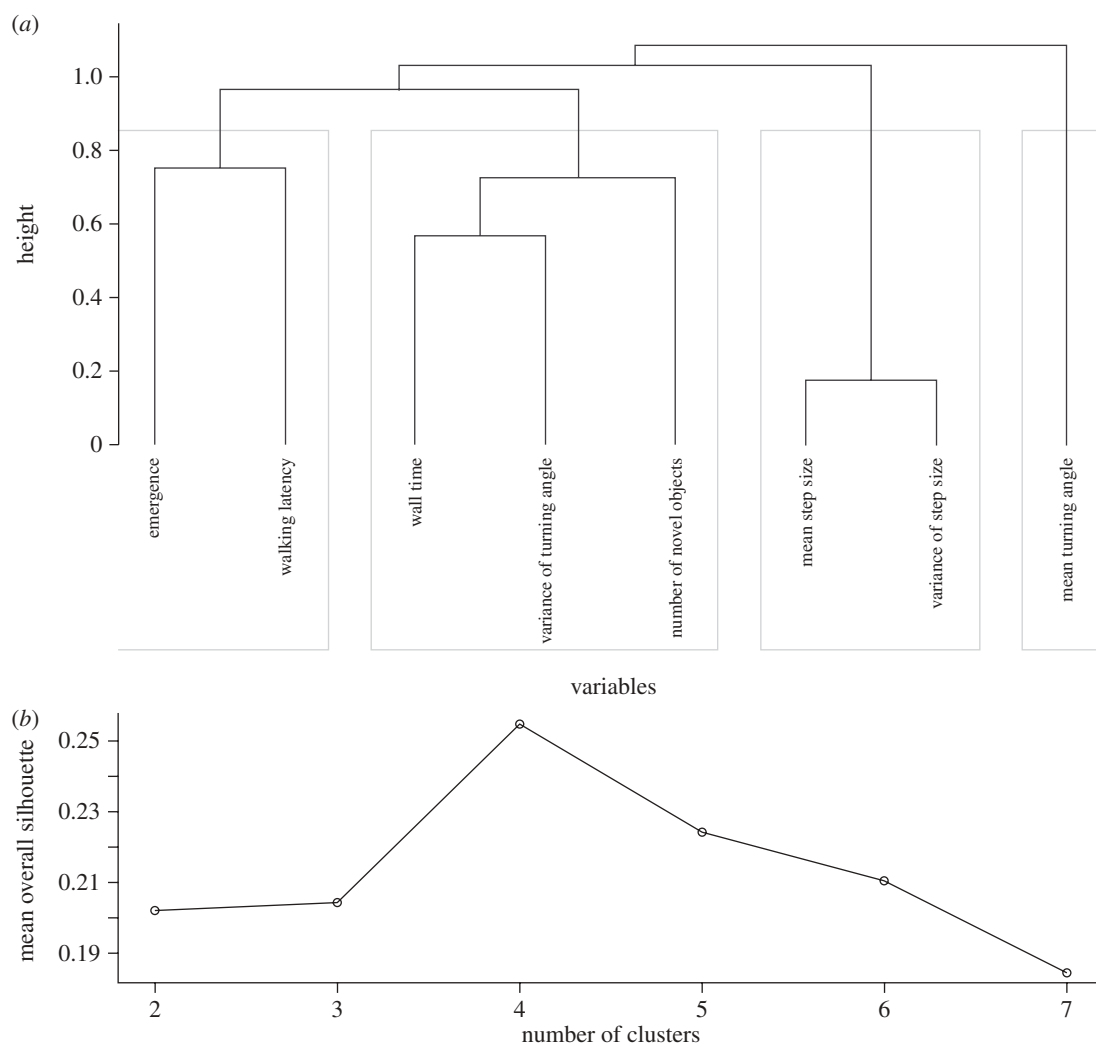
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Figure 1. (*a*) The dendrogram shows the relationship between the investigated variables according to the cluster analysis (agglomerative coefficient is 0.448). 'Height' gives similarity based on the absolute values of the Spearman correlation matrix among the variables (see text for details). Groupings indicate possible personality axes. This partitioning is robust against small random changes in the dataset as the consensus partitioning based on 1000 random perturbations gives the same result. (*b*) Silhouette plot to identify possible groupings of the variables.

interaction; $F_{1,258} = 4.666$, $p = 0.032$). No significant differences were found between sexes and morphs with respect to the other two composite variables and the mean turning angle.

Analysing each measured variable separately showed a similar picture. Macropterous females emerged sooner from the vial (sex × wing morph interaction, $\chi_1^2 = 6.32$, $p = 0.012$; figure 2) than the rest of the population, while brachypterous females visited fewer novel objects (sex × wing morph interaction, $\chi_1^2 = 8.28$, $p = 0.004$; figure 3) than the rest of the population. We found no significant effect of sex and wing morph on the other behavioural and path variables (results are not shown).

4. DISCUSSION
Our results show that there are personality differences between the individuals of the firebug as we found that they behave consistently over time and across context. According to the cluster analysis of the behavioural variables, two axes of firebug personality can be identified: boldness and explorativeness. We also found that personality of the macropterous and brachypterous females

differs; macropterous females are bolder and more explorative than the brachypterous ones. This latter result supports the model of Wolf *et al.* [11], which offers an explanation for the presence of individual differences in a population, namely that individuals choose different strategies to find the balance between present and future reproduction. In the case of firebug, it is known that there are differences in the behaviour of brachypterous and macropterous individuals, e.g. in the higher walking activity [14] and lowered mating propensity of macropterous individuals [13]. Furthermore, reproduction is delayed in the macropterous form [33], which is a common phenomenon in wing-polymorphic insects [34]. All of these indicate a difference in the life-history strategies of the two wing morphs despite the evolutionary loss of the flight capability in macropters [12]. Specifically, the lower sexual activity of macropterous individuals was found only in females and not in males [13]. This is in accord with our results on the bolder and more explorative behaviour of macropterous females compared with brachypterous ones (figures 2 and 3) [12,13]. The finding that individuals of higher dispersal tendency are bolder and more exploratory indicates the
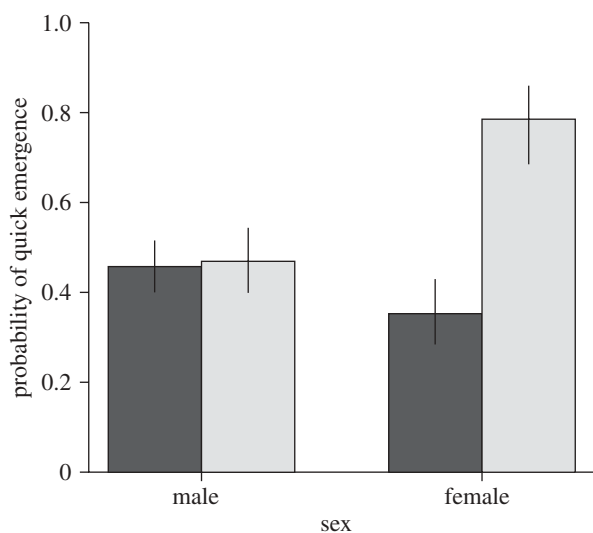
Figure 2. Macropterous females emerged quicker from the vial so they are bolder (expected probabilities, $\pm$ s.e., from binomial glm, sex $\times$ wing morph interaction, $\chi^2_1 = 6.32$, $p = 0.012$, response variable was dichotomized because of its highly skewed distribution). Wing: black bars, no; grey bars, yes.
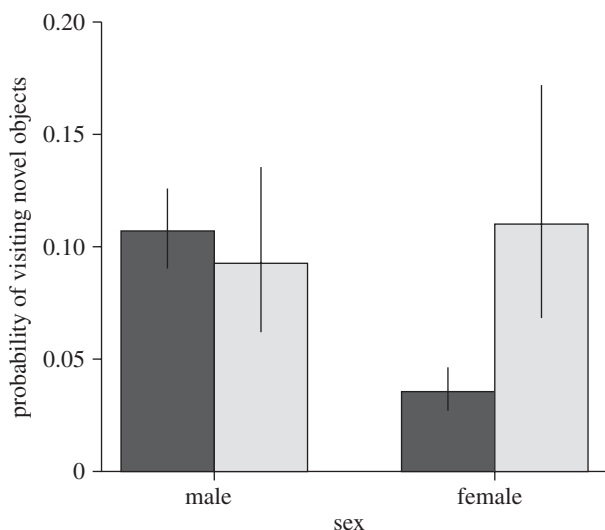

Figure 3. Brachypterous females visited fewer novel objects (expected probabilities, $\pm$ s.e., from binomial glm, sex $\times$ wing morph interaction, $\chi^2_1 = 8.28$, $p = 0.004$). Wing: black bars, no; grey bars, yes.

importance of these personality traits in dispersal. Similarly, Cote *et al.* [35] reported personality being a good predictor of dispersal tendency. The sex differences found can be attributed to the differences in investment into reproduction by the two sexes: as females invest more into reproduction, one would expect a stronger trade-off between current and future reproduction, which in turn can result in a larger difference in personality between morphs in females than in males.

Note that we studied specimens from wild populations, thereby our results validate those of Socha and co-workers [12–15] who found morph differences in firebug behaviour in captive populations maintained for many generations under laboratory conditions.

Further exciting research could investigate why it is only females among which behavioural differences can be detected, to what extent human disturbance alters a given population, whether 'city dweller' bugs that have to endure more environmental stress have different personalities compared with the specimens that live in an undisturbed environment (e.g. in a forest or a park) and to what extent the ratio of macropterous and brachypterous morphs is variable and whether it can be related to the environmental effects that influence the population. Such studies would bring us closer to the solution of an important issue of evolution, the coexistence of different morphs in terms of both life history and personality.

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Chapter IV.

Study 2: Personality traits across ontogeny in firebugs, *Pyrrhocoris apterus*

Contents lists available at SciVerse ScienceDirect

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Personality traits across ontogeny in firebugs, *Pyrrhocoris apterus*

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ARTICLE INFO

Consistent behavioural differences have long been recognized in animals but it still remains unclear how these traits change over ontogeny. As individuals can face different situations over their lives, and their life history expectation may not be the same in different life stages, one can expect that using different strategies in different life stages would be advantageous. Characteristics of animal personality across ontogeny could be measured at group and individual levels. Since personality alteration across time can be studied from various aspects one should use the following indexes: mean-level, differential, structural and individual consistency. We investigated whether common firebugs behave in the same way through a major life stage transition, namely final ecdysis. We measured activity, boldness and exploration twice in the larval stage and also twice when bugs reached the adult stage. We found that the relative value of behavioural traits was stable across ontogeny and the correlation structure among behavioural traits remained constant over time. Nevertheless, larvae differed from adults in general in that they were bolder, explored their environment more thoroughly and seemed to be more active before final ecdysis. These results indicate that personality could change differently across major life stage transitions; therefore this important factor needs to be considered in further research.

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Studying animal personalities may furnish an answer to the question of why individuals of the same sex and age within a population differ consistently in their behaviour in the same context, or to put it more generally, why persistent behavioural variation exists in populations (Sih et al. 2004; Bell 2007; Réale et al. 2007; Wolf et al. 2007). The most studied personality traits in animals are boldness, activity, aggressiveness, exploratory tendency and sociability (Réale et al. 2007). Consistent behavioural traits appear as the result of developmental pathways that are determined by an individual's genes, its developmental environment and the interactions between them (Sinn et al. 2008).

Although animal personality has been intensively studied for a long time (reviewed in Dall et al. 2004; Sih et al. 2004; Dingemanse & Réale 2005; Bell 2007; Réale et al. 2007; Biro & Stamps 2008), the effect of ontogeny on personality development in animals has just started to be explored (Stamps & Groothuis 2010). Circumstances experienced during early life can have important effects on subsequent life stages (Lindstrom 1999; Lummaa & Clutton-Brock 2002). Long-term fitness consequences of early life experiences were demonstrated, for instance, in European rabbits, *Oryctolagus cuniculus* (Rödel et al. 2009). In addition, Rödel

& Meyer (2011) suggested that early development alters ontogeny of personality traits in laboratory rats, *Rattus norvegicus*: the heavier newborns were braver and more explorative. On the other hand, the life of an individual is usually composed of several markedly different life stages (e.g. larval/adult, or sexually immature stage/sexually mature stage) and one might expect an individual's personality to change during the fundamental transitions from one life stage to the other (e.g. during morphogenesis, sexual maturation or moult).

