

Check for updates







Invasive Big-Headed Ants and Black Rats Are Dominant Arthropod Predators Across Opposing Habitats of a Degraded Oceanic Island

School of Biological Sciences, The University of Hong Kong, Hong Kong Special Administrative Region, China | 2 Conservation & Fisheries Directorate, Ascension Island Government, Georgetown, Ascension Island | 3Atlantic Island Invertebrate Specialist Group, IUCN Species Survival Commission, Salisbury, UK | ⁴Department of Life Sciences, Imperial College London, Berkshire, UK | ⁵Fera Science Ltd, York, UK

Correspondence: Adam Sharp (asharp@hku.hk)

Received: 5 November 2024 | Revised: 11 February 2025 | Accepted: 23 April 2025

Associate Editor: Jennifer Powers | Handling Editor: Xavier Arnan

Funding: This work was supported by the Darwin Plus (DPLUS135) and the Department for Environment, Food and Rural Affairs.

Keywords: ants | arthropods | caves | endemic species | invasive species | island ecology | Pheidole megacephala | predation | rats | Rattus rattus

ABSTRACT

Invasive animals threaten island-native arthropods with predation. We found that introduced ants and rats conducted 77% of experimental arthropod live bait predations on Ascension Island. Predation was mostly by big-headed ants Pheidole megacephala inland and around non-native vegetation, and by black rats Rattus rattus in coastal lowland habitats and caves.

1 | Introduction

Oceanic islands are hotspots of endemic biodiversity (Kier et al. 2009), and much of that biodiversity is threatened with extinction (Fernández-Palacios et al. 2021). Non-native species introductions cause 90% of species extinctions on islands (Roy et al. 2024) through ecological processes that include elevated competition, habitat modification, and disease transmission (Doherty et al. 2016). Island-native arthropods can be especially vulnerable to predation by introduced species (Fernández-Palacios et al. 2021). Knowledge of exactly which introduced species predate island-native arthropods in different habitats should inform their targeted eradication and local suppression. Understanding species ecologies across natural and modified habitats is vital to effective species management (Gray et al. 2019; Hoffmann et al. 2016).

Ascension, isolated in the mid-Atlantic Ocean, is one oceanic island that has been subject to many intentional and unintentional historical species introductions (Ashmole and Ashmole 2000). The volcanic landmass is around 1 million years in age (Jicha et al. 2013) and its limited native biodiversity is early successional (Ashmole and Ashmole 1997, 2000). Numerous volcanic caves and coastal lava flows are important habitats for Ascensionendemic arthropods (Ashmole and Ashmole 1997). Much of the barren landscapes below around 400 m elevation, once comprising native spurge Euphorbia origanoides and grasses, are becoming colonized by common island-invasive plants such as Mexican thorn Prosopis juliflora and common guava Psidium guajava (Lambdon et al. 2024). Most remnant native vascular plant diversity persists at higher elevations: five threatened fern species and one grass Sporobulus caespitosus scattered sparsely among dense non-native cloud forests (Lambdon et al. 2024).

Native predators are low in species richness. There are no native mammals, reptiles, or amphibians on Ascension, and the largest native terrestrial animal is the hare-lipped land crab Johngarthia lagostoma, which feeds largely on decaying plant matter (Ashmole and Ashmole 2000). There are numerous extant native bird species but none which preferentially predate

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2025 The Author(s). Biotropica published by Wiley Periodicals LLC on behalf of Association for Tropical Biology and Conservation.

arthropods. Two native bird species, the Ascension night heron *Nycticorax olsoni* and Ascension crake *Mundia elpenor*, may have consumed arthropods in significant quantity but are now extinct (Ashmole and Ashmole 2000; Bourne et al. 2003). The predatory giant pseudoscorpion *Garypus titanius* has been extirpated to a nearby sea stack from Ascension's mainland (Sherwood et al. 2024b). Ascension is therefore uniquely lacking in native predators.

