UNNATURAL SELECTION IN GALAPAGOS: THE ROLE OF DISEASE IN DARWIN'S FINCHES (GEOSPIZINAE)

By: Sharon L. Deem[1,2,3], Stephen Blake[2,3,4,5], R. Eric Miller[1] & Patricia G. Parker[1,2,3]

[1]WildCare Institute, Saint Louis Zoo, 1 Government Drive, Saint Louis, MO 63110, U.S.A. <deem@stlzoo.org>
[2]University of Missouri – Saint Louis, 8001 Natural Bridge Road, Saint Louis, MO 63121, U.S.A.
[3]Charles Darwin Research Station, Puerto Ayora, Galapagos, Ecuador
[4]Max Planck Institute for Ornithology, Vogelwarte Radolfzell, Schlossallee 2, D-78315 Radolfzell, Germany
[5]State Univ. of New York, College of Environmental Science and Forestry, 1 Forestry Drive, Syracuse, NY 13210, U.S.A.

SUMMARY

Micro-evolutionary studies, such as those of Darwin's finches (Geospizinae), have been used as indicators of rates of evolution under natural selection. Today however, such studies may be compromised by unnatural selection. Recently introduced infectious and parasitic agents in Galapagos may hamper our ability to monitor natural evolutionary change in endemic birds, by modifying such change. The opportunity to study natural selection in its iconic site may thus be lost, due to these and other forms of human environmental alteration, which may be replacing non-anthropogenic factors as the principal driver of evolution. To ensure that natural selection continues to shape the biota of Galapagos, anthropogenic impacts including introduced diseases must be managed effectively.

RESUMEN

Selección innatural en Galápagos: la influencia de las enfermedades en los pinzones de Darwin (Geospizinae). Los estudios sobre micro-evolución, tales como los de los pinzones de Darwin (Geospizinae), han sido usados como indice de evolución bajo selección natural. Sin embargo, ahora dichos estudios podrían estar comprometidos por la selección innatural. Agentes infecciosos y parasíticos introducidos recientemente en Galápagos pueden estar afectando nuestra habilidad para monitorear el cambio natural evolutivo en aves endémicas al modificar este proceso. La oportunidad para estudiar la selección natural en este sitio icónico podría perderse debido a esta y otras formas de impacto medioambiental humano, las cuales pueden estar reemplazando los factores no-antropogénicos como motor principal de la evolución. Para asegurar que la selección natural continue moldeando la biota de Galápagos, los impactos antropogénicos incluyendo las enfermedades introducidas deben ser manejados eficazmente.

The Galapagos Islands were instrumental to Charles Darwin's formulation of the theory of evolution by natural selection. Darwin's 1835 visit and his subsequent publication (Darwin 1859) mark the beginning of scientific fascination with the archipelago, which remains the world's laboratory of natural selection. In light of the many recent anthropogenic impacts on the Galapagos, we ask whether "natural" selection continues to shape evolutionary change on this archipelago laboratory or whether, with the escalating anthropogenic changes that include the arrival of invasive parasites and pathogens (Causton *et al.* 2006, Parker *et al.* 2006, Deem *et al.* 2008, Bataille *et al.* 2009), "unnatural" selection is now the major evolutionary force there. Here we define unnatural selection as the process whereby anthropogenic (human-induced) environmental changes dictate which organisms are best adapted to survive and transmit their genetic characteristics to succeeding generations (Palumbi 2001, Darimont *et al.* 2009, Stenseth & Dunlop 2009). Unnatural selection contrasts with natural selection only in that the selective pressures are anthropogenic , while the mechanisms of selection remain similar.

