

Foreword to Chapter Four



Daniel Simberloff and Anthony Ricciardi

Elton featured isolated islands as particularly devastated by invasions, focusing on Easter Island, the Tristan da Cunha group, the Hawaiian chain, and New Zealand. Had he completed a second edition, he would have noted even greater impacts at least for Tristan de Cunha and Hawaii, as he had notes from publications on invasion impacts there from 1959 through 1970.

In general, invasion impacts on islands, especially remote islands, have only worsened. For Gough in the Tristan da Cunha group, Elton's notes included records published in 1959 on house mice,^[xii] but only in 2001 was it recognized that predation by the Gough mice is responsible for massive seabird death.^[xxx] The endemic Easter Island tree *Sophora toromiro* that Elton had described as nearly extinct is now extinct in the wild (but slated for reintroduction from a botanical garden).^[xvi] Several endemic insects, as well as two endemic isopods, have since been discovered on Easter Island, particularly in caves, but these are gravely threatened by anthropogenic factors, including newly introduced species.^[xxxiii] In Hawaii, Elton mentioned the possibility that introduced Asian birds might transmit avian malaria to native birds via introduced

D. Simberloff (✉)
Department of Ecology and Evolutionary Biology,
University of Tennessee, Knoxville, TN, USA
e-mail: dsimberloff@utk.edu

A. Ricciardi
Redpath Museum and McGill School of Environment,
McGill University, Montreal, QC, Canada
e-mail: tony.ricciardi@mcgill.ca

The Ecology of Invasions by Animals and Plants

mosquitoes. He was aware by 1970 that such an event had indeed come to pass, as he had annotated a 1970 meeting report on endangered birds and mammals in Hawaii that mentioned the threat. Beginning in the late 1960s it was widely reported that native lowland birds were devastated by the pathogen, although one species recently is recolonizing lowland forests.^[XXII] For New Zealand, Elton focused primarily on introduced mammals and birds but mentioned the recently arrived and fast-spreading Palearctic wasp *Vespula germanica*, without detailing its impact. It has since become widespread, but, worse, it has been replaced in southern beech forests by the more recently introduced Palearctic *Vespula vulgaris*, with a vast array of impacts at population, community, and ecosystem levels, including competition with threatened bird species for scale insect honeydew.^[II]

Elton could have chosen other remote islands to make his case—e.g., the Galapagos^[VII] or St. Helena^[XVII]—but the four cases he chose made his case well, and many other islands have similarly suffered since he wrote. A famous case is the loss of Guam’s forest birds to predation by the introduced brown tree snake with follow-on effects on native plants and animals.^[XIX,XXIV]

For several invasions Elton discussed, recent research casts new light on impacts. On New Zealand and other islands, Elton saw the Pacific rat (*Rattus exulans*) as quite innocuous, unfairly tarred by association with the ship rat and Norway rat. In fact, on these islands it causes drastic declines in native bird, reptile, amphibian, and insect populations,^[XXI] and this species is now suspected of having been the main cause, through seed predation, of Easter Island deforestation.^[XIV] In Hawaii, one of the three Asian birds that Elton noted had penetrated into forests and might transmit avian malaria—the Japanese tit—has disappeared completely from all islands,^[XXVI] while populations of a second—the red-billed leiothrix—now fluctuate wildly, and the species has disappeared from Kauai.^[XXII]

Elton adumbrated two phenomena that subsequently became major research foci in invasion science. One is invasional meltdown, in which a group of nonnative species facilitate one another’s invasion, increasing the likelihood of survival and/or ecological impact, and possibly the magnitude of impact.^[XXVII] Elton noted that “Most of the [introduced] herbivorous insects have followed in the wake of earlier plant introductions” (p. 107). He described how the introduced Asian myna spread New World lantana in Hawaii, and he feared transmission by introduced mosquitoes of avian malaria from Asian to native birds. Similar phenomena have been recorded in many other systems,^[III] including a 3-way interaction among introduced yellow crazy ants and scale insects and

Foreword to Chapter Four

native red crabs on Christmas Island (Indian Ocean) that facilitated invasion by the giant African snail,^[xi] whose march across Pacific islands Elton described.