Potential non-native predators are numerous. There are 17 ant species on Ascension with mixed feeding behavior, but they are all introduced (Sharp and Tawatao 2023), including the generalist insectivore big-headed ant Pheidole megacephala reported since the 19th century (Dahl 1892). Black rats Rattus rattus were established around 1700 (Ashmole and Ashmole 2000) and are known arthropod predators on Ascension (Ashmole and Ashmole 2000; Chin et al. 2024). Other established nonnative arthropod predators include the red-headed centipede Scolopendra morsitans (Ashmole and Ashmole 1997; Duffey 1964), various spiders (e.g., Sherwood et al. 2023; Sherwood and Sharp 2023), and two species of scorpion including Isometrus maculatus (Sherwood et al. 2024a). Many of these are globally important invasive species, and P. megacephala and R. rattus are considered two of the "World's 100 Worst Invasive Alien Species" (Lowe et al. 2000).

Given the simplicity of the remnant native ecosystems and the diversity of natural and modified landscapes on Ascension, the island represents a unique model system on which to quantify the relative predation pressure exerted by globally widespread arthropod predators across habitats. We aimed to identify the habitats where island arthropods experienced the highest non-native predation. We hypothesized that, due to the lack of native predators and the potential difference in habitat use between diverse non-native predators (e.g., ants, centipedes, rats, and spiders), relative non-native predation occurrence not only varied across habitats but was dominated by different predators in each. We addressed our hypotheses by simulating arthropod predation across Ascension via experimental live bait trials, which accurately represent realized predation (Zvereva et al. 2024).

2 | Methods

We expanded on data collection by Chin et al. (2024) across Ascension Island from June to August 2023. This involved recording live bait predation over controlled periods (Bröder et al. 2023) at experimental "predation arenas". Arenas comprised white-painted wooden squares of 15×15 cm with a screw driven into the center. A single live arthropod was tethered to the screw by a fine nylon fishing line such that it could move freely on the arena. Most insects are nocturnal globally (Wong and Didham 2024), as is the only well-studied Ascensionendemic arthropod, the Ascension scaly cricket Discophallus ascension (Chin et al. 2024), and thus we tested predation between 7 and 10 p.m. Each predation arena was deployed at ground level and illuminated by a 350lm LED lamp. A GoPro Hero 9 Black Edition camera recorded the lit arena from a 15cm tripod via timelapse photographs taken at 10-s intervals. We recognized that illumination may alter overall predation occurrence but assumed a constant impact across treatments. Five predation arenas, separated by 10 m, were deployed along linear transects at one location per night. We recorded whether the live bait at each arena was killed and at least partly consumed in photographs within the sampling timeframe. We identified the killing predator to species level from captured photographs and prior knowledge of established non-native species, or individuals in the arena in the morning (e.g., swarming ants that were photographed killing the prey).

Sampling locations (n = 29) and live baits (n = 3) were selected to represent the range of habitats and their associated island-native arthropods on Ascension (Figure 1, S1). The arthropod species used as bait were non-native surrogates for Ascension-endemic arthropods, which we could be sure were native. Surrogates were used to avoid endangering individuals of potentially threatened species (Bröder et al. 2023). The nine locations sampled by Chin et al. (2024) were positioned on the north, west, and south of the island at the coastal edges of lava flows. Predation arenas at these locations (45 arenas) were baited with non-native tropical house crickets, Gryllodes sigillatus, that represented individuals of the similarly sized D. ascension inhabiting those areas (Mogoplistes sp. in Ashmole and Ashmole (1997); Gorochov (2009)). We sampled an additional 14 locations (70 arenas) below 400 m elevation that included land surfaces and volcanic caves. These arenas were baited with woodlice of the family Armadillidae, which represented Ascension-endemic Niambia spp. woodlice inhabiting caves and barren lowland surface habitats (Ashmole and Ashmole 1997; Taiti and Ferrara 1991). We sampled six final locations (30 arenas) above 400 m elevation. We used a larviform bait, Muscidae house fly larvae of less than 5 mm in length, to represent endemic arthropod larvae found only at higher elevations (e.g., Erechthias grayi; Davis and Mendel 2013). Our aims and hypothesis concerned realized predation, and our design did not allow the study of palatability, as we did not deploy all types of live baits at all elevations. This was partly due to logistical constraints and avoid introducing non-native species baits in habitats where they were not yet established.