Located in the Pacific Ocean 1000 km from South America, Galapagos has yet to suffer mass anthropogenic extinctions, with an estimated 95 % of its biota extant (Gibbs *et al.* 1999). In Galapagos, scientists record evolutionary changes on macro and micro scales, the latter exemplified by the studies of Darwin's finches (Geospizinae: summarized in Grant 1999, Grant & Grant 2008) that have been used as indicators of rates of change under natural selection (*e.g.* Stenseth & Dunlop 2009). Today however, rather than providing evidence for evolution by natural selection, many of these studies may be compromised by unnatural selection. For example, unnatural selection can be seen in the beak diversification of the Medium Ground Finch *Geospiza fortis*, caused by novel food sources in a human-dominated area (Hendry *et al.* 2006), where a population of historically bimodal beak size was modified to one with unimodal beak size, while bimodality was maintained in an area relatively free of human influence. The unusually strong selection pressure from anthropogenic change may render adaptation easier to study than when evolution is driven by non-anthropogenic, usually more gradual and often stabilising, selection. If natural selection is being overshadowed by unnatural selection even on Galapagos, the chances that evolution in the absence of anthropogenic selection is still occurring elsewhere in terrestrial ecosystems must be slight.

Species are prone to behaving in ways that are not adaptive when an environment changes suddenly, such as with the arrival of an introduced pathogen, because their behaviour is adapted to the previous evolutionary environment (Schlaepfer *et al.* 2002) and does not cover all anthropogenic contingencies. For example, in the absence of a particular parasite, birds may nest in ways that make them vulnerable to that parasite, should it be introduced, although their nesting behaviour may have been shaped by other parasites with which they have shared a long history (Loye & Carroll 1998). Unnatural selection has been recorded around the globe, associated with a variety of human activities including over-harvesting (Sasaki *et al.* 2008, Stenseth & Rouyer 2008, Darimont *et al* 2009), introduced predators (Blackburn *et al.* 2004), and use of pesticides and drugs stimulating resistance in insects and pathogens (Palumbi 2001). Indeed, the ultimate current anthropogenic driver of evolution may be climate change (Bradshaw & Holzapfel 2006). Humans are changing the world at an unprecedented rate, modifying phenotypic traits in surviving organisms.

Even in Galapagos, introduced parasites and pathogens (Wikelski *et al.* 2004, Parker *et al.* 2006, Deem *et al.* 2008) are influencing evolution and shaping populations, as elsewhere (Strayer *et al.* 2006). As one example, the environmental changes (*e.g.* feeding stations, fresh water) that cause Medium Ground Finches to aggregate in the town of Puerto Ayora, and which resulted in beak modifications on a population scale (Hendry *et al.* 2006), will most likely also increase transmission of density-dependent pathogens. Darwin's finches may select human-populated areas since they provide benefits over more natural habitats (*e.g.* easily available food and water). However, the finches may be unable to avoid the introduced disease vectors (*e.g. Culex quinquefasciatus*) and pathogens that are more common in areas with fresh water (Whiteman *et al.* 2005), or that are more likely to spread through a more aggregated population (*e.g.* avian poxvirus: Riper *et al.* 2002), and which thus influence their evolution.

Two recently introduced species in Galapagos, the parasitic fly *Philornis downsi* (Fessl & Tebbich 2002) and avian poxvirus (Thiel *et al.* 2005), cause mortality in endemic birds (Vargas 1987, Huber 2008). They also cause deformities of the nares and beak (Fessl *et al.* 2006, Riper & Forrester 2007) (Figs 1 & 2), hampering our ability to monitor evolutionary change in these morphological features. Further, a study on the fitness cost of avian pox for Darwin's finches on four islands found that males with pox-like lesions were significantly less likely to be pair-bonded than those without lesions (Kleindorfer & Dudaniec 2006) and thus less likely to pass their genes to succeeding generations (though other possible causes of lesions exist, such as trauma, bacterial or fungal infections: Riper & Forrester 2007). Another study of the Medium Ground Finch found that nestlings parasitized by *P. downsi* had smaller beak depths compared to unparasitized nestlings (Huber 2008). Surviving parasitized nestlings probably also have reduced fitness, based on their lower haemoglobin content and beak deformities (Dudaniec *et al.* 2006, Fessl *et al.* 2006). Therefore, Medium Ground Finches with larger beak depth may have an adaptive advantage when under pressure from these parasites. Alternatively, it is possible that nestlings surviving *P. downsi* infestations grow less (including their beaks) than they would have without parasites due to the reallocation of resources to fighting the infection: this would result in a phenotypic change without genotypic selection for beak size. These examples suggest a need for long-term studies of the impacts of invasive pathogens on the evolution of Darwin's finches and other taxa.