Individuals undergo extensive hormonal changes in the course of sexual maturation, which is obviously a period of behavioural reorganization. Edenbrow & Croft (2011) demonstrated in killifish, *Kryptolebias marmoratus*, that individuals were braver and more explorative in their early developmental stage, which, after sexual maturity, was followed by a lowered expression of such personality traits. Consequently, the developmental change in personality is a characteristic of this species.

As selection pressures can vary throughout life (McNamara et al. 2009), different behavioural traits can be advantageous at different ontogenetic stages. For instance, traits related to acquisition of food, and hence contributing to productivity (growth and/or fecundity), are expected to be expressed differently over an individual's lifetime (Biro & Stamps 2008). Therefore, we suggest that, because they are in different life stages with different fitness potentials (i.e. the juvenile must first grow, while the adult can immediately

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reproduce), juveniles and adults might respond differently to the same situation.

A sexually mature cricket, for instance, should be risk averse because it has successfully collected the costly resources that can be invested in reproduction but, at the same time, can easily be lost (Niemelä et al. 2011). As the cricket's case illustrates, a phenotype, despite being beneficial in an early period of life, does not necessarily match well with the conditions of later life stages (Roberts & Robins 2004; Taborsky 2006). Hence, it is necessary to examine which personality traits are more advantageous in the juvenile stage and which ones in the adult. A recent study in field crickets, *Gryllus integer*, indicated that in spite of predation risk, larvae are selected for feeding intensively to grow large because body size is fixed after the final moult in adults (Hedrick & Kortet 2012). Consequently, juvenile stages may be adapted to maximize growth, survival and dispersal while adults maximize reproductive output (McNamara 1996; Roff 2002). As these studies suggest, investigating personality around life stage transitions can reveal important aspects of personality development and life history as well.

The temporal changes of personality through ontogeny can be studied at two levels: individual and group (Stamps & Groothuis 2010). 'Individual stability' characterizes the extent of temporal consistency in an individual's behaviour, that is, whether a given behavioural trait in a given context will be similar later in time. At the group level we can use the following indexes: differential consistency, mean-level consistency and structural consistency (Stamps & Groothuis 2010). 'Differential consistency' describes the extent to which the scores of individuals are maintained over time compared to the scores of others in the group. 'Mean-level consistency' assesses the extent of change in the mean score of behaviour in a given group in the same context from one time to another. 'Structural consistency' describes the changes in the correlation structure among behaviours, that is, the extent to which the relations among behavioural traits are preserved over time. Structural consistency and differential consistency can change independently. For example, aggressiveness and boldness in a population of three-spined sticklebacks, *Gasterosteus aculeatus*, were positively correlated in juveniles and adults but those that had high aggressiveness and high boldness scores as juveniles were not necessarily bolder and more aggressive as adults (Bell & Stamps 2004).

Recently, we have shown that adult firebugs possess consistent behaviour across contexts and time (Gyuris et al. 2011). It is still unknown, however, how the bugs' personality changes around a major life history transition, the final ecdysis (moult) into adulthood during which they reach sexual maturation. To address this gap in knowledge, we investigated the following questions. (1) Do individuals show any consistency in terms of variation in their behaviour? (2) Does the relative performance of individuals change during sexual maturity, that is, will the bugs that are bolder than the majority as larvae be bolder as adults too? (3) How do average scores of different behavioural traits change during the transition, that is, are larvae bolder or more exploratory than adults? (4) Finally, do the relations between the different behavioural traits alter during the transition? In other words, we investigated individual stability, differential, mean-level and structural consistencies (Stamps & Groothuis 2010) across the final ecdysis in the firebug.

METHODS

Keeping Conditions

Pyrrhocoris apterus is one of the most common species of Pyrrhocoridae in Europe, and can usually be found at the base of linden (*Tilia* spp.) trees, the seeds of which are its main food. The development of the firebug is hemimetabolous, which means there are five larval stages without a pupa and the adult emerges after the fifth ecdysis (Socha 1993). Brachypterous firebugs were taken from laboratory stock cultures which originated from a wild population in Debrecen, northeast Hungary (47.52°N, 21.63°E; 130 m above sea level; subcontinental climate), and have been kept in the laboratory from 24 September 2010. Food (sunflower and linden tree seeds) and water were provided ad libitum and temperature was consistently $25 \pm 1\ °C$. The behavioural tests (hereafter runs) were carried out in January and February 2011.

Experimental Animals

Forty individuals in the fifth larval stage were selected and kept individually in separate jars between the runs. They were tested twice during their fifth larval stage and, after their final moult, twice again. 'Run a' was carried out on the third day after the bugs had moulted into the fifth larval stage and we repeated this run after 1 or 2 days (referred to as 'run b'), while the bugs were still in their fifth larval stage. Of the 40 bugs, 32 moulted successfully: nine females and 23 males. Because sex determination is very difficult in the larval stages we could not ensure a more balanced sex ratio. On the second or third day after the bugs moulted to adult we tested them again (hereafter 'run c'). 'Run d' was carried out on the 2nd or 3rd day after the third one (Fig. 1).

Behavioural Tests and Walking Path Analysis

We used the same series of tests as those in Gyuris et al. (2011), which are briefly summarized below. The runs were carried out in a circular arena of 55 cm in diameter where four plugs as novel objects were set on the floor. We used different plugs with different sizes (all plastic plugs were circular ranging from 1.5 to 5 cm in diameter) and colours (to ensure they would be treated as novel). In each series of runs every plug touched was replaced before the next individual's test (to avoid uncontrolled olfactory cues). The floor of the arena was covered with white filter paper, which was replaced before each test.

Behavioural tests consisted of two 10 min sessions. In the first test, we measured boldness while in the second we performed an open field test. The bug was put into a vial covered with paper (to prevent the bug leaving the vial) and to let it get used to its environment we waited for 1 min. After this time, we flicked the vial once (to ensure that the bug was in the bottom of the vial), removed the paper and laid it on its side. The bug had 10 min to emerge from its refuge. We registered the appearance of the antennae (hereafter 'emergence') and the time until the bug left the refuge (since the bugs left the vial in only 10 of 118 cases we omitted this variable in the rest of the study). The bugs that left the vial were put back into it immediately, while those that did not leave within 10 min were left in it. Again, 1 min habituation was allowed before the second test. In the second test, the open field test, we flicked the vial (to make sure the bug was at the bottom of the vial), then we shook the bug into the centre of the arena. In this test we measured the bug's response to a startling stimulus after it entered the new environment, referred to as 'walking latency'. Then we measured exploration, that is, how thoroughly the bug explored its environment, by recording (1) the time it took to reach the arena wall (hereafter 'wall time') and (2) the number of novel objects visited (hereafter 'number of novel objects'). Activity was also measured in the open field test by recording the pathway of the bug at 1 s intervals until it reached the wall within a 10 min period, and by calculating the following variables: (1) the mean and (2) the variance of step size

(the distance between two consecutive positions), and (3) the mean and (4) variance of turning angles.

Statistical Analyses

To measure individual stability for each variable we calculated the ISS (individual stability statistic) scores as in Sinn et al. (2008). The ISS score is a measure of the difference between an individual's trait responses at two points and therefore a relative measure of the individual's developmental change. As we measured behaviour at four points in time during ontogeny we were able to investigate how ISS scores changed over ontogeny. We calculated these scores between the first and the second, the second and the third and the third and the fourth runs, then compared the scores with a Friedman test because individual scores are not independent of each other.

To test the consistency of behaviour across ontogeny, which can be defined as differential consistency or broad-sense repeatability, we measured all the behavioural variables of the bugs four times (twice in the fifth larval stage and twice as adult, Fig. 1; see above). Then we assessed the consistency across runs by computing the Kendall's W coefficient of concordance for each measured behavioural variable separately (Legendre 2005). We also calculated a composite rank variable for each run as the sum of the individuals' ranks for each variable, and computed Kendall's W coefficient of concordance for these four composite rank variables as an overall measure of differential consistency. Kendall's $W = 1$ means that there is complete concordance among the individuals' scores at different times (across four runs); conversely, if W equals 0, there is no concordance. Since we tested the same statistical hypotheses several times we corrected for familywise errors with Holm's (1979) procedure. We also analysed the behavioural consistency between the consecutive runs with Spearman rank correlations on both the original and the composite variables.

To investigate mean-level consistency, we fitted mixed-effects models with the individuals' IDs as a random factor and run ID as a fixed factor. To control the effect of sex and moulting time (i.e. the time between moulting to the fifth larval stage and to adult) we entered these two variables as fixed effects. We fitted separate models for each behavioural variable entered as the response variable. Since the distributions of most of the behavioural variables were skewed, these variables were dichotomized (e.g. 'slow' and 'fast' emergence) and binomial mixed-effects models were fitted to them (Gyuris et al. 2011). The effect of a given explanatory variable was assessed by a likelihood ratio test (Crawley 2007).

We also investigated whether the correlation structure among the behavioural variables changed across time. We first computed a Spearman rank correlation matrix among the variables for each run. Then we compared all matrices with a Mantel randomization test in a pairwise manner (Manly 1997) with Holm's (1979) correction. If the correlation structure did not change between two runs, we expected a significant relation between the two correlation matrices representing this structure. We also computed the mean of the correlation matrices and used this average matrix, after taking one minus the absolute values of its entries, as a distance matrix to calculate a summarized clustering of the behavioural variables ('agnes' function of cluster package of the R statistical environment, Ward's clustering method).

All statistical analyses were carried out in the R interactive statistical environment (R Development Core Team 2008) with cluster (Maechler et al. 2005), ade4 (Dray & Dufour 2007), vegan (Oksanen et al. 2009) and lme4 (Bates & Maechler 2010) packages.

RESULTS

Individual Stability

We measured the individual's developmental change after calculating the ISS scores between each consecutive run and we found no significant difference between them (Table 1). This result indicates that the magnitude of possible behavioural changes over time did not differ between the life stages.

Differential Consistency (Repeatability)

Of the eight measured behavioural variables five were significantly consistent (Table 1). All of these five consistent variables measure some aspect of the movement pattern of the firebugs. For the consistency of the overall behaviour we found that the composite rank variables were also consistent between runs ($W = 0.407$, $P = 0.011$). In seven of the eight behavioural variables correlation coefficients were largest between runs c and d (Fig. 2; binomial test against the null hypothesis that the probability of the largest coefficients being between runs c and d is 1/3: $P = 0.003$).
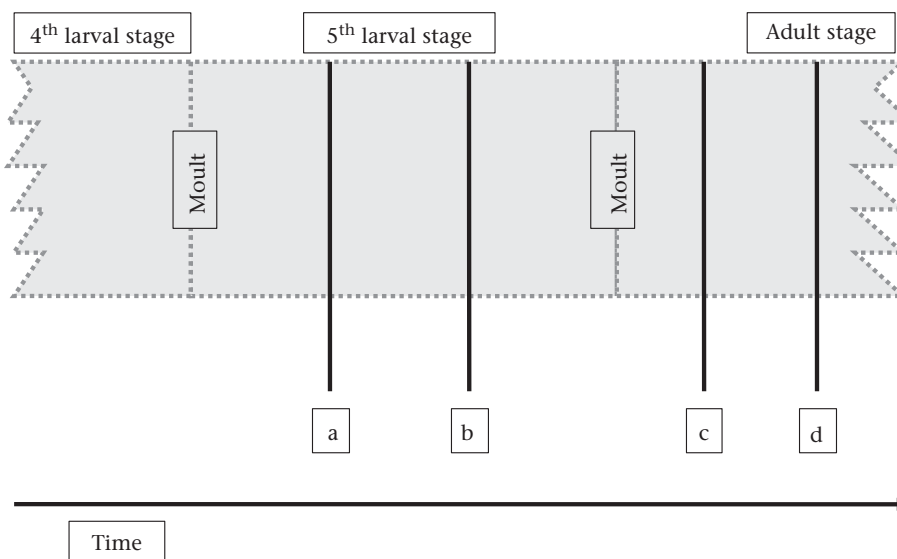

Figure 1. The timing of behavioural tests, marked here as runs, over a period of a firebug's life. Vertical continual lines labelled from 'a' to 'd ' indicate the runs.