There were eight locations inside volcanic caves, eight in naturally barren areas, 10 in areas colonized by non-native vegetation, and three in areas of native vegetation. We distinguished habitats by six variables to explain spatial differences in predator presence and activity. Locations spanned coast to a maximum of 748 m elevation and, separately, 3.79 km distance inland. We downloaded Copernicus Sentinel-2 composites of 2019-2023 Normalized Difference Vegetation Index (NDVI), describing vegetation cover, and Normalized Difference Moisture Index (NDMI), describing vegetation moisture, at 10×10 m resolution from the Sentinel Hub at www.sentinel-hub.com (2024). From each independent variable of cave habitat (true or false), distance inland, elevation (log-10 transformed), native habitat (true or false), NDMI, and NDVI, we separately predicted three dependent variables: overall predation occurrence (true or false) and predation occurrence (true or false) by each of P. megacephala and R. rattus (the most frequently recorded predators). Models were mixed-effects logistic regressions (18 in total), fitted in R version 4.3.1 (R Core Team 2023) using the lme4 package (Bates et al. 2015), which predicted binomial odds of predation occurrence given counts of success and failures per location (n = 29; S2). All models included bait type (cricket/larva/woodlouse) as

2 of 6 Biotropica, 2025

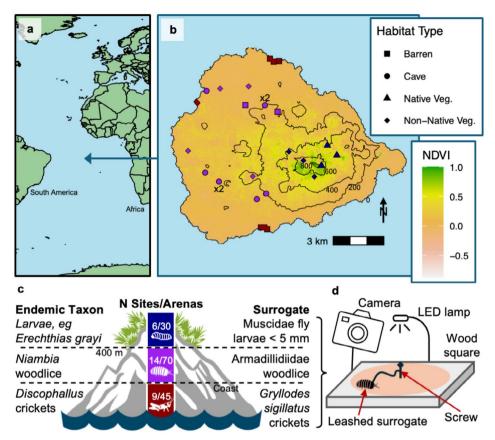


FIGURE 1 | Sampling locations and experimental design on Ascension Island. (a) Location of Ascension in the South Atlantic. (b) Locations of sampling sites. Each represents a site of five predation arenas. (c) Elevational separation in predation baits. (d) Design of one predation arena.

a random intercept to control for potential differences in their detectability and palatability.

3 | Results

Across sampling locations, 33% of baits were predated. Of those occurrences, 44% were conducted by ants and 39% by *P. megacephala* specifically (the remainder by longhorn crazy ant *Paratrechina longicornis* at a single site; S2). A further 33% of the recorded predation was by *R. rattus*. Cricket (at the coastline) and woodlice baits (<400 m elevation) were predated by both *P. megacephala* and *R. rattus*, while larva baits (>400 m elevation) were predated only by *P. megacephala*. Other recorded non-native predators were the American cockroach *Periplaneta americana*, coconut palm gecko *Hemidactylus mercatorius*, and ring-legged earwig *Euborellia annulipes*. There were five observations of Ascension-native animals, all *D. ascension*, feeding on a bait item. We did not observe predation by centipedes, spiders, or scorpions.