In 2009, a year of Darwin anniversaries, it appears that the opportunity to study natural selection in its iconic site (Boag & Grant 1981, Grant & Grant 1989) may soon be lost, due to unnatural selection by invasive pathogens and parasites, and other forms of human environmental alteration. Such anthropogenic selection

Figure 1. An adult male Common Cactus Finch *Geospiza scandens* with deformity to the beak and nare caused by *Philornis downsi*.

Figure 2. An adult Woodpecker Finch *Cactospiza pallida* with avian pox lesions on dorsal mandible and lower eyelid.

may overshadow, confound and ultimately replace non-anthropogenic factors as the principal driver of evolution. To prevent further degradation of natural selection, global concern for the conservation of Galapagos ecosystems must be translated into effective management of anthropogenic impacts, including introduced diseases. Preventing the arrival of more parasites and pathogens to the islands, and mitigating the impacts of those already introduced, are imperative to ensure that natural selection continue to shape the biota of Galapagos.

ACKNOWLEDGMENTS

We thank the Galapagos National Park and Charles Darwin Foundation for the Galapagos Islands (CDF) for supporting our work. This is contribution 2021 of the CDF.

LITERATURE CITED

Bataille, A., Cunningham, A.A., Cedeño, V., Cruz, M., Eastwood, G., Fonseca, D.M., Causton, C.E., Azuero, R., Loayza, J., Cruz Martinez, J.D. & Goodman, S.J. 2009. Evidence for regular ongoing introductions of mosquito disease vectors into the Galapagos islands. *Proceedings of the Royal Society* B 276: 3769–3775.

Blackburn, T.M., Cassey, P., Duncan, R.P., Evans, K.L. & Gaston, K.J. 2004. Avian extinction and mammalian introductions on oceanic islands. *Science* 305: 1955–1958.

Boag, P.T. & Grant, P.R. 1981. Intense natural selection in a population of Darwin's finches (Geospizinae) in the Galápagos. *Science* 214: 82–85.

Bradshaw, W.E. & Holzafpel, C.M. 2006. Evolutionary response to rapid climate change. *Science* 301: 1477–1478.

Causton, C.E., Peck, S.B., Sinclair, B.J., Roque-Albelo, L., Hodgson, C.J. & Landry, B. 2006. Alien insects: threats and implications for conservation of Galápagos islands. *Annals of the Entomological Society of America* 99: 121–143.

Darimont, C.T., Carlson, S.M., Kinnison, M.T., Paquet, P.C., Reimchen, T.E. & Wilmers, C.C. 2009. Human predators outpace other agents of trait change in the wild. *Proceedings of the U.S. National Academy of Science* 106: 952–954.

Darwin, C. 1859. *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*. John Murray, London.

Deem, S.L., Cruz, M., Jiménez-Uzcátegui, G., Fessl, B., Miller, R.E. & Parker, P.G. 2008. Pathogens and parasites: an increasing threat to the conservation of Galapagos avifauna. Pp. 125–130 *in* Watkins, G., Cruz, F. & Cayot, L. (eds) *Galapagos Report 2007–2008*. Charles Darwin Foundation, Puerto Ayora.

Dudaniec, R.Y., Kleindorfer, S. & Fessl, B. 2006. Effects of the introduced ectoparasite *Philornis downsi* on haemoglobin level and nestling survival in Darwin's Small Ground Finch (*Geospiza fuliginosa*). *Austral Ecology* 31: 88–94.

Fessl, B. & Tebbich, S. 2002. *Philornis downsi* — a recently discovered parasite on the Galapagos archipelago — a threat for Darwin's finches? *Ibis* 144: 445–451.

Fessl, B., Sinclair, B.J. & Kleindorfer, S. 2006. The life-cycle of *Philornis downsi* (Diptera: Muscidae) parasitizing Darwin's finches and its impacts on nestling survival. *Parasitology* 133: 739–747.