Table 1
Different aspects of developmental effects on personality

Indexes		Variables							
		Emergence	Walking latency	Wall time	Number of novel objects	Mean step size	Variance of step size	Mean turning angle	Variance of turning angle
Individual stability	χ_2^2	0.724	0.311	3.111	4.741	2.551	7.103	0.482	0.482
	P	1	0.855	1	0.653	1	1	0.229	1
Differential consistency	W	0.211	0.325	0.454	0.262	0.544	0.521	0.488	0.382
	P	0.687	0.115	**0.001***	0.414	**0.001***	**0.001***	**0.001***	**0.015**
Mean-level consistency	χ_3^2	1.086	16.662	3.001	18.781	8.813	6.887	3.860	3.194
	P	0.780	**0.0008***	0.391	**0.0003***	**0.031**	0.075	0.277	0.362

'Individual stability' characterizes temporal consistency in an individual's behaviour (results of Friedman tests are shown). 'Differential consistency' describes how scores of individuals are maintained over time relative to others in the group (Kendall's W coefficients of concordance are given). 'Mean-level consistency' assesses the change in the mean score of behaviour in a given group in the same context from one time to another (likelihood ratio tests of mixed-effect models are given). P values in bold were significant and those marked by an asterisk remained significant after correcting for familywise error by Holm's (1979) method.

Correlation coefficients calculated between the composite rank variables of consecutive runs supported this result: we found a significant correlation only between runs c and d (between a and b: $r_S = 0.165$, $P = 0.366$; b and c: $r_S = 0.188$, $P = 0.300$; c and d: $r_S = 0.381$, $P = 0.031$; all $N = 32$). These results show that behaviour was more consistent during adulthood than during development.

Mean-level Consistency

Neither the effect of sex nor the moulting time was significant (all $P > 0.078$ for sex and all $P > 0.138$ for moulting time). By analysing the effect of runs we found that the mean values differed strongly across runs for the following behavioural variables: walking latency, number of novel objects, mean step size; in addition, the variance of step size was nearly significantly affected (Table 1). Walking latency was largest after the moult, while the mean and variance of step size were smallest at the same time but later they increased (Fig. 3). The number of novel objects visited peaked immediately after moulting again (Fig. 3).

Structural Consistency

All the pairwise Mantel's tests between the correlation matrices were significant (Table 2). This result means that the correlational structure of the measured variables was similar across the runs.
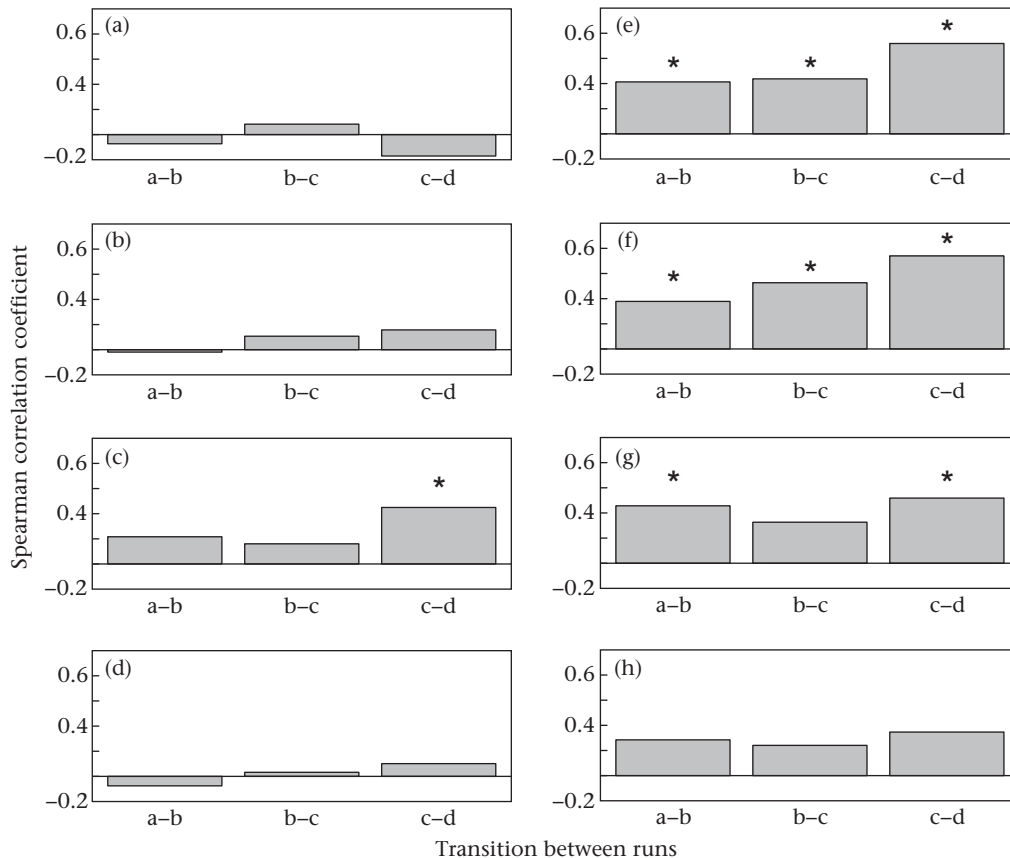

Figure 2. Extent of behavioural consistency between consecutive runs for each variable based on Spearman correlations between pairs of consecutive runs. Variables: (a) emergence, (b) walking latency, (c) wall time, (d) number of novel objects visited, (e) mean step size, (f) variance of step size, (g) mean turning angle and (h) variance of turning angle. Letters from 'a' to 'd' on the horizontal axes mark the runs. Runs 'a' and 'b' were carried out in the final larval stage while 'c' and 'd' were carried out in the adult stage. Asterisks mark significant correlations between runs at $P < 0.05$. The figure is based on the behavioural analyses of 32 firebugs.
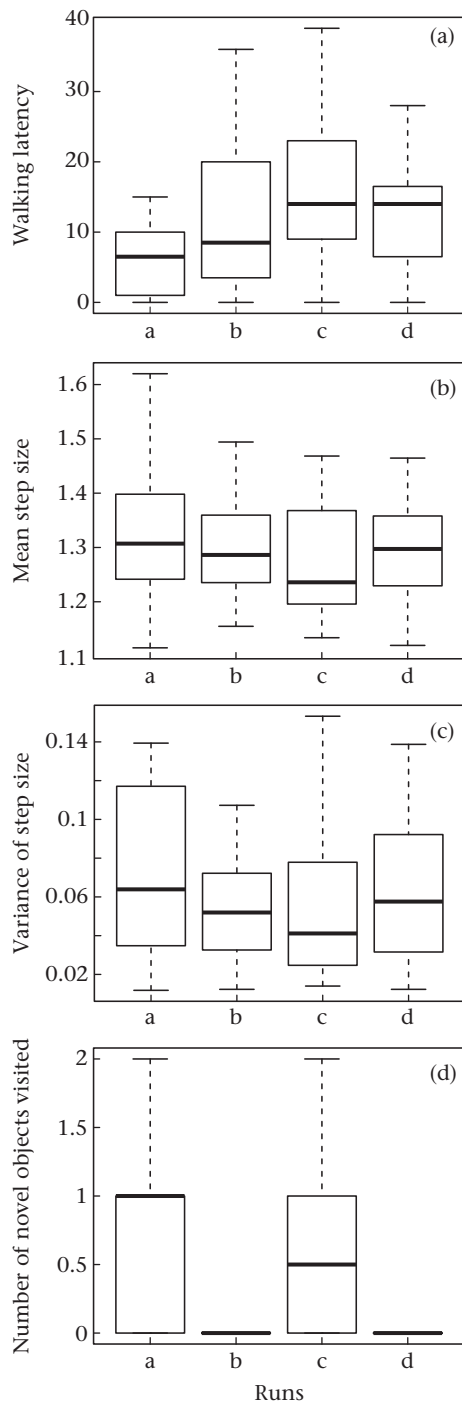
Figure 3. Effect of runs ('a', 'b': in larval stage, 'c', 'd': in adult stage) on different behavioural traits. (a) Walking latency, (b) mean step size, (c) variance of step size, (d) number of novel objects visited. The box plots show the median and 25th and 75th percentiles; the dashed lines indicate the range. The figure is based on the behavioural analyses of 32 firebugs. For further details see text.

Figure 4. Dendrogram showing the relation between the measured behavioural traits, calculated from the average correlation matrix of the four runs. The figure is based on the behavioural analyses of 32 firebugs. For further details see text.

step size and the variance of step size, which can be interpreted as variables of general activity.

DISCUSSION

The final ecdysis, during which firebugs reach sexual maturity, is thought to be a major life stage transition in this insect. In this study we found that firebugs behaved consistently through this transition. The relative value of the individuals' behavioural traits, compared to each other, did not change across ontogeny (differential consistency). The correlation structure of behavioural variables also remained the same during this transition (structural consistency). Rödel & Meyer (2011) similarly found in laboratory rats that personality traits within contexts at different ages are consistent. Niemelä et al. (2011) have also shown in field crickets that personality can change around maturity, but the rank order repeatability between individuals can remain. Our results show that behaviour in firebugs is most consistent during adulthood. This finding is in accordance with human studies, which find that personality changes less over time with greater level of maturity (Roberts et al. 2001).

By investigating the absolute value of the behavioural traits, however, we found that some of them changed across metamorphosis (mean-level consistency). Larvae seemed to be bolder (i.e. they started to explore the new environment sooner), explored their environment more thoroughly (visited more novel objects in the first runs) and seemed to be more active before the final transition (Fig. 3). Hedrick & Kortet (2012) found similar results, with boldness changing across ontogeny in field crickets.

Consistent differences between individuals can be explained by the integrative pace-of-life syndrome (POLS, Réale et al. 2010). This is based on the growth–mortality trade-off (Stamps 2007), which means individuals with a 'slow lifestyle' are expected to have low metabolic rate and to be less aggressive, facilitating risk-averse behaviour (Mathot et al. 2009). Consequently, they have a long

Based on the summarized cluster dendrogram, our variables can be divided into the following groups (Fig. 4). The first group consisted of emergence, variance of turning angle, walking latency and wall time, which can be considered as proxies for the shy–bold personality axis. The second group consisted of mean turning angle and number of novel objects, which can indicate the individual's tendency for exploration. The third group contained mean
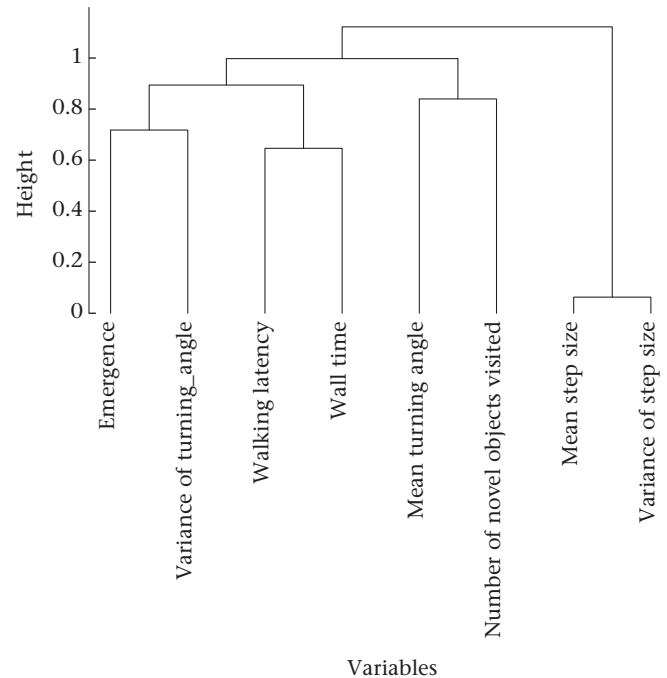
Table 2
Structural consistency of the relations among behavioural traits in firebugs

Distance matrices	r_S	P
a vs b	0.665	0.031
a vs c	0.709	0.010
a vs d	0.808	0.010
b vs c	0.647	0.031
b vs d	0.676	0.031
c vs d	0.787	0.002

Pairwise Mantel tests between rank correlation matrices (r_S) of behavioural scores and their significance (P value). 'a'–'d' represent the runs. All of these P values remained significant after Holm's (1979) correction.

