Are introduced spiders displacing native species on Galápagos? Observations on pholcid spiders (Araneae: Pholcidae)

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Abstract

The spider family Pholcidae includes several species that have followed humans to other continents and around the world. Negative impacts of these species on the local faunas have never been reported. Here, we present results of a short collecting trip to Galápagos in 2019, focusing on two species that have been introduced to the archipelago by humans and whose spread appears correlated with, if not causally linked to, the decline or disappearance of two native species occupying the same microhabitats: 1) the local abundance of the introduced *Modisimus culicinus* (Simon, 1893) appears negatively correlated with the abundance of the native *Galapa bella* (Gertsch & Peck, 1992), and 2) the recently introduced *Smeringopus pallidus* (Blackwall, 1858) is now abundant in caves where a few decades ago the native *Aymaria jarmila* (Gertsch & Peck, 1992) was present. The last species was not found in any of the six caves visited on Santa Cruz Island in 2019, suggesting that it may be seriously threatened. In addition, we present new records of Pholcidae from Galápagos and re-emphasize the need to reconsider the distinction between the two epigean *Aymaria* species on Galápagos: *A. conica* (Banks, 1902) and *A. insularis* (Banks, 1902).

Keywords: alien species • genital variation • invasion biology • island • synanthropic

Introduction

Alien species are widely recognized as one of the main sources of biodiversity loss (Sala *et al*. 2000; Clavero & García-Berthou 2005; Courchamp *et al*. 2017; Pyšek *et al*. 2020; Gentili *et al*. 2021). This is particularly true for oceanic islands, most of which have lost a large percentage of their pristine (often endemic) flora and fauna long before these could be studied in any detail (Simberloff 1986; Tye *et al*. 2002; Wood 2012; Régnier *et al*. 2015). The Galápagos Islands are unique in this respect because their colonization happened relatively late, with no permanent settlements before 1832 (González *et al*. 2008). A large percentage of the introductions did probably occur after approximately 1970 when the tourism industry and the number of inhabitants started to grow exponentially (Peck *et al*. 1998; González *et al*. 2008; Toral-Granda *et al*. 2017). This has made Galápagos a living laboratory of invasion biology where large inventories and focused ecological studies on a variety of taxa coincide temporally with the advent of alien species and the decline and loss of native species (Tye *et al*. 2002; Causton *et al*. 2006; Cooke *et al*. 2019; Parent *et al*. 2020). This is an ongoing process, despite massive efforts by governmental and nongovernmental entities to minimize introductions and their impacts (Causton, Sevilla & Porter 2005; Atkinson *et al*. 2012; Toral-Granda *et al*. 2017; Cayot, Campbell & Carrión 2021). Demographic growth and tourist numbers are highly correlated with numbers of alien species (Trueman *et al*. 2010; Toral-Granda *et al*. 2017) and tourist numbers have more than tripled between 2003 and the covid-19 pandemic (Díaz-Sánchez & Obaco 2020).

Spiders are highly suited to contribute to our knowledge about the recent and ongoing faunal exchange on Galápagos. Spiders are probably among the best-studied orders of terrestrial invertebrates on Galápagos, due mainly to the extensive efforts by L. Baert and colleagues since 1982. Serious spider collecting on Galápagos started slightly earlier, in the 1960s (see reviews in Gertsch & Peck 1992 and Baert *et al*. 2008) and, by 2014, more than 11,400 specimens from over 700 localities were available in collections (Baert 2014). The available data have recently been updated and analysed further (Buchholz *et al*. 2020) but collecting efforts have been very limited over the last decade.

Pholcidae is among the most species-rich spider families (World Spider Catalog 2021), with the large majority of species in tropical and subtropical regions (Huber & Chao 2019). They are known for their substantial number of synanthropic species that have followed humans to other continents and around the world (~19 species in 11 genera), which, in turn, might be related to the widespread tendency within the family to readily occupy caves and cave-like sheltered habitats if available (Huber 2018). On Galápagos, 14 species of Pholcidae were previously known (Baert 2013; Buchholz *et al*. 2020), with only two of them being certain or near-certain human introductions: *Modisimus culicinus* (Simon, 1893) and *Physocyclus globosus* (Taczanowski, 1874). A possible negative impact of these two species on the native fauna has never been studied nor suggested, neither on Galápagos nor in any other part of the world.