Baits in non-native vegetation habitats were predated most (51%), followed by baits in barren habitats (41%), native vegetation habitats (15%), and cave habitats (11%; Figure 2a). Arthropod baits in caves were less likely to be taken compared with other habitats (Z=-3.19, p<0.01) and all observed cave predation events were by R. rattus and within twilight zones, which are dimly lit and close to cave entrances, as opposed to dark zones, which are completely unlit and further underground. Distance inland had

no impact on total predation occurrence (Z=-0.30, p>0.05; Figure 2b) but there was turnover whereby R. rattus predated more baits at the coast (Z=-2.39, p<0.05) and P. megacephala more baits inland (Z=3.46, p<0.001). Rattus rattus also predated more baits at lower elevations (Z=-2.20, p<0.05) but there was no significant elevation effect on P. megacephala (Z=-1.28, p>0.05). We found no effect of NDMI (multiple tests, p>0.05), but P. megacephala predated more baits at locations of higher NDVI (Z=3.09. p<0.01). Arthropod baits in native habitats were less likely to be predated than in non-native habitats (Z=-2.97, p<0.001) and there were significantly fewer predations by P. megacephala in native habitats (Z=-4.16, p<0.01). Conversely, 100% of predation by R. rattus was in natively barren habitats. Full model outputs are reported in the S3.

4 | Discussion

These results support our initial hypothesis that arthropod predation is dominated by different non-native animals across habitats. Two of the "World's 100 Worst Invasive Alien Species" (Lowe et al. 2000), *P. megacephala* and *R. rattus*, are implicated as the key arthropod predators on our study island. Ants (McGlynn 1999; Suarez et al. 2009) and rats (Doherty et al. 2016; Puckett et al. 2016) are frequently introduced to oceanic islands and many species of both consume arthropods (St Clair 2011; Tercel et al. 2023), hence our findings may be broadly representative of oceanic islands with few native arthropod predators. Both *P. megacephala* (Wetterer and Lester 2012) and *R. rattus*

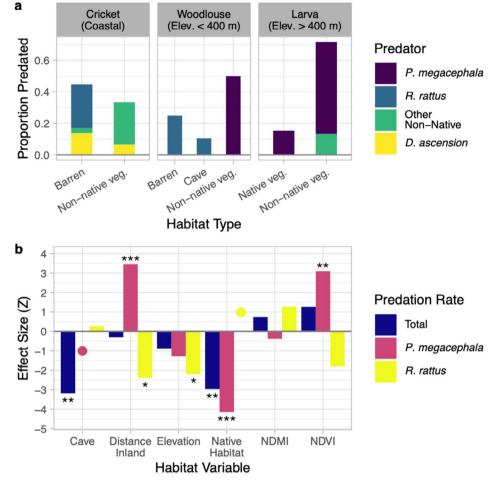


FIGURE 2 | Simulated predation occurrences on Ascension. (a) Observed proportions of baits predated (i.e., killed and consumed) across arenas. (b) Modeled effect sizes of six variables on predation occurrence. Each bar represents the only predictor of one mixed-effects logistic regression. Significance of variables at the p < 0.05, p < 0.01, and p < 0.001 levels are represented by *, **, and ***, respectively. Circles at Z = 1 indicate that 100% of predation occurred in that habitat. Circles at Z = -1 indicate that 0% of predation occurred in that habitat. In these cases, the associated mixed-effects model did not converge and therefore a valid effect size could not be reported.

(St Clair 2011) are known invasive predators of importance to arthropod species conservation on islands, and previous work on Ascension has shown that one comparatively closely related non-native taxon, the ants, divide feeding niches but not site occupancy (Sharp and Tawatao 2023). These current results are novel in that they show significant segregation across common island habitats in the relative predatory impact exerted by distantly related non-native taxa. The results also show that other non-native predators which might have been assumed to be important arthropod predators were less so than expected. For example, predatory Scolopendra centipedes, which are non-native to Ascension (Ashmole and Ashmole 1997; Duffey 1964) and can consume various arthropods (Guizze et al. 2016), have been loosely implicated in the mainland extirpation of the endemic giant pseudoscorpion Garypus titanius (Wilkins et al. 2019) but did not take a single prey item in our study.