life and long developmental time in contrast to those with a 'fast lifestyle'. Accordingly, one may expect that bugs with a more active, exploratory personality may develop faster. We examined whether the length of the fifth larval stage has any effect on personality traits but found no correlation between any of the behavioural variables and the duration of the fifth stage. Further investigations are needed because we observed only a given life period of the bugs. Another explanation for interindividual differences might be the different life history expectations in different life stages (Roff 2002; Wolf et al. 2007; McNamara et al. 2009). By sexual maturity, the rate of growth decreases or becomes zero in many species and therefore we expect maturity to change the value of different behaviours and hence their level of expression (Niemelä et al. 2011). Weed et al. (1997) reported that home cage activity of male rhesus monkeys, *Macaca mulatta*, declined during their early adulthood. Human studies have shown that the greatest decrease in physical activity occurs during adolescence rather than during adulthood and is related to sexual maturation (Bijnen et al. 1998). Several studies (e.g. Wirth-Dzieciolowska et al. 1996; Walsh et al. 2006; Johnson & Sih 2007) have found that juvenile growth rate correlates positively with adult size and thereby with fecundity (Anholt et al. 1991; Plaistow & Siva-Jothy 1996, 1999). Consequently, larvae should first feed, while for an adult reproduction might be more relevant (Roff 1992), that is, larvae might tolerate a higher risk of predation than adults. Therefore, different behaviours or different levels of the same behaviour could be beneficial in different life stages (Wolf et al. 2007). Accordingly, we found that firebug larvae show more risk-prone behaviour than adults and, similarly, nymphs of field crickets use different strategies from adults, as they are bolder (Hedrick & Kortet 2012). However, Hedrick & Kortet (2012) proposed an alternative explanation for the differences between larval and adult behaviour: they assumed that the two forms differ because they are often challenged by different predators. Note, however, that adult variability of phenotype may not always be an adaptive strategy for the current circumstances; it can be a behavioural 'carryover' which remains from an early life stage (Stamps 2003; West et al. 2003; Taborsky 2006).

By comparing which variables showed differential consistency and mean-level consistency, we could infer that the measured personality traits changed in different ways. Age had a strong effect on all variables that identified activity traits: bugs' activity decreased immediately after the final moult, but later it seemed to increase again (Fig. 3). One may argue that this is simply the effect of the physiological changes induced by the final moult. When bugs were tested after moult, however, they always had fully hardened exoskeletons. Therefore we presume that moult-induced changes were over by the time of the tests.

In conclusion, we found that different behaviours changed differently across a major life stage transition in the firebug. To catch this complexity fully we need the indexes proposed by Stamps & Groothuis (2010). It is still a mystery how and why personality changes during this important transition. To answer the former question, studying hormonal reorganization at sexual maturity (O'Dor & Wells 1978) may be useful. For the latter, detailed study of personality changes during the final ecdysis in individuals with different life history expectations, that is, the winged and unwinged forms of the firebug (Gyuris et al. 2011), could be a promising direction.

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Chapter V.

Study 3: *Hemipteroseius adleri* **Costa, 1968 collected on red firebug: the first record of the family Otopheidomenidae Treat, 1955 (Acari: Mesostigmata) in Hungary**

Hemipteroseius adleri Costa, 1968 collected on red firebug: the first record of the family Otopheidomenidae Treat, 1955 (Acari: Mesostigmata) in Hungary

J. Kontschán[1] and E. Gyuris[2]

Abstract. The parasitic mite *Hemipteroseius adleri* Costa, 1968 was collected on red firebug, *Pyrrhocoris apterus* (Linnaeus, 1758) for the first time in Hungary. Short description and drawings of the specimens are presented.

INTRODUCTION

The family Otopheidomenidae Treat, 1955 is a characteristic group of phytoseioid mites. All stages of its species are parasites of insects in the tropical and temperate regions throughout the world (Lindquist *et al.,* 2009). The family is divided into three subfamilies on the basis of the host preferences: Otopheidomeninae Treat, 1955 species are parasites of butterflies and moths, Treatiinae Wainstein, 1972 species are parasites of heteropterans and Katydiseiinae Fain & Lukoschus, 1983 are mainly parasites of termites (Lewandowski & Szafranek, 2005).

The genus *Hemipteroseius* Evans, 1963 belongs to the subfamily Treatiinae, species of this genus are distributed in Central America, Central Africa, India, Oceania, Middle East and Europe (Lewandowski & Szafranek, 2005). Only one species of them (*Hemipteroseius adleri* Costa, 1968) is known from Europe (Poland and Lithuania (Lewandowski & Szafranek, 2005, Chmielewski 2006) and from the Middle East (Israel) (Costa 1968). This species is associated to a very common bug species, the red firebug [*Pyrrhocoris apterus* (Linnaeus, 1758)].

MATERIAL AND METHODS

Specimens were cleared in lactic acid, mounted in lactic acid and gelatin mixture and stored on slides. Drawings were made with the aid of a drawing tube. Specimens examined are deposited in the Collections of Soil Zoology of the Hungarian Natural History Museum. Measurements are given in micrometers (µm), width of idiosoma was taken at the level of the coxae IV.

RESULTS

Hemipteroseius adleri Costa, 1968
(Figs. 1–7)

Hemipterus adleri Costa 1968: 1–10. Figs 1–13.

Hemipteroseius adleri: Lewandowski & Szafranek 2005: 251–257; Chmielewski 2006: 157-161, Figs. 1–4.

Material examined. Two females. Hungary, Debrecen, Egyetem tér, from red firebugs, leg. Enikő Gyuris, 05.V.2010.

Short description. Idiosoma oval, approximately 380–390 µm long and 230–235 µm wide.

Dorsal idiosoma (Fig. 1). Holodorsal shield divided into podonotal and opistonotal plates. Podonotal plate with nine pairs of needle-like setae (cca. 20–25 µm) and one pair of lateral incisions. Opistonotal plate with one pair of very short setae (J5, cca. 4–5 µm), one pair of very long setae (S5) (45–50 µm) with bulbiform tip (Fig. 2) and with other three setae cca. 20–25 µm (one seta lacking).

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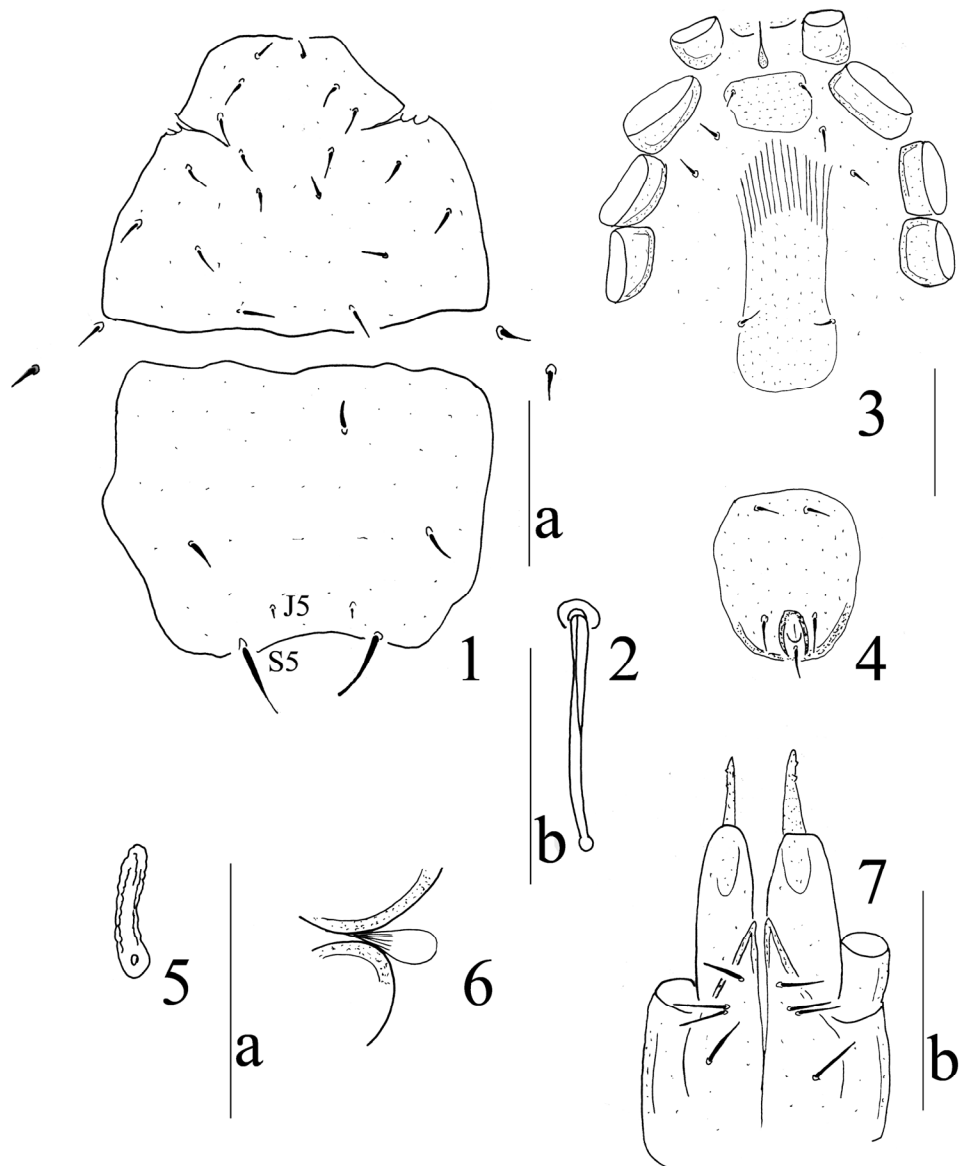
Figures 1–7. *Hemipteroseius adleri* Costa, 1968, female. 1 = Dorsal plates, 2 = S5 seta, 3 = intercoxal region, 4 = anal shield, 5 = peritreme, 6 = spermatheca, 7 = ventral view of gnathosoma. (Scale bar: a: 100 mμ, b: 50 μm)

Ventral idiosoma (Fig 3–4). Sternal shield bearing only one pair of setae, two other pairs of setae placed on membranous cuticle near coxae II. Genital shield hatchet shaped, with one pair of setae. Shape of anal shield oval, with one pair of setae near anterior margin and one pair of adanal setae and one postanal seta. Peritremes short (Fig. 5). Investigated part of spermatheca rounded (Fig. 6) it opens between coxae III and IV.

Gnathosoma (Fig. 7). Hypostomal setae smooth. Movable digit of chelicerae bidentate.

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DISSCUSSION

In the description of the species, Sellnick (1968) mentioned the variations of the dorsal chaetotaxy. Additional setae or lacking setae can often be observed on the opistonotal plate, hence the lacking opisthonotal setae of our specimens is not an extraordinary phenomenon of this species.

Hemipteroseius adleri have previously been recorded only from Israel, Poland and Lithuania. However, *H. adleri* is perhaps distributed in all the regions where its host species occurs.

Chmielewski (2006) mentioned the number of the live parasite mites per host insect varied from single adults to several dozen. In addition, Lewandowski and Szafranek (2005) gave the maximum number of found specimens on a host (124 individuals). We found only two specimens on a firebug, but according to our assumption more mite specimens can be found on other host specimens. The parasitic mites were located on the abdomen, under the wings, mostly near the wing base and anterior abdominal tergites; Chmielewski (2006) named it as "acarinarium" (our specimens were found on the same area of the host's body). Lewandowski and Szafranek (2005) found the mite specimens on the same locations, but they recorded some females also from the ventral side of thorax.

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Chapter VI.

Study 4: Ectoparasitic mites (*Hemipteroseius adleri*) and firebugs' (*Pyrrhocoris apterus*) personality traits

Ectoparasitic mites (*Hemipteroseius adleri*) and firebugs' (*Pyrrhocoris apterus*) personality traits

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ABSTRACT

Individuals of the same species often differ in their behavioural tendencies across time and context. These consistent differences are termed to animal personality. Parasitism as an ecological factor could significantly influence the evolution of animal personality. A recent study suggests that parasitism can have an impact on personality traits in two different ways. On the one hand, the differences in behaviour can be considered as a consequence of infections (i.e. parasite infection affects behaviour), while on the other hand, the behavioural type of the host can influence the chance to be infected (i.e. behaviour affects the probability of infection). We tested the relation between the firebugs' personality traits and its ectoparasitic mites and examined statistically these two scenarios in a wild population. Previously, we demonstrated that consistent individual differences (boldness, activity, exploration) can be measured in firebugs. Here we examined whether the degree of the infections have any effects on behavioural variables, and contrarily, the measured variables have any effect on the number of mites. We detected a trend that females behave in a shier way than males and with the increase of the number of mites they become braver. At the same time, if we consider the second scenario, it resulted in that braver and more active females have a higher chance to be infected. We also showed that symmetry in morphological traits can correlate with the rate of infection, that is the more symmetric the spot and the more symmetric the antenna in female firebugs the fewer mites they have.