The present report is based on a short field expedition in 2019, with a total of no more than 16 collecting days limited to Santa Cruz and Isabela Islands. Our data on introduced species are thus necessarily preliminary in many respects. However, our observations suggest that two introduced species may be affecting the native fauna adversely. These are the first such cases in Pholcidae (cf. Huber *et al*. 2017), and should be the focus of further research. This is particularly true for a species that we newly report from Galápagos, the circumtropical (originally African) *Smeringopus pallidus* (Blackwall, 1858).

Material and methods

Spiders were collected manually, mostly by turning rocks on the ground, by inspecting cave walls, niches, and crevices, and by searching leaf litter and other near-ground

sheltered spaces. Specimens collected do not necessarily reflect the number of individuals seen, i.e. only a few specimens were collected even in cases of high abundance. Specimens in 80% EtOH are deposited in the Invertebrates Collection of the Charles Darwin Research Station (ICCDRS), Galápagos, Ecuador; specimens in pure ethanol are currently at Zoological Research Museum Alexander Koenig (ZFMK), Bonn, Germany, for molecular study, but will eventually also be deposited in ICCDRS.

Results and Discussion

We collected a total of 12 or 13 species of Pholcidae (the uncertainty refers to a dubious pair of species of *Aymaria* Huber, 2000: see Appendix). Three of them are certain or near-certain human introductions and these are the main focus of this report: *Modisimus culicinus*, *Physocyclus globosus*, and *Smeringopus pallidus*. The second focus is on a couple of native species that seem to have declined or even disappeared (at least locally) during the last decades: *Galapa bella* (Gertsch & Peck, 1992) and *Aymaria jarmila* (Gertsch & Peck, 1992). The latter species is most conspicuous by its absence from the list below (we could not find a single specimen). Since we suspect that this absence might be related to the fact that the caves that originally harboured *A. jarmila* now harbour the introduced *S. pallidus*, we discuss this species under *S. pallidus*. For the remaining species collected during the 2019 expedition, we refer to Appendix and Huber *et al*. (in press). Photos of live specimens of the species treated below are shown in Figs. 1–7.

Introduced species

Modisimus culicinus (Simon, 1893) (Fig. 5)

Remarks: This small litter- and ground-dwelling species has spread around the globe and is commonly found in and around human buildings (Huber *et al*. 2017). The closest putative known relatives range from Mexico to the coastal regions of mainland Ecuador (B. A. Huber, unpubl. data). The oldest known Galápagos record is from 1970 (from Floreana; Huber *et al*. 2017), suggesting that the species has been on the archipelago for a long time. Gertsch & Peck (1992) reported very few specimens from near the towns of Puerto Ayora (Santa Cruz) and Baquerizo (San Cristóbal). Baert *et al*. (2008), Baert (2013), and Buchholz *et al*. (2020) reported the species from several islands, but without providing precise collection data.

We found *M. culicinus* in high densities at several localities around Puerto Ayora and around Puerto Villamil, both in altered habitats (e.g. under rocks along trails near Charles Darwin Research Station, along the trail between Puerto Ayora and Tortuga Bay, along a trail W of Puerto Villamil) and in seemingly pristine habitats (e.g. 700 m E of Charles Darwin Research Station, 850 m NNE of Charles Darwin Research Station, 600 m W of Muro de Las Lágrimas). The densities appeared much lower in localities farther away from human settlements, as for example near Garrapatero beach, and 1.3 km SW of Tunel del Estero, both in pristine environments. Even further away, *M. culicinus* was not found (e.g. 2 km NE of Los Gemelos, 0.6150°S 90.3700°W; near Canal de Itabaca, 0.4936°S 90.2860°W; around Cueva del Sucre, 0.843°S 91.029°W).