We found evidence of non-native predation across all studied island habitats, but native habitats, and in particular caves, were least impacted. Native habitats and associated specialist species may confer some resilience to non-native species colonization through limiting available niche space (Delavaux et al. 2023) and thus such habitat could accordingly be resilient

to non-native predator colonization also. We found no evidence of non-native predation in the dark zones of caves-the most distant and physically inaccessible areas from cave entrances. In line with the current understanding that environmental filtering in caves often prevents colonization by non-native species (Nicolosi et al. 2023), we suggest that non-native predation, especially deep within caves, is low. This may explain why caves remain globally significant reservoirs of threatened islandendemic arthropods, which are often not threatened by invasive species (Sharp and Gray 2025). Rattus rattus are likely most abundant at barren coastlines where native biodiversity is low (Ashmole and Ashmole 1997) but they are able to scavenge on marine animal carcasses. In contrast, P. megacephala predated baits in inland, vegetated, and non-native habitats. In line with understanding from oceanic islands elsewhere (Wetterer and Lester 2012) Pheidole megacephala are likely associated with spreading non-native vegetation.

These results show habitat separation and contrasting predation pressures exerted by non-native species and can help inform invasive species management on oceanic islands. We recommend maintaining or restoring native habitat structures to reduce overall non-native predation pressure on arthropods. On

4 of 6 Biotropica, 2025

the many islands colonized by P. megacephala (Wetterer and Lester 2012), we suggest that local stakeholders specifically trial non-native vegetation clearance and fine-scale chemical suppression at those sites (e.g., Gaigher et al. 2012) to reduce predatory pressure associated with vegetation. For islands where R. rattus has been established (St Clair 2011), we suggest deploying poison baits (e.g., Auld et al. 2010) specifically along coastlines and cave openings. Such barren habitats may be perceived as depauperate of arthropod biodiversity but accommodate undetected and predation-threatened species; for example, the Ascension-endemic coastal pseudoscorpion Garypus ellickae (Sherwood et al. 2024b) was discovered only during the wider project associated with this analysis. Our recommendations are unlikely to prove failsafe solutions for reducing non-native predation of island-native arthropods but might provide a starting point from which to research and plan locally optimized strategies.

Acknowledgments

This work was funded by Darwin Plus grant DPLUS135 From Pseudoscorpions to Crickets: Securing Ascensions Island's Unique Invertebrates. We thank the Department for Environment, Food and Rural Affairs (DEFRA) for supporting this project. We also thank three anonymous Reviewers for their constructive support in developing this manuscript.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in the Zenodo Repository: https://zenodo.org/records/15299995.

References

Ashmole, P., and M. Ashmole. 2000. St Helena and Ascension Island: A Natural History. Anthony Nelson.

Ashmole, P. N., and M. J. Ashmole. 1997. "The Land Fauna of Ascension Island: New Data From Caves and Lava Flows, and a Reconstruction of the Prehistoric Ecosystem." *Journal of Biogeography* 24: 549–589.

Auld, T. D., I. Hutton, M. K. J. Ooi, and A. J. Denham. 2010. "Disruption of Recruitment in Two Endemic Palms on Lord Howe Island by Invasive Rats." *Biological Invasions* 12: 3351–3361.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 6: 1–48

Bourne, W. R. P., N. P. Ashmole, and K. E. L. Simmons. 2003. "A New Subfossil Night Heron and A New Genus for the Extinct Rail Ascension Island, Central Tropical Atlantic Ocean." *Ardea* 91: 45–51.

Bröder, L., L. Tatin, and A. Hochkirch. 2023. "Quantifying Predation to Insects: An Experimental Approach." *Global Ecology and Conservation* 44: e02485.

Chin, W. Y., V. Wilkins, and A. Sharp. 2024. "Invasive Vegetation Encroachment Modulates Dual Threats Faced by Island-Endemic Scaly Crickets." *Biological Invasions* 26: 2941–2954.

Dahl, F. 1892. "Die Landfauna von Ascension (Anhang zu Kapitel VII)." In Ergebnisse der in dem Atlantischen Ocean von Mitte Juli bis Anfang November 1889 Ausgeführten Plankton-Expedition der Humboldt-Stifttung, edited by V. Hensen, 204–209. Verlag Lipsius & Tischer.