INTRODUCTION

An increasing number of evidence shows that animals have personality that is differences in the same behaviour between individual are maintained over time and in different contexts (Dingemanse and Wolf. 2010). For instance, if an individual is shy in a feeding context, it will behave in the same way consistently in a mating context, i.e. it will take fewer risks than a braver individual in both cases would do. The adaptive significance of risk taking may depend on how the cost of being bold changes from situations to situations and over time. For example, brave individuals can have higher fitness benefits if predation risk is low, whereas shy individuals can benefit more if predation risk is high (Sih *et al.* 2004). Besides predation, parasitism can also be a crucial ecological factor, which, although has not been considered with due attention so far, can significantly influence the evolution of personality (Barber and Dingemanse 2010).

According to a common definition of parasitism, the health status of a parasitized individual can deteriorate through a wide variety of mechanisms compared to an unparasitized one (Bush *et al.* 2001, Poulin 2007). Therefore parasitism can have an important effect on the host's fitness, similarly to predation (e.g. Raffel *et al.* 2008; Schmid-Hempel 2009). While in most cases predators kill the prey and hence have immediate effects on its state, parasites, on the other hand, live inside their hosts or on their surface and feed from their body causing less dramatic, but nevertheless, long-term consequences. Such consequences can be, for instance, that parasites cause low fecundity (Newey and Thirgood 2004) or decrease the host's mating success due to the other sex's avoidance of parasitized individuals as mating partners (Hamilton and Zuk 1982). They can also have an effect on the host's feeding rate, sociability and migration (Lozano 1991; Hart 1997; Jog and Watve 2005). Furthermore, parasites might manipulate the host's behaviour in order to increase their own transmission rate by making the host to behave in a more risk-taking way (Libersat *et al.* 2009)

Barber and Dingemanse (2010) suggest that parasites can exert influence on animal personality as follows: First, parasites can have a selective effect on personality and behavioural traits, as the risk of acquiring parasites can be influenced by the individual's behavioural type, that is different personality types can contribute to end up as a host differently. For instance, exploratory individuals, because of their thorough investigation of their environment, might encounter parasites more often and hence their risk of infection can be increased. Second, parasites can promote individual differences in host-behaviour type in a population, since the host's state, an important determinant of behaviour (Dingemanse and

Wolf 2010), can change considerably as a consequence of an infection.

Individuals can develop a wide range of antiparasitic behavioural strategies to avoid or remove parasites (Hart 1997, 1990). Parasite avoidance behaviour can have similar cost than the avoidance of predators, so one would only expect an antiparasitic strategy to manifest when the risk of parasitic infection is high (Lafferty 1992). Zemek and Socha (2009) found for instance, that common firebugs (*Pyrrhocoris apterus*) show an interesting vertical arrangement, i.e. many of them climb up trees. The authors hypothesise that bugs do this for two reasons: first, to find optimal abiotic conditions for their ecdycis or, second, to avoid the ectoparasitic mite, *Hemipteroseius adleri*. The second hypothesis was investigated by collecting bugs from the ground and from linden tree trunks at the height of about 1 meter and counting the number of mites they harboured. The authors have shown that 29 % of the bugs collected from the ground, while only 5 % of the bugs from linden tree trunks were infected by mites. The authors concluded that climbing up on a tree can contribute to decrease the risk of being parasitized. The mite, *Hemipteroseius adleri*, has been recently detected in our study population of common firebugs (*Pyrrhocoris apterus*) in Hungary (Konstchán and Gyuris 2010). The finding that common firebug has personality (Gyuris *et al*. 2011, 2012), makes these bugs an ideal system to study the effects of parasites on animal personality.

Here we investigate the followings: First, how does the personality of the firebugs (*Pyrrhocoris apterus*) infected by *Hemipteroseius adleri* differ from that of the non-infected ones? In order to statistically take into account both scenarios by which parasitism and personality can be related (Barber and Dingemanse 2010) we analyse our data in two ways: In one set of analyses we set behavioural traits as response variable and the number of mites as one of the explanatory variable among other control variables like sex. This configuration might represent the case when parasite infection affects behaviour. In the other set of analyses the number of mites is entered as response variable and the behavioural traits as one of the explanatory variables among other control variables like sex. This set might correspond to the case when behaviour affects the probability of infection. Second, along the habitat switch phenomenon described by Zemek and Socha (2009), do individuals collected from different habitats show differences in their mite load and behaviour?

Differences in states – that can be well observable e.g. in size, sex, dominance or can be less observable e.g. in stress response, experience – provide a strong reason to the presence of stable individual differences in behaviour (Wolf *et al.* 2013). Therefore, we investigated whether stable state differences – e.g. sex, morphological traits measured the most frequently in insects and symmetry traits – have any impact on (i) behaviour and (ii) degree of infection.

MATERIALS AND METHODS

(a) Studied species and area

Firebug (*Pyrrhocoris apterus*) is a common and widely distributed Palearctic species of the heteropteran family Pyrrhocoridae. It can be found mostly around linden trees the seed of which provides its food. We collected 87 experimental animals from a wild population in Debrecen (47.52º N, 21.62º E; 130 m a.s.l.; subcontinental climate), Northeast Hungary, from September to October, 2011. We categorized the bugs based on their collection habitat:

i. from the ground

ii. from linden tree trunks at the height of 20 to 50 cm

iii. from linden tree trunks at a height exceeding 50 cm

After their collection, the bugs were put individually into jars and kept under laboratory conditions until the experiments (for further details on the keeping conditions see Gyuris *et al*. 2011). Sunflower seeds as food and water were provided *ad libitum*.

The parasitic mite, *Hemipteroseius adleri* (Costa 1968) of the *Hemipteroseius* genus is the only species which is described in Europe (Poland and Lithuania (Lewandowski and Szafranek 2005, Chmielewski 2006) and in the Middle East (Israel; Costa 1968) and which is associated with firebugs. Previously, we reported the occurrence of this mite on firebugs in Hungary, 2010, in the same population from which we collected the bugs for this study (Kontschán and Gyuris 2010). *H. adleri* has a negative effect on firebugs that was supported by the findings of Lewandowski and Szafranek (2005). They observed that firebugs with more than three mites entered hibernation in a bad condition could explain their higher winter mortality.

(b) Personality tests

We used the same behavioural tests as Gyuris *et al.* (2011), which are briefly summarized below. The tests were carried out in an arena of 55 cm in diameter. The floor of the arena was covered with filter paper, and 4 plugs were placed on the floor as novel objects. Filter paper and plugs were replaced before every run to avoid uncontrolled chemical cues of previous runs. Personality tests consisted of two parts: (i) "boldness test" and (ii) "open field test." In the first part we put the bug into a vial, covered with paper and waited for 1 minute to let it get used to its new environment. After one minute, we flicked the vial (to be sure that the bug is at the bottom of the vial), removed the paper, laid the vial on its side and waited (for a

maximum of ten minutes) when the bug's antenna would appeared in the opening of the vial. This was registered as the "emergence" of the bugs from the vial. Before the second part of the test, we put 4 plugs as novel objects into the arena to measure how thoroughly the bug explores its environment. The second part also began with a one minute habituation in the vial. After the habituation we shook the bug into the centre of the arena, registered when it started to move after a starting stimulus (hereafter "walking latency"), and recorded its movement pattern with a webcam. By this we could measure how soon the bug responded to a startling stimulus when it entered the new environment, how thoroughly they explored their environment (referred to by the "number of novel objects" visited), and the time it took for them to reach the arena wall (hereafter "wall time"). Behaviour in the open field test was also characterised by calculating the following variables: (i) the mean and (ii) the variance of step size (the distance between two consecutive positions 1 sec apart), and (iii) the mean and (iv) variance of turning angle. This is a well applicable method in firebugs for measuring boldness, explorativeness and activity personality axes (Gyuris *et al.* 2011, 2012).

(c) Infestation rate and morphological measurements

After personality tests, we put the bugs into 97% propanol in Eppendorf vials and then counted the mites on them with the help of a microscope. In addition, we measured the following morphological traits:

(1) body length in dorsal view from the tip of the head to the distal end of the abdomen (Figure 1/1.)

(2) pronotum width (Figure 1/2.)

(3) scape (the first segment of the antenna) length on both the left and the right sides (Figure 2/3.)

(4) funiculus (part of the antenna without the scape) length on both the left and the right sides (Figure 2/4.)