New records: GALÁPAGOS ISLANDS: Santa Cruz: 2♂, 1♀, ICCDRS, and 1♂, 5♀ in pure ethanol, ZFMK (Gal40), near Charles Darwin Research Station, 0.743°S 90.303°W–0.744°S 90.299°W, 5–15 m, under rocks, 17 August 2019, B. A. Huber and A. Acurio; 1♂, 1♀, ICCDRS, and 1♂, 1♀ in pure ethanol, ZFMK (Gal43), near Playa Tortuga, 0.7648°S 90.3405°W, 10 m, under rocks, 18 August 2019, B. A. Huber and A. Acurio; 1♀, ICCDRS, and 2♀ in pure ethanol, ZFMK (Gal51), W Puerto Ayora, small canyon, 0.7459°S 90.3198°W, 10 m, under rock, 20 August 2019, B. A. Huber; 1♂, ICCDRS, near Garrapatero beach, 0.6908°S 90.2249°W, 20 m, under rocks, 22 August 2019, B. A. Huber. Isabela: 1 juv. in pure ethanol, ZFMK (Gal61), outside Tunel del Estero, 0.9607°S 90.9897°W, 10 m, under rock, 26 August 2019, B. A. Huber; 2♂, 3♀, ICCDRS, and 1♂, 2♀ 1 juv. in pure ethanol, ZFMK (Gal64), W Puerto Villamil, 0.960°S 90.996°W–0.959°S 91.019°W, 20–50 m, under rocks, 27 August 2019, B. A. Huber; 1♀ in pure ethanol, ZFMK (Gal66), lava field E Puerto Villamil, 0.9546°S 90.9559°W, 20 m, in dead cactus leaves on ground, 27 August 2019, B. A. Huber; 1♀ in pure ethanol, ZFMK (Gal70), 1.3 km SW Tunel del Estero, 0.9675°S 90.9994°W, 20 m, in cave entrance, 28 August 2019, B. A. Huber.

Physocyclus globosus (Taczanowski, 1874) (Fig. 2)

Remarks: The genus *Physocyclus* Simon, 1893 is native to North and Central America, reaching no further south than Costa Rica (Valdez-Mondragón 2010). Only *P. globosus* has attained a circumtropical distribution, by the late 19th century at the latest. The species is not listed for Galápagos in Gertsch & Peck (1992) and in early papers by L. Baert and colleagues (Baert & Maelfait 1986; Baert, Maelfait & Desender 1989a,b; Baert Desender & Maelfait 1991) but by 2008 it is listed for four islands (Baert *et al*. 2008; without precise collection data). It may thus have reached Galápagos in the 1990s, approximately.

We found *P. globosus* at numerous localities on Santa Cruz and Isabela Islands. The species occupied a variety of habitats, ranging from buildings in Puerto Ayora and Villamil to pristine or near-pristine habitats (under rocks). In contrast to Baert *et al*. (2008: 59), who reported the species also from "caves on Floreana and Santa Cruz" (without further details), we never found *P. globosus* in caves.

New records: GALÁPAGOS ISLANDS: Santa Cruz: 1♀, ICCDRS, Puerto Ayora, small canyon, 0.7459°S 90.3198°W, 10 m, among rocks, 20 August 2019, B. A. Huber; 1♂, 1♀ in pure ethanol, ZFMK (Gal37), Puerto Ayora, 0.7409°S 90.3124°W, 20 m, at building, 16 August 2019, B. A. Huber and A. Acurio; 5♀ in pure ethanol, ZFMK (Gal39), near Charles Darwin Research Station,

Figs. 1–7: Pholcidae from Galápagos, live specimens (males). **1** *Smeringopus pallidus* (Blackwall, 1858); **2** *Physocyclus globosus* (Taczanowski, 1874); **3** *Anopsicus banksi* (Gertsch, 1939); **4** *Aymaria conica* (Banks, 1902); **5** *Modisimus culicinus* (Simon, 1893); **6** *Modisimus modicus* (Gertsch & Peck, 1992); **7** *Galapa bella* (Gertsch & Peck, 1992). At different scales.

0.743°S 90.303°W–0.744°S 90.299°W, 5–15 m, among rocks, 17 August 2019, B. A. Huber and A. Acurio; 2 juvs in pure ethanol, ZFMK (Gal57), trail to Garrapatero beach, 0.6906°S 90.2224°W, 20 m, under rocks, 22 August 2019, B. A. Huber; 1♂, 2♀, ICCDRS, and 1♂, 3 juvs in pure ethanol, ZFMK (Gal59), near Charles Darwin Research Station, 0.7432°S 90.3034°W, 5 m, under rocks, 17 August 2019, B. A. Huber and A. Acurio. Isabela: 1♀ in pure ethanol, ZFMK (Gal65), lava field E Puerto Villamil, 0.9544°S 90.9586°W, 20 m, in small cavity, 27 August 2019, B. A. Huber; 1♀ in pure ethanol, ZFMK (Gal75), Puerto Villamil, 0.9565°S 90.9682°W, 10 m, in building, 30 August 2019, B. A. Huber.