Davis, D. R., and H. Mendel. 2013. "The Genus Erechthias Meyrick of Ascension Island, Including Discovery of a New Brachypterous Species (Lepidoptera, Tineidae)." *ZooKeys* 341: 1–20.

Delavaux, C. S., T. W. Crowther, C. M. Zohner, et al. 2023. "Native Diversity Buffers Against Severity of Non-Native Tree Invasions." *Nature* 621: 773–781.

Doherty, T. S., A. S. Glen, D. G. Nimmo, E. G. Ritchie, and C. R. Dickman. 2016. "Invasive Predators and Global Biodiversity Loss." *Proceedings of the National Academy of Sciences* 113: 11261–11265.

Duffey, E. 1964. "The Terrestrial Ecology of Ascension Island." *Journal of Applied Ecology* 1: 219–251.

Fernández-Palacios, J. M., H. Kreft, S. D. H. Irl, et al. 2021. "Scientists' Warning – The Outstanding Biodiversity of Islands is in Peril." *Global Ecology and Conservation* 31: e01847. https://doi.org/10.1016/j.gecco. 2021.e01847.

Gaigher, R., M. J. Samways, K. G. Jolliffe, and S. Jolliffe. 2012. "Precision Control of an Invasive Ant on an Ecologically Sensitive Tropical Island: A Principle With Wide Applicability." *Ecological Applications* 22: 1405–1412.

Gorochov, A. V. 2009. "Crickets of the Family Mogoplistidae (Orthoptera) From Ascension and Saint Helena Islands, Atlantic Ocean." *Proceedings of the Zoological Institute RAS* 313: 23–32.

Gray, A., V. Wilkins, D. Pryce, et al. 2019. "The Status of the Invertebrate Fauna on the South Atlantic Island of St Helena: Problems, Analysis, and Recommendations." *Biodiversity and Conservation* 28: 275–296.

Guizze, S., I. Knysak, K. Barbaro, M. Karam-Gemael, and A. Chagas-Jr. 2016. "Predatory Behavior of Three Centipede Species of the Order Scolopendromorpha (Arthropoda: Myriapoda: Chilopoda)." *Zoologia* (Curitiba) 33: e20160026.

Hoffmann, B. D., G. M. Luque, C. Bellard, N. D. Holmes, and C. J. Donlan. 2016. "Improving Invasive Ant Eradication as a Conservation Tool: A Review." *Biological Conservation* 198: 37–49.

Jicha, B. R., B. S. Singer, and M. J. Valentine. 2013. "40Ar/39Ar Geochronology of Subaerial Ascension Island and a Re-Evaluation of the Temporal Progression of Basaltic to Rhyolitic Volcanism." *Journal of Petrology* 54, no. 12: 2581–2596. https://doi.org/10.1093/petrology/egt058.

Kier, G., H. Kreft, M. L. Tien, et al. 2009. "A Global Assessment of Endemism and Species Richness Across Island and Mainland Regions." *Proceedings of the National Academy of Sciences of the United States of America* 106: 9322–9327.

Lambdon, P., J. Sim, and S. Stroud. 2024. Flowering Plants & Ferns of Ascension Island. NatureBureau. https://www.nhbs.com/flowering-plants-ferns-of-ascension-island-book.

Lowe, S., M. Browne, S. Boudjelas, and M. De Poorter. 2000. 100 of the World's Worst Invasive Alien Species A Selection From the Global Invasive Species Database. Invasive Species Specialist Group (ISSG) a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN).

McGlynn, T. P. 1999. "The Worldwide Transfer of Ants: Geographical Distribution and Ecological Invasions." *Journal of Biogeography* 26, no. 3: 535–548. https://doi.org/10.1046/j.1365-2699.1999.00310.x.

Nicolosi, G., S. Mammola, L. Verbrugge, and M. Isaia. 2023. "Aliens in Caves: The Global Dimension of Biological Invasions in Subterranean Ecosystems." *Biological Reviews* 98: 849–867.

