REFERENCES

1. Suddendorf, T. (2013). The Gap: The Science of What Separates Us from Other Animals (New York: Basic Books).
2. Chittka, L., and Niven, J. (2009). Are bigger brains better? Curr. Biol. *19*, R995–R1008.
3. Herculano-Houzel, S. (2012). The remarkable, yet not extraordinary, human brain as a scaled-up primate brain and its associated cost. Proc. Natl. Acad. Sci. USA *109*, 10661–10668.
4. Quian Quiroga, R. (2019). Plugging in to human memory: advantages, challenges and insights from human single neuron recordings. Cell *179*, 1015–1032.
5. Quian Quiroga, R., Reddy, L., Kreiman, G., Koch, C., and Fried, I. (2005). Invariant visual representation by single neurons in the human brain. Nature *435*, 1102–1107.
6. Quian Quiroga, R., Kraskov, A., Koch, C., and Fried, I. (2009). Explicit encoding of multimodal percepts by single neurons in the human brain. Curr. Biol. *19*, 1308–1313.
7. Moscovitch, M., Cabeza, R., Winocur, G., and Nadel, L. (2016). Episodic memory and beyond: the hippocampus and neocortex in transformation. Annu. Rev. Psychol. *67*, 105–134.
8. Squire, L. (2009). The legacy of patient H.M. for neuroscience. Neuron *61*, 6–9.
9. Ison, M., Quian Quiroga, R., and Fried, I. (2015). Rapid encoding of new memories by individual neurons in the human brain. Neuron *87*, 220–230.
10. De Falco, E., Ison, M., Fried, I., and Quian Quiroga, R. (2016). Long-term coding of personal and universal associations underlying the memory web in the human brain. Nat. Commun. *7*, 13408.
11. Tsao, D.Y., Freiwald, W.A., Tootell, R.B., and Livingstone, M. (2006). A cortical region consisting entirely of face-selective cells. Science *311*, 670–674.
12. Chang, L., and Tsao, D. (2017). The code for facial identity in the primate brain. Cell *169*, 1013–1028.
13. Sliwa, J., Plante, A., Duhamel, J.R., and Wirth, S. (2016). Independent neuronal representation of facial and vocal identity in the monkey hippocampus and inferotemporal cortex. Cereb. Cortex *26*, 950–966.
14. von Heimendahl, M., Rao, R., and Brecht, M. (2012). Weak and nondiscriminative responses to conspecifics in the rat hippocampus. J. Neurosci. *32*, 2129–2141.
15. Moser, E., Moser, M.-B., and McNaughton, B. (2017). Spatial representation in the hippocampal formation: a history. Nat. Neurosci. *20*, 1448–1464.
16. Eichenbaum, H., and Cohen, N. (2014). Can we reconcile the declarative memory and spatial navigation views on hippocampal function? Neuron *83*, 764–770.
17. Eichenbaum, H., Dudchenko, P., Wood, E., Shapiro, M., and Tanila, H. (1999). The hippocampus, memory, and place cells: is it spatial memory or a memory space? Neuron *23*, 209–226.
18. Rolls, E.T., and Wirth, S. (2018). Spatial representations in the primate hippocampus, and their functions in memory and navigation. Prog. Neurobiol. *171*, 90–113.
19. Gulli, R., Duong, L., Corrigan, B., Doucet, G., Williams, S., Fusi, S., and Martinez-Trujillo, J. (2020). Context-dependent representations of objects and space in the primate hippocampus during virtual navigation. Nat. Neurosci. *23*, 103–112.

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Quick guide

The island syndrome

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What is the island syndrome?
Organisms on islands predictably differ from their continental counterparts in a host of ecological, behavioural, and morphological traits. Together, the differences are referred to as the 'island syndrome'. The phenomenon has been described in a wide variety of animal and plant species (Figure 1).

Can you give examples of such traits?
The life-span of animals from island populations tend to be longer than those of mainland relatives. This is one of several recurrent life-history changes observed in island organisms. Reduced fecundity is a second — island animals typically produce smaller clutches or litters, funnelling their reproductive effort into fewer, but larger, and more competitive offspring.

What about body size? Some island animals are larger than their mainland relatives, others are not. Rodents, iguanas, geckos, monitor lizards, tortoises and most species of bird tend to grow larger on islands. Spectacular examples of this tendency towards 'island gigantism' include the giant tortoises of the Galápagos and the Seychelles archipelago (*Chelonoidis*, *Aldabrachelys*; Figure 1), Saint Martin's giant hutias (*Amblyrhiza inundata*), and the giant earwig of Saint Helena (*Labidura herculeana*). In contrast, hippopotamuses, elephants, rabbits, deer, pigs, foxes, raccoons, snakes show the opposite tendency: the miniature hippopotamuses (*Hippopotamus creutzburgi*) and elephants (*Mammuthus creticus*) of Pleistocene Crete represent extreme cases of dwarfism. In addition to being larger, or smaller, than their mainland counterparts, island animals often also differ in body shape and colouration. A common theme in island evolution is the reduction of body parts implicated in locomotion (Figure 1). The wings of several species of weevils (Curculionidae), rails (Rallidae), and pigeons (Columbidae, such as the dodo, *Raphus cucullatus*), for instance, have shrunk to the extent that the animals have lost their ability to fly. In several species of lizard and snake, island populations exhibit an increased incidence of melanism (Figure 1). The colours of island birds tend to be less bright and less intense.