Smeringopus pallidus (Blackwall, 1858) (Fig. 1)

Remarks: The genus *Smeringopus* Simon, 1890 is native to sub-Saharan Africa and the Arabian Peninsula (Huber 2012). Only two species have followed humans to other continents; of these, only *S. pallidus* has attained a circumtropical distribution, by the mid-19th century at the latest. It is a conspicuous long-legged species that builds large

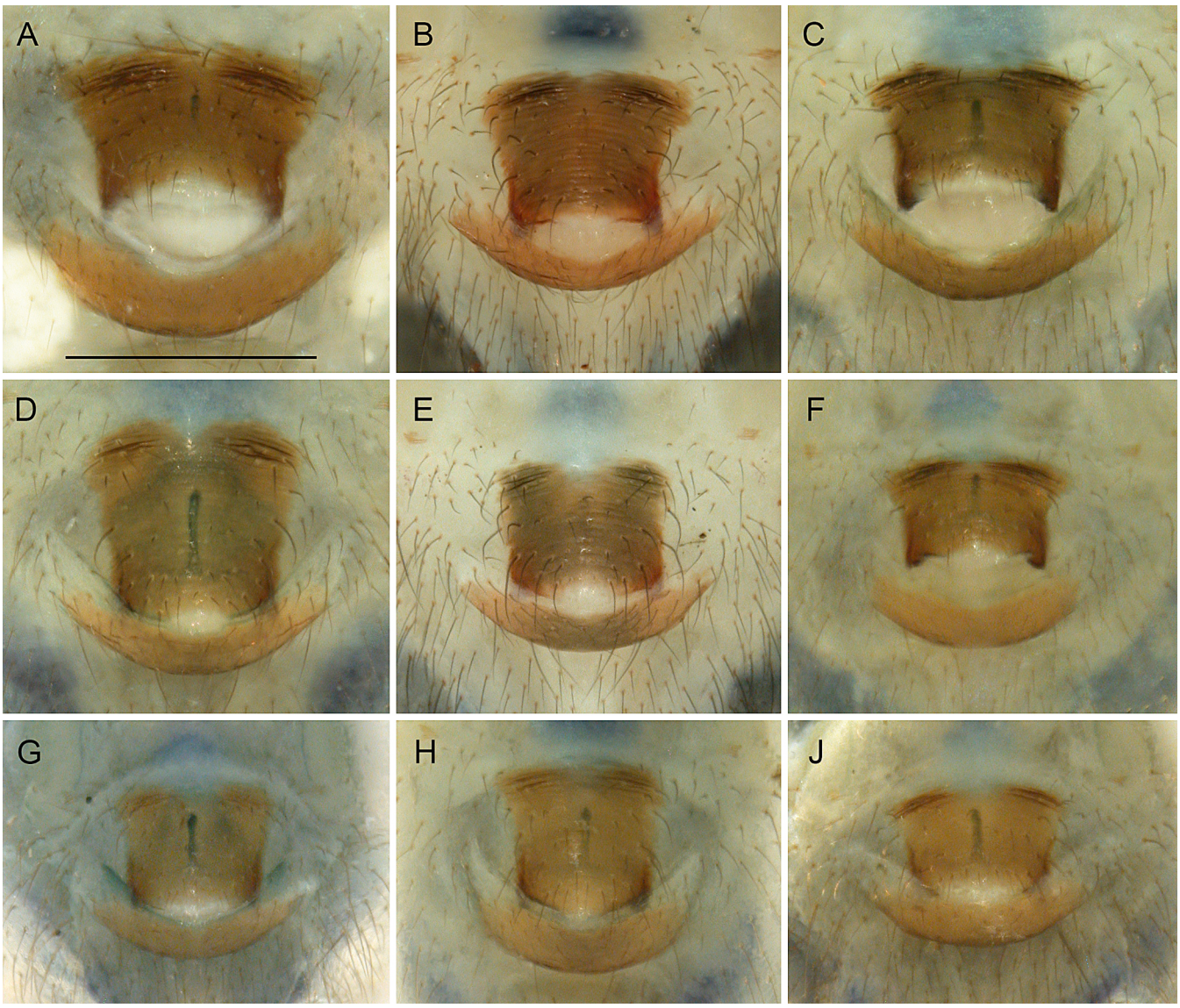

Fig. 8: *Aymaria conica* (Banks, 1902) (= *A. insularis* (Banks, 1902)?). Epigyna in ventral views (vertical to ventral sides of abdomens); all specimens from within ~100 m at Cerro Puntudo, Santa Cruz Island; arranged from largest to smallest according to tibia 1 length (cf. Fig. 10). Scale bar (identical for all) = 0.5 mm.

domed sheet webs. It is thus remarkable that it has not been reported from Galápagos before.

We found *S. pallidus* at numerous localities on Santa Cruz Island, often in high densities. The species occupied a variety of habitats, ranging from buildings in Puerto Ayora and shaded places near rural houses and gardens to tunnels under roads and caves. In several of the caves visited, *S. pallidus* appeared to be among the dominant macroscopic animals. *Smeringopus pallidus* was never found to share a cave with a species of *Aymaria* Huber, 2000, even in three caves where *A. jarmila* had been reported by Gertsch & Peck (1992) (Cueva Finca Kastdalen, Cueva Señora