Puckett, E. E., J. Park, M. Combs, et al. 2016. "Global Population Divergence and Admixture of the Brown Rat (*Rattus norvegicus*)." *Proceedings of the Royal Society B: Biological Sciences* 283: 20161762.

R Core Team. 2023. "R: A Language and Environment for Statistical Computing."

Roy, H. E., A. Pauchard, P. Stoett, et al. 2024. "IPBES Invasive Alien Species Assessment: Summary for Policymakers." Zenodo Available at: https://zenodo.org/doi/10.5281/zenodo.7430692.

Sharp, A., and A. Gray. 2025. "Tiny Habitats of Tiny Species: The Importance of Micro-Refugia for Threatened Island-Endemic Arthropods." *Oryx.* https://doi.org/10.1017/S0030605324001509.

Sharp, A., and N. Tawatao. 2023. "Colonization and Coexistence of Non-Native Ants on a Model Atlantic Island." *Diversity and Distributions* 29: 1278–1288.

Sherwood, D., L. F. De Armas, A. Sharp, L. Fowler, and V. Wilkins. 2024a. "Scorpions (*Arachnida Scorpiones*) of the United Kingdom Overseas Territories: Current Knowledge and Future Directions." *Biodiversity Journal* 15: 41–52.

Sherwood, D., V. Grignet, M. Harvey, et al. 2024b. "David and Goliath: On the Pseudoscorpions of Ascension Island, Including the World's Largest, *Garypus titanius* Beier, 1961, and a New, Minute, Neocheiridium Beier, 1932 (Arachnida: Pseudoscorpiones)." *Natura Somogyiensis* 42: 131–150.

Sherwood, D., Y. M. Marusik, A. Sharp, and P. Ashmole. 2023. "A Survey of Gnaphosidae (Arachnida, Araneae) From Ascension Island With Description of a New Species of Australoechemus Schmidt & Piepho, 1994." *African Invertebrates* 64: 291–302.

Sherwood, D., and A. Sharp. 2023. "A Caribbean in the South Atlantic: First Records of *Hentzia antillana* Bryant 1940, With Notes on Other Previously Reported Jumping Spider Species (Araneae: Salticidae), From Ascension Island." *Peckhamia* 310: 1–7.

St Clair, J. J. H. 2011. "The Impacts of Invasive Rodents on Island Invertebrates." *Biological Conservation* 144: 68–81.

Suarez, A. V., T. P. McGlynn, and N. D. Tsutsui. 2009. "Biogeographic and Taxonomic Patterns of Introduced Ants." In *Ant Ecology*, 233–244. Oxford University Press. https://academic.oup.com/book/26117/chapt er/194138991.

Taiti, S., and F. Ferrara. 1991. "Two New Species of Terrestrial Isopoda (Crustacea, Oniscidea) From Ascension Island." *Journal of Natural History* 25: 901–916.

Tercel, M. P. T. G., J. P. Cuff, W. O. C. Symondson, and I. P. Vaughan. 2023. "Non-Native Ants Drive Dramatic Declines in Animal Community Diversity: A Meta-Analysis." *Insect Conservation and Diversity* 16: 733–744.

Wetterer, J. K., and P. J. Lester. 2012. "Worldwide Spread of the African Big-Headed Ant, *Pheidole megacephala* (Hymeno-Ptera: Formicidae)." *Myrmecological News* 17: 51–62.

Wilkins, V. L., V. Knight, and A. Gray. 2019. "Garypus titanius. The IUCN Red List of Threatened Species 2019." https://www.iucnredlist.org/species/135739408/135745815.

Wong, M. K. L., and R. K. Didham. 2024. "Global Meta-Analysis Reveals Overall Higher Nocturnal Than Diurnal Activity in Insect Communities." *Nature Communications* 15: 3236.

Zvereva, E., B. Adroit, T. Andersson, et al. 2024. "Predation on Live and Artificial Insect Prey Shows Different Global Latitudinal Patterns." *Global Ecology and Biogeography* 33: 1–11.

Supporting Information

Additional supporting information can be found online in the Supporting Information section.

6 of 6 Biotropica, 2025