In Hawaii Elton also foresaw the explosion of interest in non-target impacts of introduction of natural enemies for biological control of nonnative pests following Howarth's suggestion that such nontarget impacts on native insects are common.^[xiii] Subsequent research shows that one such case adduced by both Elton and Howarth, the loss or possible extinction of native moths owing to the introduction of wasp parasitoids to control introduced pest moths, is doubtful, but several other instances on both islands and mainland are confirmed.^[xxviii] One case hinted at by Elton and updated by Howarth is the impact of the predatory New World rosy wolf snail, introduced to Hawaii and many other islands in a futile attempt to control the giant African snail. Elton noted that the rosy wolf snail was being trialed as a possible control agent and seemed to hint at its threat to native amastrid snails. In fact, the introduction led to one of the great conservation hecatombs of modern times, delivering the coup de grace to already declining amastrids^[xxiii] and causing the extinction of many other Pacific island snails, including endemic achatinellid tree snails in Hawaii.^[vi]

Elton's attitude towards biological control was enigmatic. In Chap. 4 he extensively paraphrased Weber,^[xxxii] about how "Every new insect pest may cause a train of operations with foreign counterpests," with no mention of possible non-target impacts. This passage may be read as either an endorsement of the approach or as a wry, ironic commentary on the endless build-up of invaders, in the spirit of the poem about great fleas having little fleas upon their backs to bite 'em. In notes inserted in the proof copy for Chap. 7, Elton wrote extensively, based on comments by Nicholson,^[xx] about many successful or promising projects for biological control of plants, never cited in his book, with no mention of possible non-target impacts on native species.

Elton did not foresee several subsequent developments in invasion science. One is extensive research on ecosystem-wide impacts of invasions following research by Vitousek and colleagues on how myriad impacts of the nitrogen-fixing Atlantic shrub *Morella faya* "change the rules of the game" for the entire mid-elevation ecosystem on the island of Hawaii,^[xxix] in a meltdown involving introduced earthworms and seed-dispersers.^[xxv] Another is the increasing role of genetics in invasion science. Molecular tools unavailable in 1958 have been used to track pathways of introduction to islands and mainland, as for the cane toad,^[ix] to detect hybridization of native species with invaders, as for the

The Ecology of Invasions by Animals and Plants

Hawaiian duck,^[X] to determine cause of eradication failure, as for rats in the St. Anne Peninsula,^[II] and to determine that a legendary invader, the rosy wolf snail, is actually two species.^[XVIII]

Elton was not sanguine about eradication of invaders, on mainland or islands, though in Chaps. 1 and 6 he noted the eradication of the malaria mosquito, *Anopheles gambiae*, from a large region in Brazil and in Chap. 6 he described eradicating a small North American muskrat population in Great Britain. Previously he had foreseen the possibility of eradicating ship rats and Norway rats from Great Britain and many other islands;^[VIII] had he become more pessimistic? If so, this was unwarranted, as recent advances have led to successful eradication of both species from hundreds of islands^[XXI] with notable conservation benefits of these and other invasive mammal eradications.^[XV] Many technologies unavailable in 1958 have been used in projects on increasingly large islands—for instance, the use of GIS, aircraft, and synthetic hormones in eradicating goats from Santiago and the entire northern part of Isabela in the Galapagos Archipelago.^[IV,V]