Colombia, "Cueva Bellavista" = Cueva Gallardo). Gertsch & Peck (1992) found *A. jarmila* in several further caves in the Bellavista area that we were not able to locate precisely (Cueva de los Huesos, Cueva Enrique Sevilla, Cueva de Vargas). On the other hand, we visited another cave in the area not listed in Gertsch & Peck (1992) (Tunel Ballena), and here, too, we found only *S. pallidus* but not *A. jarmila*.

We did not find *S. pallidus* on Isabela, neither in the town of Villamil nor in any of the caves visited (Cueva de Sucre, Cueva de Los Trillizos, two unnamed caves 1.3 km SW of Tunel del Estero). This suggests that *S. pallidus* has arrived and spread on Santa Cruz Island very recently (probably within the last decade, after L. Baert and colleagues collected on the archipelago) and that it may not yet have reached Isabela Island.

New records: GALÁPAGOS ISLANDS: Santa Cruz: 1♂, 1♀ in pure ethanol, ZFMK (Gal38), Puerto Ayora, 0.7409°S 90.3124°W, 20 m, at building, 16 August 2019, B. A. Huber and A. Acurio; 1♂, 1♀, ICCDRS, and 1♀ in pure ethanol, ZFMK (Gal45), Bellavista, Cueva Gallardo, 0.6947°S 90.3168°W [= "Cueva Bellavista No. 1" and "Cueva Bellavista No. 2" of S. Peck; Hernández, Izquierdo & Oromí 1992; Baert, Maelfait & Desender 1995), 220 m, in cave, 19 August 2019, B. A. Huber; 2♀, ICCDRS, near Bellavista, shady brook bed near road, 0.6905°S 90.3115°W, 210 m, 22 August 2019, B. A. Huber; 1♂,