(5) length of the front tibia on the right side (after removal of the leg) (Figure 3/5.)
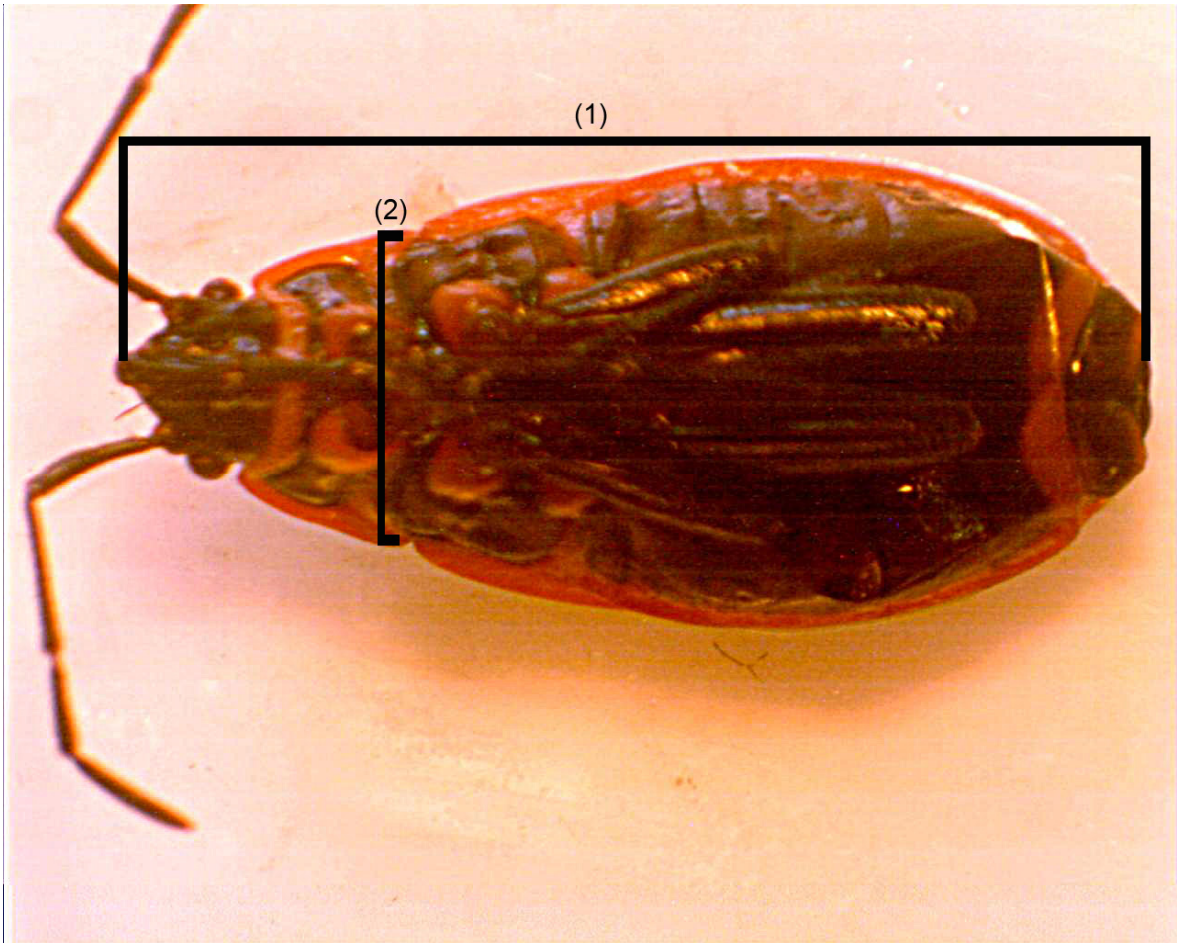
Figure 1. Measured morphological traits: 1. body length, 2. pronotum width.
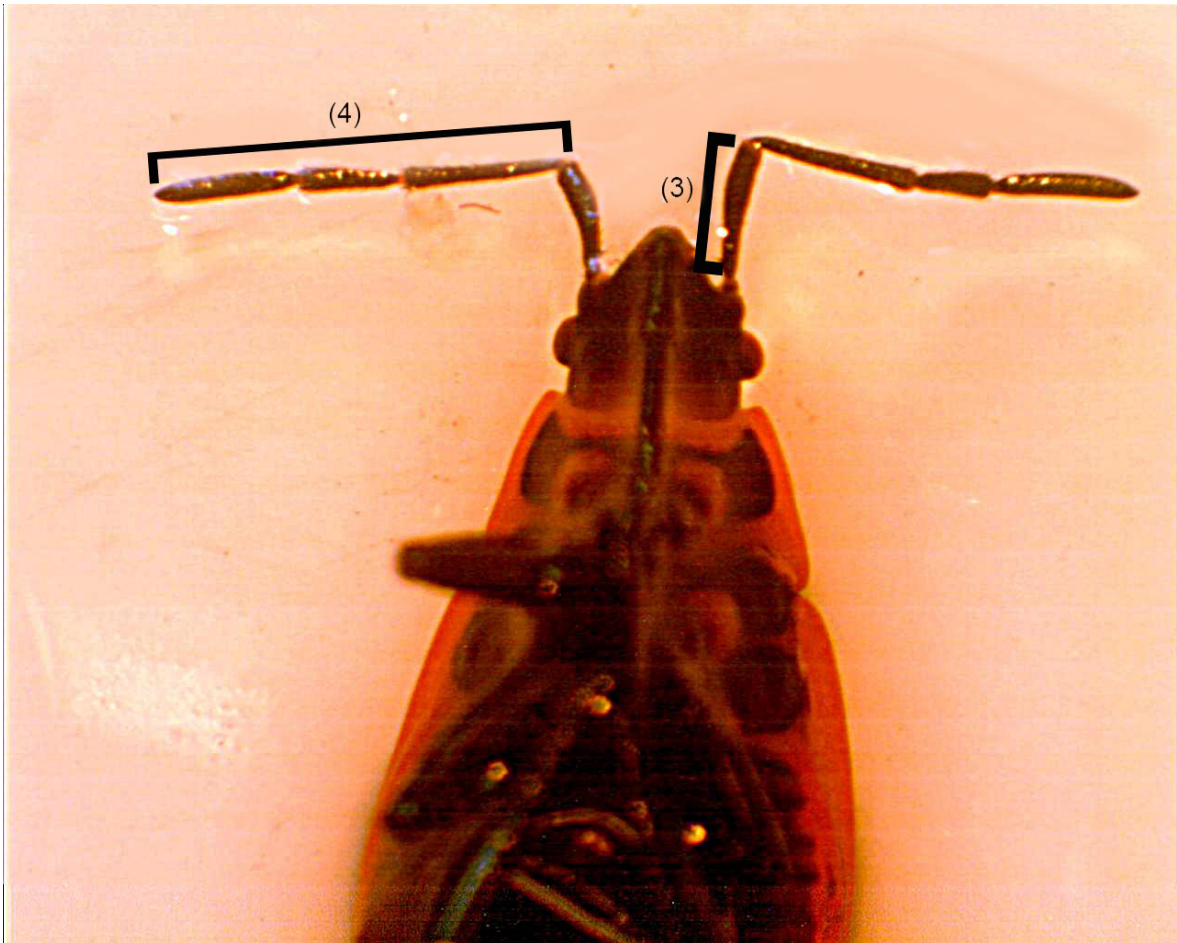
Figure 2. Measured morphological traits: 3.scape length, 4. funiculus length.
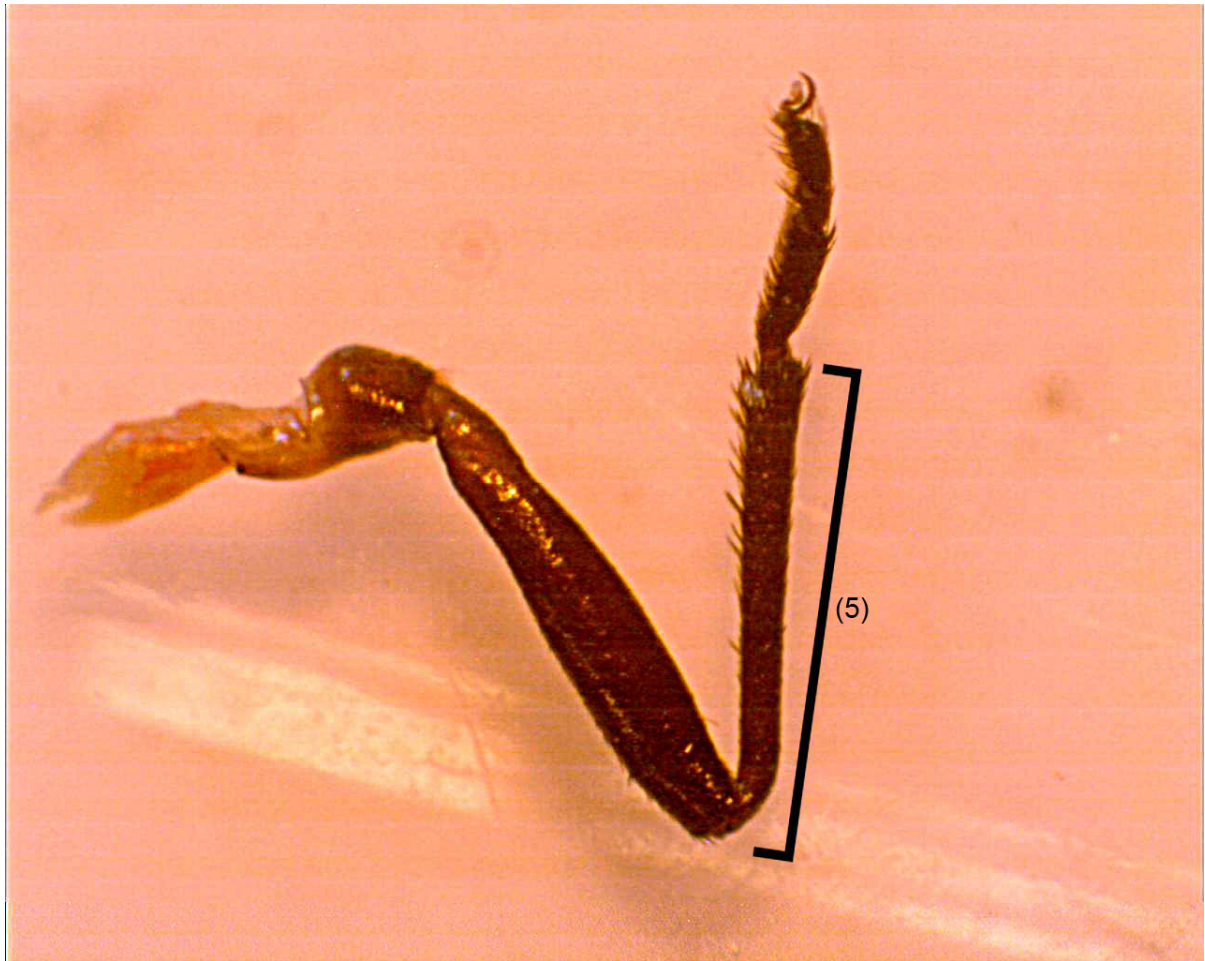
Figure 3. Measured morphological traits: 5. length of the front tibia

After measuring these linear dimensions, we removed the wings, and prepared them for photography. In the photos we measured the extent of the wing spots (as the number of the pixels) with ImageJ (Rasband 1997-2012) for further analysis. Photos were taken at the same settings one after the other to be sure that one pixel is equal in each photo. We separately measured the extent of "small" black spots (Figure 4/6.), "big" black spots (Figure 4/7.), and the black margin of the wings. Since the extent of the margin area highly depends on shabbiness and the age of the firebug, we did not consider this variable later on.

Figure 4. Measured morphological traits: 6. "small black spot", 7. "big black spot"

(d) Statistical analysis

Behavioural consistency was measured by computing the Kendall's W coefficient of concordance, which shows how similar are the ranks of individuals' based on the rank scores of different variables. To separate the personality axes we used the absolute value of pairwise Spearman rank correlation coefficients between behavioural variables as similarity values for computing clu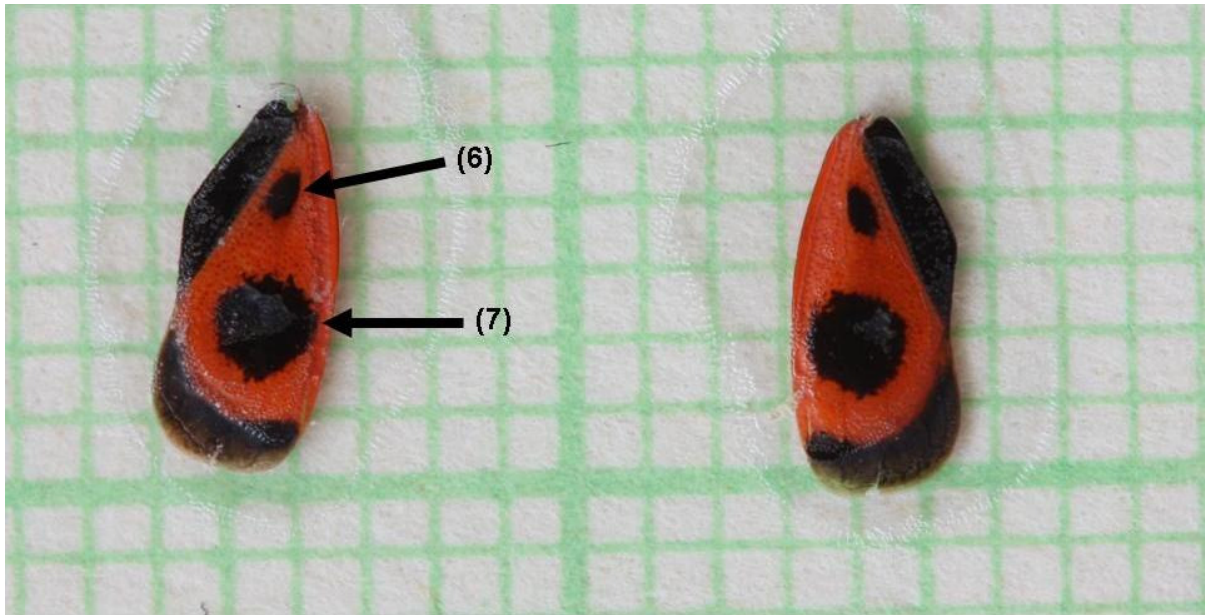ster analysis to investigate whether there are any groupings between behavioural variables (Legendre 2005). We categorised the collected bugs based on whether they had any mites or not (infested and non-infested), and we investigated if the correlation structure of the two groups differed from each other (structural consistency, Stamps and Groothuis 2010, Gyuris et al. 2012). First, we calculated a Spearman rank correlation matrix among variables for each group, and then we compared these two matrices with a Mantel randomization test (Manly 1997). We determined the prevalence values of each group – groups were categorized based on where they were collected – that is the proportion of the hosts infested by the studied parasitic species in the group sample size (Rózsa 2005). Besides, we compared the number of mites in each group with Kruskal-Wallis test to examine whether there are any differences among the three habitats in infestation rate. Subsequently, we used Principal Component Analysis to investigate which morphological traits (length of antenna (i.e. the mean of the right and the left antenna length), width of pronotum, length of body, length of tibia, extent of small and big spot) explain the total size variance primarily. We measured the effect of PC1, PC2, sex and their interactions on behavioural variables with a

series of generalised linear models where each behavioural variable was entered as response variable in separate models. After that we investigated the effect of PC1, PC2 and the sex on the number of mites, which was the dependent variable here (we corrected for distribution and adjusted to Poisson distribution). Since we tested the same statistical hypotheses several times we corrected for family wise errors with Holm's (1979) procedure.