References

- I. Abdelkrim, J., M. Pascal, and S. Samadi. 2007. Establishing causes of eradication failure based on genetics: case study of ship rat eradication in Ste. Anne archipelago. *Conservation Biology* 21: 719–730.
- II. Beggs, J.R., E.G. Brockerhoff, J.C. Corley, M. Kenis, M. Masciocchi, F. Muller, Q. Rome, and C. Villemant. 2011. Ecological effects and management of invasive alien Vespidae. *BioControl* 56: 505–526.
- III. Braga, R.R., L. Gómez-Aparicio, T. Hegers, J.R.S.Vitule, and J.M. Jeschke. 2018. Structuring evidence for invasional meltdown: broad support but with biases and gaps. *Biological Invasions* 20: 923–936.
- IV. Campbell, K. J., G.S. Baxter, P.J. Murray, B.E. Coblenz, and C.J. Donlan. 2007. Development of a prolonged estrus effect for use in Judas goats. *Applied Animal Behaviour Science* 102: 1–2,12–23.
- V. Carrion, V., C.J. Donlan, K.J. Campbell, C. Lavoie, and F. Cruz. 2011. Archipelago-wide island restoration in the Galapagos Islands: Reducing costs of invasive mammal eradication programs and reinvasion risk. *PLoS ONE* 6(5): e18835. doi:10.1371/journal.pone.0018835
- VI. Cowie, R.H. 2001. Can snails ever be effective and safe biocontrol agents? *International Journal of Pest Management* 47: 23–40.
- VII. Eckhardt, R.C. 1972. Introduced plants and animals in the Galápagos Islands. *BioScience* 22: 585–590.
- VIII. Elton, C.S. 1944. The biological cost of modern transport. *Journal of Animal Ecology* 13: 87–88.
- IX. Estoup A., I.J. Wilson, C. Sullivan, J.-M. Cornuet, and C. Moritz. 2001. Inferring population history from microsatellite and enzyme data in serially introduced cane toads, *Bufo marinus*. *Genetics* 159: 1671–1687.