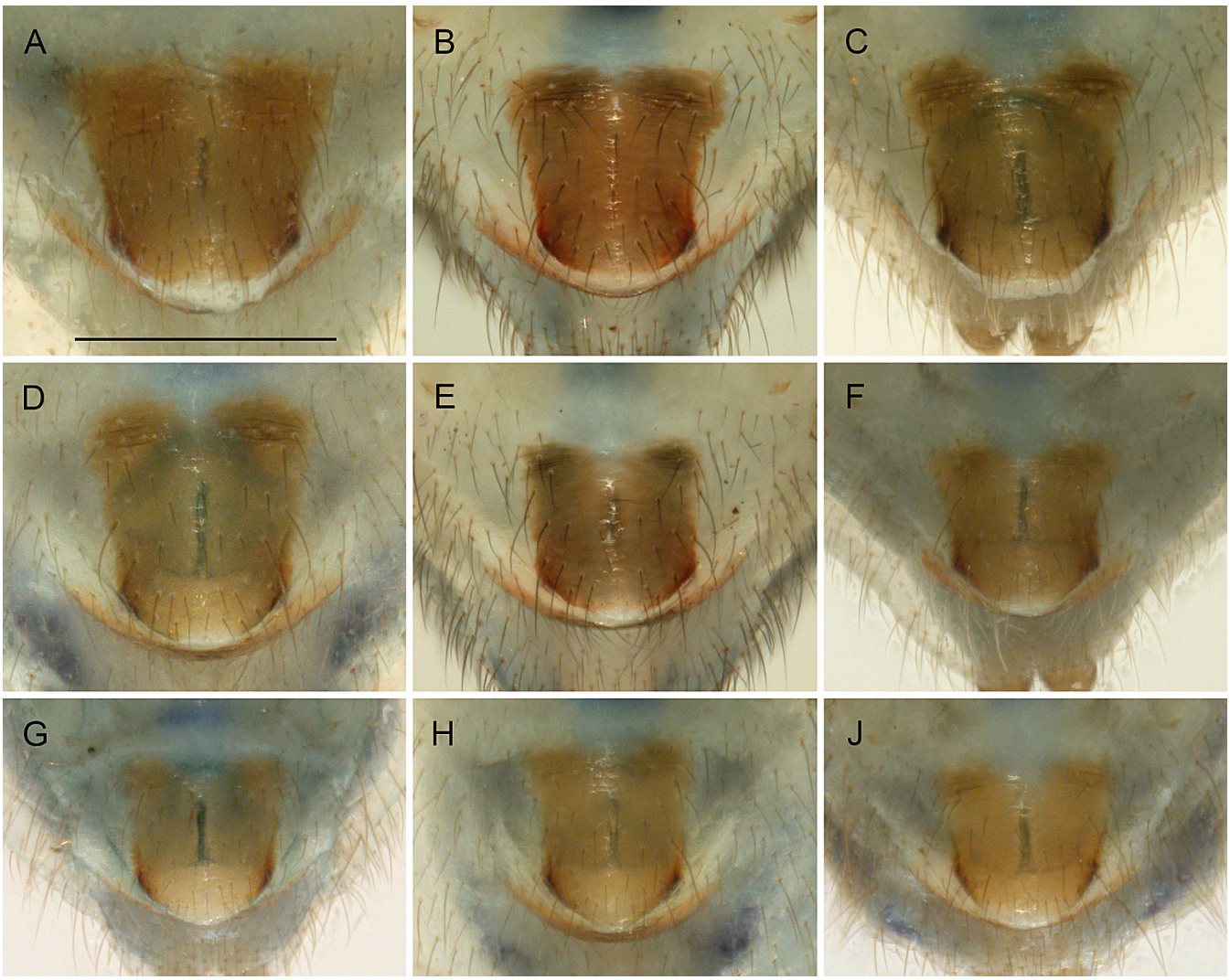

Fig. 9: *Aymaria conica* (Banks, 1902) (= *A. insularis* (Banks, 1902)?). Epigyna in ventral-frontal views (vertical to anterior epigynal plate); same specimens and arrangement as in Fig. 8. Scale bar (identical for all) = 0.5 mm.

ICCDRS, and 1♂ in pure ethanol, ZFMK (Gal49), Bellavista, Cueva Señora Colombia, 0.6958°S 90.3239°W, 160 m, in cave, 20 August 2019, B. A. Huber and A. Acurio; 1♂, ICCDRS, and 1♂ in pure ethanol, ZFMK (Gal79), El Cascajo, Tunel Ballena, 0.6735°S 90.2628°W, 250 m, in cave, 01 September 2019, B. A. Huber and A. Acurio; 1♂ 1♀, ICCDRS, Bellavista, cave at Finca Kastdalen, 0.6850°S 90.3164°W, 230 m, in cave, 21 August 2019, B. A. Huber, A. Acurio, and L. Betancourt; 1♀, ICCDRS, near Los Gemelos, in artificial tunnel under road, 0.6231°S 90.3825°W, 605 m, 21 August 2019, B. A. Huber, A. Acurio, and L. Betancourt.

Native species

Galapa bella (Gertsch & Peck, 1992) (Fig. 7)

Remarks: This tiny ground-dwelling species was originally described from specimens collected in 1964 at the Charles Darwin Research Station on Santa Cruz Island (Gertsch & Peck 1992). Later, it was reported from a couple of small islets a few hundred metres off the eastern coast of Santa Cruz (Plaza Sur and Plaza Norte) and from Genovesa and Pinta Islands. The last record did not appear in the list of Buchholz *et al*. (2020), and none of these records is accompanied by precise collection data. We have not seen any of these specimens except for the types (Huber 2000) and therefore cannot further comment on them.