Do island animals behave differently?
Island mammals, birds and lizards tend to be less territorial and more tame. For instance, in comparison to their mainland conspecifics, deer mice (*Peromyscus maniculatus*), song sparrows (*Melospiza melodia*) and bronze anoles (*Anolis aeneus*) all have smaller, more overlapping territories and are more tolerant towards intruders. Falkland Island foxes (*Dusicyon australis*) and tammar wallabies (*Macropus eugenii*) from Kangaroo Island have lost their natural fear of large predators, including humans, a phenomenon called 'island tameness'.

What is driving the island syndrome?
Compared to their mainland counterparts, island biota are exposed to a predictably different set of environmental conditions. Due to small size and remoteness, islands tend to house fewer species. Especially, the paucity of larger predators turn islands into safe havens, where prey species can afford to be slower or less wary. The scarcity of competitor species allows island species to expand their ecological niche. Islands often also enjoy relatively mild, predictable climates. Combined, these favourable environmental conditions allow island populations to reach higher, more stable densities, a phenomenon called 'density compensation'. This may shift the balance of interspecific versus intraspecific competition towards the latter, prompting changes in morphology, behaviour and life-history characteristics. Along these lines, many of the features typical for island populations are thought to be adaptive, resulting from natural selection or plasticity responses goaded by the insular environment. However, some of the more unique and eccentric characteristics of creatures found on islands may be coincidental, products of genetic drift.

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Figure 1. The island syndrome in animals and plants.
Top left: Gigantism in tortoises (*Chelonoidis nigra*; Galápagos Islands; photo: Rory Stansbury/Island Conservation). Top right: Dwarfism in foxes (*Urocyon littoralis*; Channel Islands of California; photo: Island Conservation). Center left: Flightlessness in birds (*Strigops habroptila*; Anchor Island, New Zealand; photo: Jake Osborne). Center right: Melanism in lizards (*Podarcis melisellensis*; Brusnik, Croatia; photo: Simon Baeckens). Bottom left: Megaherbs (*Anisotome latifolia*; Enderby Island, New Zealand; photo: Tobias Hayashi). Bottom right: Seed gigantism in plants (*Coprosma propinqua* var. *martinii*; Chatham Islands, New Zealand; photo: Kevin Burns).

What about plants? Freed of (vertebrate) herbivores, many island plants have lost protective structures such as prickles, spines, and thorns and produce smaller amounts of defensive chemicals. The relative rarity of fires on islands has induced the loss of an extra-thick, fire-resisting bark or fire-adapted fruits or cones. As in animals, island life can induce both gigantism and dwarfism in plants. The aptly-called 'megaherbs' (e.g. *Pleurophyllum*, *Stilbocarpa*) of several sub-Antarctic islands, for instance, are herbaceous plants that grow much taller than related plants on the continent (Figure 1). Populations of the giant elephant cactus (*Pachycereus pringlei*) on islands in the Sea of Cortez are an example of island dwarfism. Increased woodiness and seed gigantism (Figure 1) are recurrent trends in island floras. Self-compatibility, in which pollen of one plant can fertilize eggs of the same individual, is also found more often on islands than on continents. In response to a lack of dedicated pollinators, island plants will typically adopt an opportunistic strategy, trying to attract as many alternative pollinator species as possible. Thus, island plants tend to have small, inconspicuously coloured and easily accessible flowers. In turn, island pollinators (usually insects, but sometimes unusual pollinators such as lizards) tend to be catholic with respect to the plant species they visit. Island plants will also often rely on unexpected seed dispersers (e.g. giant tortoises).

Is there an island syndrome in humans? In 2004, paleoanthropologists discovered the fossil remains of a small-sized hominin that roamed the island of Flores in Indonesia about 18,000 years ago. The discovery of these one-meter short, hobbit-like islanders is interpreted by some researchers as an example of human dwarfism due to insularity.

What is next? The island syndrome is often seen in some but not all animal or plant groups. Why some species obey the rule, and others do not, is not clear. The exact mechanism producing the changes in phenotype (genetic drift, natural selection, phenotypic plasticity) is also rarely known. Recently, repeated changes in other characteristics have come to light. Island populations may be more sexually dimorphic, and less resistant to parasite attacks, for instance.

Why does the island syndrome matter? Islands are natural laboratories of evolutionary experimentation, in which we can observe how animals and plants adapt to special, recurring environmental conditions. Islands have greatly inspired modern evolutionary and ecological thinking. The mere existence of a taxon-wide syndrome suggests that evolution is predictable to at least some extent. On the down side, island faunas and floras are among the earth's most-threatened systems. Island environments have produced some of the world's gaudiest life forms, many of which are endemic. Elements of the island syndrome render these island forms especially vulnerable to anthropogenic threats, in particular overharvesting and the introduction of competitor or predator species. Understanding insular ecology and evolution is crucial to prevent island species from suffering the same fate as the emblematic dodo.

Where can I find out more?

Burns, K.C. (2019). Evolution in Isolation: The Search for an Island Syndrome in Plants (Cambridge: Cambridge University Press).
Losos, J.B., and Ricklefs, R.E. (2009). Adaptation and diversification on islands. Nature *457*, 830–836.
Whittaker, R.J., and Fernández-Palacios, J.M. (2007). Island Biogeography: Ecology, Evolution, and Conservation (Oxford: Oxford University Press).
Whittaker, R.J., Férnandez-Palacios, J.M., Matthews, T.J., Borregaard, M.K., and Triantis, K.A. (2017). Island biogeography: taking the long view of nature's laboratories. Science *357*, eaam8326.

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