Foreword to Chapter Four

- X. Fowler, A.C., J.M. Eadie, and A. Engilisi, Jr. 2009. Identification of endangered Hawaiian ducks (*Anas wyvilliana*), introduced North American mallards (*A. platyrhynchos*) and their hybrids using multilocus genotypes. *Conservation Genetics* 10: 1747–1758.
- XI. Green, P.T., D.J. O'Dowd, K.L. Abbott, M. Jeffery, K. Retallick, and R. MacNally. 2011. Invasional meltdown: Invader-invader mutualism facilitates a secondary invasion. *Ecology* 92: 1758–1768.
- XII. Hill, J.E. 1959. Rats and mice from the islands of Tristan da Cunha and Gough, South Atlantic Ocean. Results of the Norwegian Scientific Expedition to Tristan da Cunha 1937–1938, No. 46.
- XIII. Howarth, F. G. 1983. Classical biological control: panacea or Pandora's Box? *Proceedings of the Hawaiian Entomological Society* 24: 239–244.
- XIV. Hunt, T., and C. Lipo. 2011. *The Statues that Walked*. Free Press, NY.
- XV. Jones, H.P., N.D. Holmes, S.H.M. Butchart, B.R. Tershy, P.J. Kappes, et al. 2016. Invasive mammal eradication on islands results in substantial conservation gains. *Proceedings of the National Academy of Sciences (USA)* 113: 4033–4038.
- XVI. Maunder, M., A. Culham, A. Bordeu, J. Allainguillaume, and M. Wilkinson. 1999. Genetic diversity and pedigree for *Sophora toromiro* (Leguminosae): a tree extinct in the wild. *Molecular Ecology* 8: 725–738.
- XVII. Maunder, M., T. Upton, B. Spooner, and T. Kendle. 1995. Saint Helena: sustainable development and conservation of a highly degraded island ecosystem. Pp. 205–217 in: P.M. Vitousek, L.L. Loope, and H. Adersen (eds.), *Islands. Biological Diversity and Ecosystem Function*. Springer, Berlin.
- XVIII. Meyer, W.M., III, N.W. Yeung, J. Slapcinsky, and K.A. Hayes. 2017. Two for one: inadvertent introduction of *Euglandina* species during a failed bio-control attempt. *Biological Invasions* 19: 1399–1405.
- XIX. Mortensen, H.S., Y.L. Dupont, and J.M. Olesen. 2008. A snake in paradise: Disturbance of plant reproduction following extirpation of bird flower-visitors on Guam. *Biological Conservation* 141: 2146–2154.
- XX. Nicholson, A.J. 1950. Progress in the control of *Hypericum* by insects. Pp. 96–99 in: *Eighth International Congress of Entomology*. Axel B. Elfstroms Boktryckeri ab, Stockholm.
- XXI. Pascal, M. 2011. Rats. Pp. 571–575 in: D. Simberloff and M. Rejmánek (eds.), *Encyclopedia of Biological Invasions*. University of California Press, Berkeley.
- XXII. Ralph, C.J., S.G. Fancy, and T.D. Male. 1998. Demography of an introduced red-billed leiothrix population in Hawaii. *Condor* 100: 468–473.
- XXIII. Régnier, C., P. Bouchet, K.A. Hayes, N.W. Yeung, C.C. Christensen, D.J.D. Chung, B. Fontaine, and R.H. Cowie. 2015. Extinction in a hyperdiverse endemic Hawaiian land snail family and implications for the underestimation of invertebrate extinction. *Conservation Biology* 29: 1715–1723.
- XXIV. Rogers, H., J. Hille Ris Lambers, R. Miller, and J.J. Tewksbury. 2012. 'Natural experiment' demonstrates top-down control of spiders by birds on a landscape level. *PLoS ONE*. e43446. doi:10.1371/journal.pone.0043446.
- XXV. Simberloff, D. 2006. Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? *Ecology Letters* 9: 912–919.
- XXVI. Simberloff, D., and W. Boecklen. 1991. Patterns of extinction in the introduced Hawaiian avifauna: A reexamination of the role of competition. *American Naturalist* 138: 300–327.
- XXVII. Simberloff, D., and B. Von Holle. 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* 1: 21–32.
- XXVIII. Van Driesche, R., D. Simberloff, B. Blossey, C. Causton, M. Hoddle, C. Marks, K. Heinz, D. Wagner, and K. Warner (eds.). 2016. *Integrating Biological Control into Conservation Practice*. Wiley-Blackwell, Chichester, UK.

The Ecology of Invasions by Animals and Plants

- XXIX. Vitousek, P.M., and L.P. Walker. 1989. Biological invasions by *Myrica faya* in Hawaii: plant demography, nitrogen fixation and ecosystem effects. *Ecological Monographs* 59: 247–265.
- XXX. Wanless, R.M., A. Angle, R.J. Cuthbert, G.M. Hinton, and P.G. Ryan. 2007. Can predation by mice drive seabird extinctions? *Biology Letters* 3: 241–244.
- XXXI. Weber, P.W. 1956. Recent introductions for biological control in Hawaii. I. *Proceedings, Hawaiian Entomological Society* 16: 162–164.
- XXXII. Woodworth, B.L., C.T. Atkinson, D.A. LaPointe, P.J. Hart, C.S. Spiegel, E.J. Tweed, C. Henneman, J. LeBrun, T. Denette, R. DeMots, K.L. Kozar, D. Triglia, D. Lease, A. Gregor, T. Smith, and D. Duffy. 2005. Host population persistence in the face of introduced vector-borne diseases: Hawaii amakihi and avian malaria. *Proceedings of the National Academy of Sciences (USA)* 102: 1531–1536.
- XXXIII. Wynne, J.J., E.C. Bernard, F.G. Howarth, S. Sommer, F.N. Soto-Adames, S. Taiti, E.L. Mockford, M. Horrocks, L. Pakarati, and V. Pakarati-Hotus. 2014. Disturbance relicts in a rapidly changing world: the Rapa Nui (Easter Island) factor. *BioScience* 64: 711–718.