In 2019, we failed to find *G. bella* around Puerto Ayora even though this species was one of the main reasons for the entire trip, i.e. a very significant amount of time was dedicated to finding this species. In the microhabitat of *G. bella* around Puerto Ayora we found massive numbers of the introduced *M. culicinus* (see above). At a location 10 km from Puerto Ayora (near Garrapatero beach) we found *G. bella* in reasonable densities, but only a single specimen of *M. culicinus*. At another locality, 27 km from Puerto Ayora, we found *G. bella* but no *M. culicinus*.

New records: GALÁPAGOS ISLANDS: Santa Cruz: 2♂, ICCDRS, and 3♂, 7♀ 9 juvs in pure ethanol, ZFMK (Gal55), 1 km SW Garrapatero beach, 0.7007°S 90.2280°W, 30 m, under rocks, 22 August 2019, B. A. Huber; 1♀, 1 juv. in pure ethanol, ZFMK (Gal77), near Canal de Itabaca, 0.4936°S 90.2860°W, 20 m, under rocks, 31 August 2019, B. A. Huber.

Conclusions

We found two species pairs where the increase or appearance of the introduced species over the last decades appears correlated with the decline or disappearance of the native species: *Modisimus culicinus*/*Galapa bella*, and *Smeringopus pallidus*/*Aymaria jarmila*.

In the case of *Modisimus culicinus*/*Galapa bella*, it seems that the first has entirely replaced the second at the type locality (Charles Darwin Research Station) and around Puerto Ayora, but *M. culicinus* seems slow at spreading across the island. More than 40 years after the collection of the type specimens it was still rare or absent at two localities far away from human settlements where *G. bella* still persisted. Our field observations do not allow a statement about the possible mechanism(s) involved and whether there is any direct connection between the increase of one species and the decline of the other.

The case of *Smeringopus pallidus*/*Aymaria jarmila* appears more alarming. The introduced *S. pallidus* has spread rapidly within approximately a decade and has massively invaded caves, at least some of which originally contained the native troglobite *A. jarmila*. In 1985, S. & J. Peck found numerous specimens of *A. jarmila* in several caves in the Bellavista area of Santa Cruz (17 specimens from seven caves: Gertsch & Peck 1992). We could not find a single specimen of *A. jarmila* in any of the six caves we visited on Santa Cruz Island, including three caves where *A. jarmila* had been collected in 1985. Judging from the general morphology of these two species (body size, leg length), they presumably occupy the same microhabitat within the caves, i.e. spaces and niches that allow for the construction of relatively large horizontal domed webs. Thus, they presumably compete for the same type of prey (in contrast to endemic *Metagonia* Simon, 1893 spiders that live close to the ground and under rocks and that appear unaffected by *S. pallidus*; Huber *et al*. in press). In addition, both species probably avoid areas with air currents (as is generally the case in pholcids: Huber, Pavlek & Komnenov 2021; B. A. Huber pers. observation). We thus hypothesize that *S. pallidus* is directly involved in the displacement of *A. jarmila*.

Our field observations provide a baseline for further monitoring. Elucidating interspecific interactions and other factors affecting species distributions such as climate change, habitat reduction, and exposure to agrochemicals, will require controlled experiments and more detailed field observations. In the current scenario of massive decline of invertebrates worldwide, such information will be pivotal for the improvement of conservation policies.

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Appendix

Other Pholcidae collected during the 2019 expedition. Not listed here are five species of *Metagonia* Simon, 1893 (all presumably native) that are treated in another context (Huber *et al*. in press).

Anopsicus banksi (Gertsch, 1939) (Fig. 3)

New records: GALÁPAGOS ISLANDS: Santa Cruz: 1♂, 2♀, ICCDRS, and 3♀, 3 juvs in pure ethanol, ZFMK (Gal56), 1 km SW Garrapatero beach, 0.7007°S 90.2280°W, 30 m, under rocks, 22 August 2019, B. A. Huber; 1♂, 1♀, ICCDRS, and 1♀, 1 juv. in pure ethanol, ZFMK (Gal76), near Canal de Itabaca, 0.4921°S 90.2855°W, 15 m, under rocks, 31 August 2019, B. A. Huber.