We measured the effect of the number of mites on behavioural variables with generalized linear models. Each behavioural variable were entered as dependent variable into separate models where the explanatory variables were the number of mites, sex, and their interaction. We corrected for the distribution of the dependent variables, namely we logarithmised wall latency and move latency variables; we dichotomised emergence, mean turning angle and variance of step size variables, and used quasibinomial error distribution to the number of novel objects variable and applied gamma distribution to mean steps size and variance of turning angle variables. We added habitat type as explanatory variable to each of the models, but since it didn't have any effect on any dependent variables we excluded it from the final analyses.

In addition, we tested the effect of behaviour on the number of mites with generalised linear models. In this case the number of mites was the dependent variable, while the habitat type, sex, behavioural variable (each entered into separate models) and the interaction of the latter two were the explanatory variables. We corrected for the distributions: as we had count data (number of mites) we used Poisson distribution in these models. We calculated "antenna symmetry" from left and right antennae length and also calculated "spot symmetry" from the wings' big and small spots of the wings by subtracting the left side values of each measured traits from the corresponding right side values then dividing this difference by the sum of the two values and finally taking the absolute value of the result. We carried out this process at every trait in the case of which we measured the right and left sides then we summed these values, that is in the case of antenna symmetry (length of funiculus and scape) and at spot symmetry (extent of small - and big spot). We measured with Spearman rank correlation whether these two symmetry indices correlate with each other, and also we measured the differences between them with paired Wilcoxon test. After that we tested the effect of spot or antenna symmetry on each behavioural variable with the generalized linear model (each behavioural variable was dependent variable, while explanatory variables were sex, each symmetry index and their interactions). Here we also examined the effect of the spot and antenna symmetry on the number of mites (we used the same GLM model procedure as mentioned above, so the dependent variable was the number of mites, while the explanatory

variable was the sex and each symmetry index). All statistical analyses were carried out in the R interactive statistical environment (R Development Core Team 2008) with cluster (Maechler *et al.* 2005), ade4 (Dray and Dufour 2007) and vegan (Oksanen *et al.* 2009) packages.

RESULTS

Kendall concordance for the total number of bugs were W=0.150, p=0.081, but when we separated them we got W=0.314, p<0.001 for the infested ones (n=21) and W=0.178, p=0.008 for the non-infested ones (n=66). It shows that personality differences were detected in observed firebugs because different individuals behaved in the same way in different situations.

Based on the results of cluster analysis, the measured variables can be classified as the following: brave-shy personality axis (emergence, wall time, wall latency) explorativeness (mean step size, variance of step size, and number of novel objects) and activity (mean turning angle, variance of turning angle) personality axes. This clustering of behavioural variables corresponds well to those that were previously demonstrated in firebugs (Gyuris *et al.* 2011, 2012). Result of Mantel test showed that the structure of behavioural variables in groups of infested and non-infested bugs was similar (obs=0.719, p=0.0004).

We show the prevalence of mites collected from three different habitats in Table 1. It reveals that the ratio of the infected bugs in each total sample did not differ from each other ($\chi^2_2 = 0.16$, p = 0.923).

	I.	II.	III.
Infested bugs	12	5	4
Total number of bugs	48	19	20
Prevalence	0.25	0.26	0.20

Table 1. Prevalence of parasitic mite (*Hemipteroseius adleri*) on firebugs

We also compared the number of mites per individuals collected from each habitat with Kruskal-Wallis test, which shows that there is no significant differences between the habitats (chisq=0.148, df=2, p=0.928).

We carried out Principal Component Analysis with the measured morphological traits (length of antennae, width of pronotum, body length, tibia length, extent of small and big spot). The result shows that the first principal component explains 62% of the total variance,

while the second PC explains 12% of the total variation (Figure 5). The first PC was mainly consisted of the linear size measurements with high loading, while the extent of the small spot on the wing contributed mainly to the second PC.
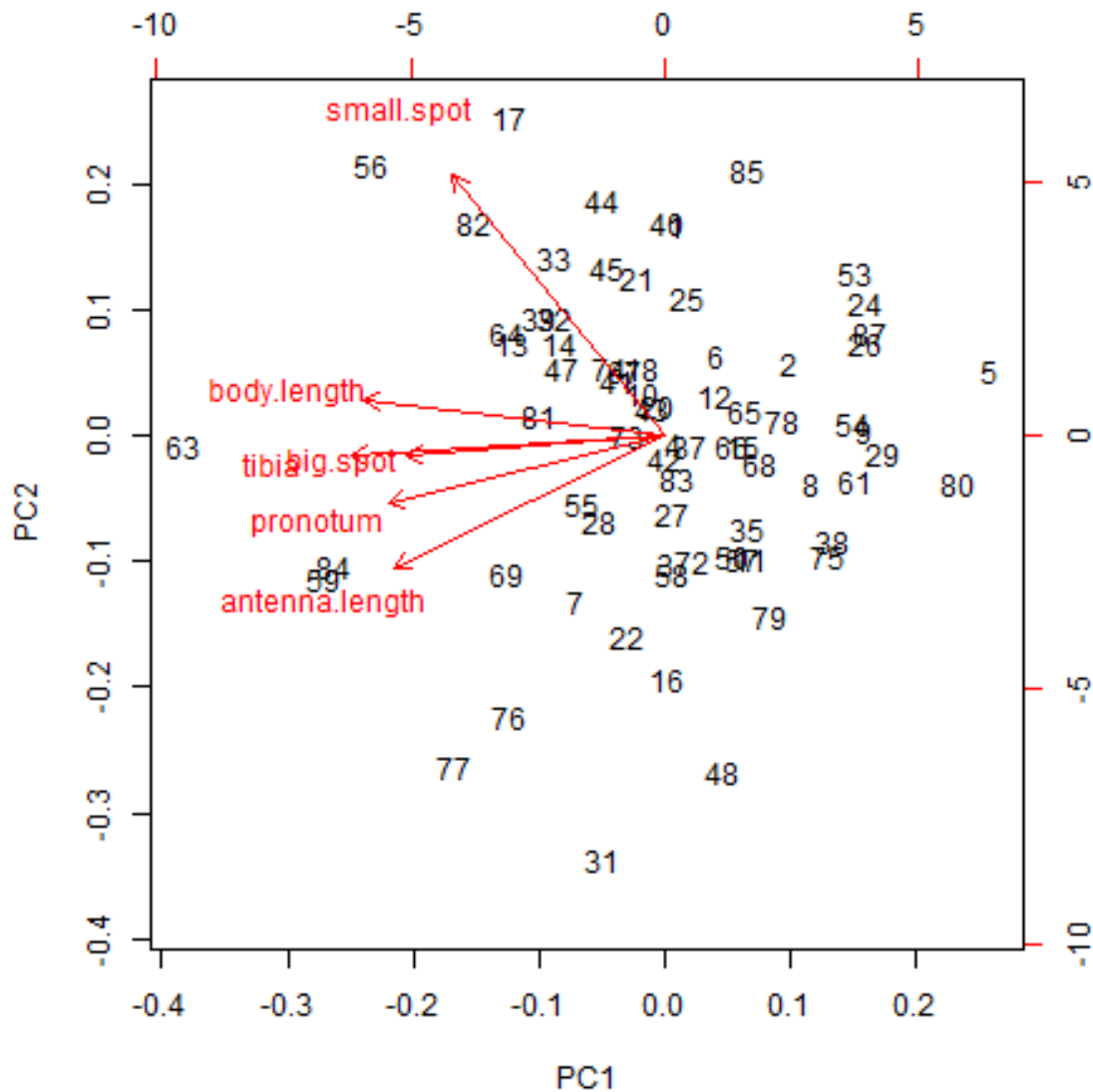
Figure 5. Distributions of individuals and morphological traits based on PCA. Linear measurement of size of firebugs contributes mainly to the first principal component (PC1), while "small black spot" to the second one (PC2).

We found a tendency at each behavioural variable that sex has effect on the variance of step size (ß=0.962, z=1.948, p=0.051), which disappears after Holm correction. Individually, neither PC1 nor PC2 have an impact on the behavioural variable, but the interaction of the sex and PC2 has a significant effect on three of the variables. At female firebugs the bigger the

extent of the small spot (PC2) (i) the higher is the mean turning angle (ß=1.297, z=2.037, p=0.041), (ii) the higher is the variance of turning angle (ß=1.307, z=3.328, p=0.001), and also (iii) the higher is their move latency time, which means they start to move later (ß=0.723, t=2.264, p=0.026). Only the effect on variance of turning angle will remain after Holm correction. Examining the effect of PC1, PC2 and sex on the number of mites we found the following: the bigger they are (PC1), and the smaller their small black spots (PC2) are in females, the more mites they have (Table 2.).

	estimate (ß)	z value	p value
Number of mites ~			
Sex (female)	0.344	4.022	**<0.001***
PC1	-0.325	-9.374	**<0.001***
Sex (f):PC1	0.078	2.019	**0.043***
Number of mites ~			
Sex (female)	0.128	1.616	0.106
PC2	0.400	6.669	**<0.001***
Sex (f):PC2	-1.172	-13.647	**<0.001***

Table 2. Sex and PC1 (body length) and PC2 (small black spot) effect on number of mites. P values in bold were significant and those marked by an asterisk remained significant after correcting for familywise error by Holm's (1979) method.

Based on GLM model results it can be seen that female firebugs started to move later than males, and their step sizes were less variable (Table 3.). At the same time, females show higher wall latency value, so they roamed in the arena for a longer time than males, and this roaming time became shorter with the increase of the number of mites. They visited fewer novel objects than males, so they seem to behave in a shier way. We did not find any further significant association between sex and number of mites and the other behavioural traits (emergence, mean step size, mean turning angle and variance of turning angle).

	estimate (ß)	z / t value	p value
Wall latency ~			
Sex (female)	0.991	3.370	**0.001***
No. of mites	0.001	0.080	0.936

Sex(f): no. mites	-0.024	-2.059	**0.042**
Emergence ~			
Sex (female)	-0.849	-1.780	0.075
No. of mites	-0.001	-0.135	0.892
Sex(f): no. mites	0.0002	0.012	0.990
Mean step size ~			
Sex (female)	0.041	0.477	0.634
No. of mites	0.003	1.096	0.276
Sex(f): no. mites	-0.004	-1.092	0.278
Mean turning angle ~			
Sex (female)	-0.084	-0.179	0.858
No. of mites	-0.014	-0.859	0.391
Sex(f): no. mites	0.0003	0.015	0.988
Variance of step size ~			
Sex (female)	1.205	2.475	**0.013***
No. of mites	0.003	0.268	0.788
Sex(f): no. mites	-0.025	-1.279	0.200
Variance of turning angle ~			
Sex (female)	-0.270	-0.622	0.536
No. of mites	-0.011	-1.181	0.241
Sex(f): no. mites	-0.001	-0.091	0.928
Number of novel objects ~			
Sex (female)	-1.407	-2.067	**0.041**
No. of mites	-0.021	-1.310	0.193
Sex(f): no. mites	0.068	1.326	0.188
Move latency ~			
Sex (female)	0.621	2.152	**0.034**
No. of mites	0.003	0.434	0.665
Sex(f): no. mites	-0.011	-0.973	0.333

Table 3. Effect of the sex and number of mites on each behavioural variable based on GLM model.

P values in bold were significant and those marked by an asterisk remained significant after correcting for familywise error by Holm's (1979) method.