Aymaria conica (Banks, 1902) (Figs. 4, 8–10) and *A. insularis* (Banks, 1902)

Remarks: In 2000, one of us has expressed doubts about the supposedly diagnostic characters separating these two nominal species (Huber 2000: 158). Subsequent authors

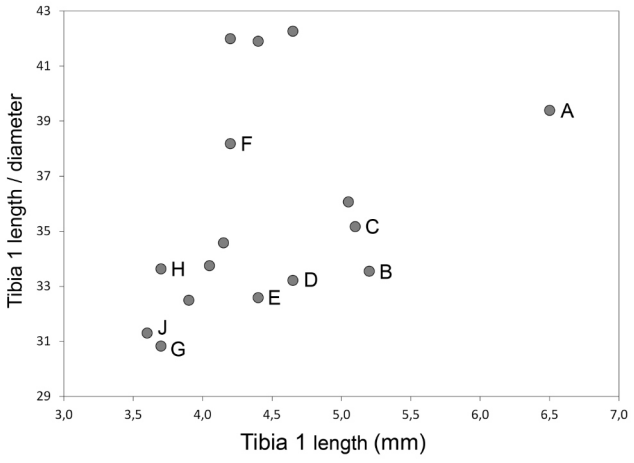

Fig. 10: Tibia 1 length and stoutness (length/diameter) of the 16 females of *Aymaria conica* (Banks, 1902) (= *A. insularis* (Banks, 1902)?) collected at Cerro Puntudo, Santa Cruz Island. Letters indicate specimens shown in Figs. 8–9.

have maintained the separation without commenting on these doubts (e.g. Baert *et al*. 2008; Buchholz *et al*. 2020). Our new material from Cerro Puntudo (Santa Cruz Island) originates from a small patch of forest and a single type of microhabitat, strongly suggesting that all these specimens are conspecific. This series of 16 females supports the idea that *A. conica*/*insularis* is unusually variable in several respects (leg length and stoutness, abdomen shape, even epigynum shape: Figs. 8–10). At the same time, CO1 sequences of specimens from Cerro Puntudo and an unnamed cave 1.3 km SW of Tunel del Estero (Isabela Island) had a P-distance of 4.9% (G. Meng & B. A. Huber, unpublished data). This question clearly requires a much denser sampling and is beyond the scope of this contribution. Thus, the specimens listed below may in fact represent one species or two.

New records: GALÁPAGOS ISLANDS: Santa Cruz: 3♂, 12♀ 1 juv., ICCDRS, and 1♂, 4♀, 3 juvs in pure ethanol, ZFMK (Gal58), ~1 km N Cerro Puntudo, 0.636°S 90.335°W, *Scalesia* forest, 700 m, at tree bases and among other plants near ground, 23 August 2019, B. A. Huber. Isabela: 1♂, ICCDRS, small cave near Tunel del Estero, 0.9601°S 90.9895°W, 10 m, at cave entrance, 26 August 2019, B. A. Huber; 2♀, 2 juvs in pure ethanol, ZFMK (Gal60), Tunel del Estero, 0.9607°S 90.9897°W, 5 m, in cave, 26 August 2019, B. A. Huber; 1♂, 4♀, ICCDRS, and 3♀, 2 juvs in pure ethanol, ZFMK (Gal71), 1.3 km SW Tunel del Estero, 0.9675°S 90.9994°W, 20 m, among plants at cave entrance, 29 August 2019, B. A. Huber; 2 juvs in pure ethanol, ZFMK (Gal69), same data but 28 August 2019; 2♀, 2 juvs in pure ethanol, ZFMK (Gal72), unnamed cave 1.3 km SW Tunel del Estero, 0.9676°S 90.9993°W, 20 m, in cave, 29 August 2019, B. A. Huber.

Modisimus modicus (Gertsch & Peck, 1992) (Fig. 6)

New record: GALÁPAGOS ISLANDS: Santa Cruz: 7♂, 2♀, ICCDRS, and 4♀ in pure ethanol, ZFMK (Gal54), 2 km NE Los Gemelos, 0.6150°S 90.3700°W, 570 m, under rocks, 21 August 2019, B. A. Huber, A. Acurio, and L. Betancourt.