Investigating the factors that have influence on the number of mites, based on GLM models we found at every behavioural variable that the second habitat type (that is linden tree trunks at the height of 20 to 50 cm) has a negative effect on the number of mites, which might mean that the probability to be infected is the lowest there (all p < 0.001). At the interaction of each behavioural variable and sex we found significant association in the case of seven out of eight variables (Table 4.). This means that the sooner the females emerge from their refuge, the sooner they start to move after an alarm, the bigger is their mean step size, the lower is their mean turning angle, the more novel objects they visit and the lower their variance of step size and turning angle, the more mites they have compared to males. We may conclude that braver and more active females have higher chance to be infected.

	estimate (ß)	z / t value	p value
No. of mites ~			
Habitat type II.	-0.876	-7.794	**<0.001***
Habitat type III.	0.041	0.515	0.606
Sex (female)	0.157	1.879	0.060
Wall latency	-0.001	-4.269	**<0.001***
Sex (f):wall latency	0.001	1.511	0.130
No. of mites ~			
Habitat type II.	-0.729	-6.468	**<0.001***
Habitat type III.	0.021	0.256	0.798
Sex (female)	0.614	6.641	**<0.001***
Emergence	0.0001	0.822	0.411
Sex(f):emergence	-0.001	-6.884	**<0.001***
No. of mites ~			
Habitat type II.	-0.626	-5.450	**<0.001***
Habitat type III.	0.053	0.625	0.532
Sex (female)	-1.676	-6.476	**<0.001***
Mean step size	-2.123	-7.257	**<0.001***
Sex(f):mean step size	2.550	7.079	**<0.001***
No. of mites ~			
Habitat type II.	-0.561	-4.903	**<0.001**

Habitat type III.	0.023	0.261	0.794
Sex (female)	0.952	5.223	**<0.001**
Mean turning angle	6.838	12.125	**<0.001**
Sex(f):mean turning angle	-3.958	-5.470	**<0.001**
No. of mites ~			
Habitat type II.	-0.603	-5.307	**<0.001***
Habitat type III.	-0.097	-1.046	0.295
Sex (female)	0.540	3.550	**<0.001***
Variance of turning angle	3.588	9.778	**<0.001***
Sex(f):variance of turning angle	-1.706	-3.947	**<0.001***
No. of mites ~			
Habitat type II.	-0.799	-7.125	**<0.001***
Habitat type III.	0.052	0.616	0.537
Sex (female)	0.656	2.743	**0.006***
Variance of step size	1.610	2.135	**0.032**
Sex(f):variance of step size	-1.815	-2.383	**0.017***
No. of mites ~			
Habitat type II.	-0.756	-6.717	**<0.001***
Habitat type III.	0.120	1.441	0.15
Sex (female)	-2.766	-10.577	**<0.001***
Number of novel objects	-1.318	-11.586	**<0.001***
Sex(f):no.nov.objects	3.326	12.228	**<0.001***
No. of mites ~			
Habitat type II.	-0.750	-6.680	**<0.001***
Habitat type III.	0.133	1.620	0.105
Sex (female)	0.543	6.238	**<0.001***
Move latency	0.005	3.816	**<0.001***
Sex(f):move latency	-0.015	-7.584	**<0.001***

Table 4. Effect of the habitat type, sex and each behavioural variable on number of mites based on GLM model. P values in bold were significant and those marked by an asterisk remained significant after correcting for familywise error by Holm's (1979) method.

We did not find significant correlation between antenna symmetry and spot symmetry (Rs= -

0.111, p=0.340), but Figure 6. illustrates, that antennae are more symmetric than wing's spots (V=2453, p <0.001). Based on GLM models we found only one significant result showing that interaction of sex and antennae symmetry explains the variance of turning angle (ß=-15.510, t=-2.274, p=0.025). It means that the more symmetric the antenna, the less variable is the turning angle in females. Effects of the two symmetry indices on the number of mites are illustrated in Table 5. We showed that the more symmetrical the spots found on the wings of firebugs are, the fewer mites they have and at the same time the more symmetrical the antennae are the fewer mites were found on females.

	estimate (ß)	z value	p value
Number of mites ~			
Sex (female)	0.189	1.391	0.164
Spot symmetry	3.478	4.702	**<0.001***
Sex(f):spot symmetry	-0.559	-0.643	0.520
Number of mites ~			
Sex(female)	-0.964	-8.560	**<0.001***
Antenna symmetry	-2.140	-2.116	**0.034***
Sex(f):antenna symmetry	18.288	14.157	**<0.001***

Table 5. Effect of antenna and spot symmetry on number of mites. P values in bold were significant and those marked by an asterisk remained significant after correcting for familywise error by Holm's (1979) method.
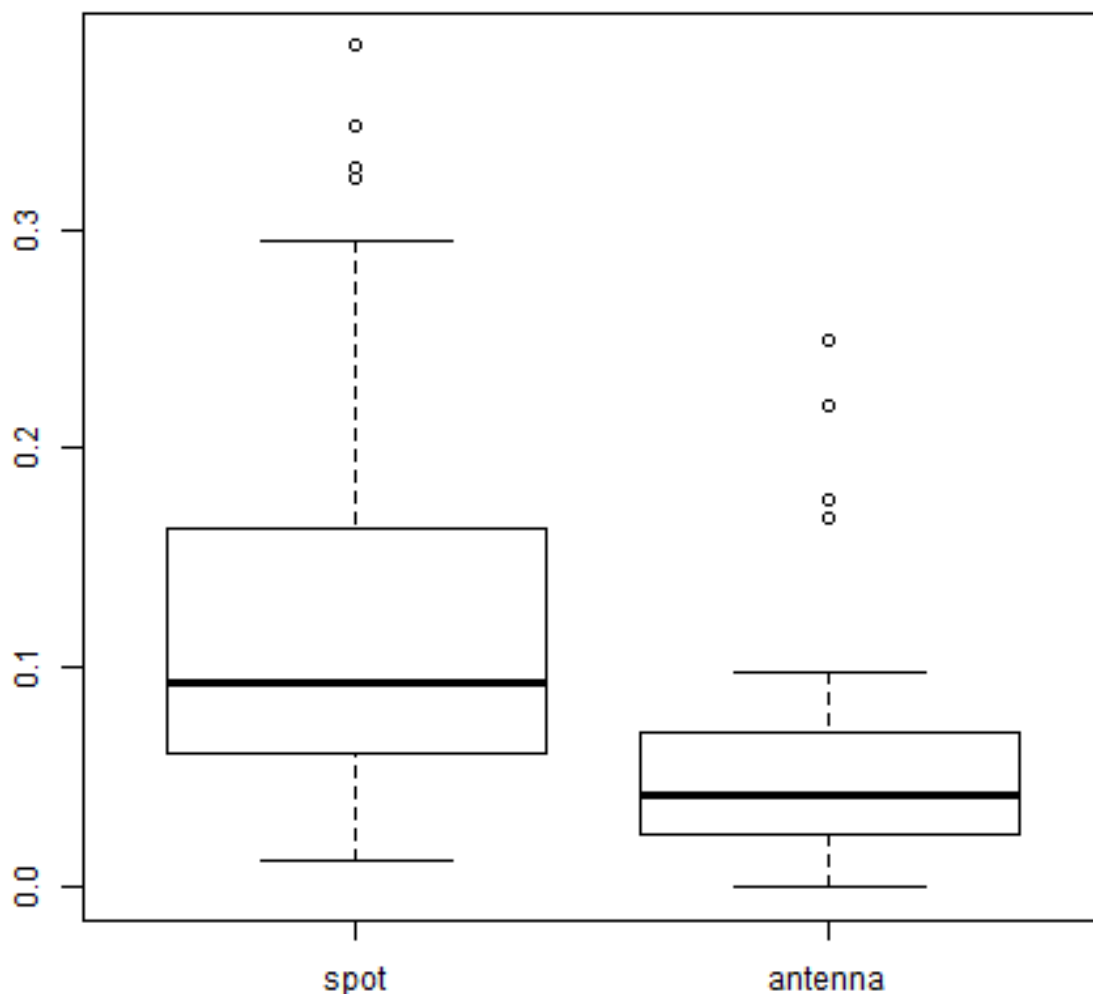
Figure 6. Symmetry of antennae and spot. It shows that "antenna" is more symmetric.

DISCUSSION

Parasitism can be an important factor at shaping the evolution of consistent individual differences because infection may often lead to specific changes in axes of personality. In this paper we examined a wild population of firebugs naturally infected by a mite. We found that the structures of observed behavioural traits are similar in infected and non-infected bugs (structural consistency, Stamps and Groothuis 2010) and these personality axes refer to those previously described in healthy firebugs (Gyuris *et al.* 2011, 2012). In summary at the first

sight we can conclude that the position of the measured personality traits relative to each other do not differ in infected and non-infected individuals.

Recently, Zemek and Socha (2009) found significant differences in prevalence of mites on firebugs collected from the ground (29%) and from linden tree trunks (5%), while in our study the prevalence did not differ between vertical habitats, they were between 20 and 26% in the three different habitats. It means that our data do not support clearly the hypothesis that firebugs climbed up to trees to avoid infection. Nevertheless, we found that the intensity of infection is the lowest in habitat type two (linden tree trunks at the height of 20 to 50), but not in habitat type three as we expected. Previously it was observed (Lewandowski and Szafranek 2005) that, in the autumn, *Hemipteroseius adleri* mites switch their firebugs' hosts intensively to maximise food intake in order to prepare for the winter. Since we collected firebugs from September to October but not in the summer like Zemek and Socha (2009), the host changing appearing in the autumn could be a possible explanation why we did not find any differences between prevalence in firebugs. We assume that since *Hemiperoseius adleri* mites' mean intensity of infestation changes intensively from spring to autumn in relation to the life cycle of the host and the parasite, hence stable individual differences in firebugs may not evolve so rapidly. We can suppose that the presence of this antiparasitic strategy is seasonal or depends on the extent of exposure of parasites because the investment to this behaviour is costly (Lafferty 1992).

Association between parasite infection and host behaviour could develop in two ways (Barber and Dingemanse 2010). It can be one way that an individual is parasitized because it behaves in a given way (for example more active and brave individuals since they move more, have higher chance to meet parasites). The other scenario can be that parasites will change the individuals' behaviour after the infection (e.g. Berdoy *et al.* 1995, 2000). Since causes and consequences are not obvious at studying a wild population we investigated statistical surrogates of these scenarios. First, we examined whether the number of mites have any effect on the measured behavioural variables, and second, whether behavioural variables have any effect on the number of mites. In the first case we found that with increasing number of mites females are shier compared to males and become more active and braver. In the second case we found that the chance was higher in females who behaved in a braver way (started to move sooner after an alarm, emerged from a refuge after a shorter time, and visited more novel objects) to be infected, but the same relation could not be found in males. *H.adleri* spreads from one firebug to another by climbing over (Lewandowski and Szafranek 2005); therefore we suppose that if the host becomes braver and more active after an infection, it

would facilitate the transmission of the mites.

We have just suspected this trend so further studies are necessary to distinguish these causes and consequences, but similar results can be found in literature, so the presence of the effect is presumable. Giles (1983) found that infested stickleback approaches the model predator more readily than non-infested ones while Barber *et al.* (2004) found reduced escape response after an infection at the same species. Webster (1994) demonstrated increased activity in rats infected by *T.gondii* while reduced activity was found in a copepod parasitized by *Diphyllobothrium* (Pasternak *et al.* 1995).

In our study, we examined whether stable morphological traits have any effect on behaviour and on the rate of infection (here number of mites). We found that the small black spot has a slight effect on three behavioural variables in females, but this effect remains after correction in only one case, that is the more variable the turning angle, the bigger small black spot the female has. Nevertheless, body length, small black spot and the symmetry indices have a remarkable effect on the degree of infection. It means that the more mites the females have, the bigger they are, and the smaller the extent of small black spot. Nevertheless, the fewer mites were on firebugs, the more symmetrical the spot, and the more symmetrical the antennae are in females. Symmetry could be a quality signal because all organisms exert to develop symmetrically, which has numerous benefits, so deviation from it can be considered as a developmental abnormality (*fluctuating asymmetry*, Valen 1962). In our case, it can be conceivable that the asymmetry refer to a weaker immune system which associates to having more mites.

Our results illustrate that the number of mites have a slight effect on female behaviour, namely they will behave in a brayer way. Nevertheless, we showed that our observed behavioural traits have an impact on the number of mites, that is females behave in a braver way with the increase of infection This paper is an initial, explorative study, which examined the relationship between firebugs and their ectoparasitic mites and provides a basis of further fruitful experiments. For instance it would be important to investigate the alteration of personality traits before and after an infection considering the extent of and exposure to infestation, and the mites' life cycle. Current research is on-going in which we also test whether the above mentioned infection can be modelled in an experimental way, and to what extent is the immune reaction associated with personality traits.

ACKNOWLEDGEMENTS

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