Gibbs, J.P., Snell, H.L., & Causton, C.E. 1999. Effective monitoring for adaptive wildlife management: lessons from the Galapagos islands. *Journal of Wildlife Management* 63: 1055–1065.

Grant, P.R. 1999. *Ecology and Evolution of Darwin's Finches*. Princeton University Press, Princeton NJ.

Grant, B.R. & Grant, P.R. 1989. Natural selection in a population of Darwin's finches. *American Naturalist* 133: 377–393.

Grant, P.R. & Grant, B.R. 2008. *How and Why Species Multiply: The Radiation of Darwin Finches*. Princeton University Press, Princeton NJ.

Hendry, A.P., Grant, P.R., Grant, B.R., Ford, H.A., Brewer, M.J., & Podos, J. 2006. Possible human impacts on adaptive radiation: beak size bimodality in Darwin's finches. *Proceedings of the Royal Society* B 273: 1887–1894.

Huber, S.K. 2008. Effects of the introduced parasite *Philornis downsi* on nestling growth and mortality in the medium ground finch (*Geospiza fortis*). *Biological Conservation* 141: 601–609.

Kleindorfer, S. & Dudaniec, R.Y. 2006. Increasing prevalence of avian poxvirus in Darwin's finches and its effect on male pairing success. *Journal of Avian Biology* 37: 69–76.

Loye, J.E. & Carroll, S.P. 1998. Ectoparasite behavior and its effects on avian nest site selection. *Annals of the Entomological Society of America* 91: 159–163.

Palumbi, S. 2001. Humans as the world's greatest evolutionary force. *Science* 293: 1786–1790.

Parker, P.G., Whiteman, N.K. & Miller, R.E. 2006. Conservation medicine on the Galápagos Islands: partnerships among behavioral, population and veterinary scientists. *Auk* 123: 625–638.

Riper, C. van, III, Riper, S.G. van & Hansen, W. 2002. The epizootiology and effect of avian pox on Hawaiian forest birds. *Auk* 119: 929–942.

Riper, C. van & Forrester, D.J. 2007. Avian Pox. Pp. 131–176 *in* Thomas, N.J., Hunter, D.B. & Atkinson, C.T. (eds), *Infectious Diseases of Wild Birds*. Blackwell, Oxford.

Sasaki, K., Fox, S.F. & Duvall, D. 2008. Rapid evolution in the wild: changes in body size, life-history traits, and behaviour in hunted populations of the Japanese Mamushi snake. *Conservation Biology* 23: 93–102.

Schlaepfer, M.A., Runge, M.C. & Sherman, P.W. 2002. Ecological and evolutionary traps. *Trends in Ecology and Evolution* 17: 474–480.

Stenseth, N.C. & Dunlop, E.S. 2009. Unnatural selection. *Nature* 457: 803–804.

Stenseth, N.C. & Rouyer, T. 2008. Destabilized fish stocks. *Nature* 452: 825–826.

Strayer, D.L., Eviner, V.T., Jeschke, J.M. & Pace, M.L. 2006. Understanding the long-term effects of species invasions. *Trends in Ecology and Evolution* 21: 645–651.

Thiel, T., Whiteman, N.K., Tirape, A., Baquero, M.I., Cedeño, V., Walsh, T., Jiménez Uzcátegui, G. & Parker, P.G. 2005. Characterization of canarypox-like viruses infecting endemic birds in the Galapagos islands. *Journal of Wildlife Diseases* 41: 342–353.

Vargas, H. 1987. Frequency and effect of pox-like lesions in Galapagos mockingbirds. *Journal of Field Ornithology* 58:101–102.

Whiteman, N.K., Goodman, S.J., Sinclair, B.J., Walsh, T., Cunningham, A.A., Kramer, L.D. & Parker, P.G. 2005. Establishment of the avian disease vector *Culex quinquefasciatus* Say, 1823 (Diptera: Culicidae) on the Galápagos Islands, Ecuador. *Ibis* 147: 844–847.

Wikelski, M., Fousopoulos, J., Vargas, H. & Snell, H. 2004. Galapagos birds and diseases: invasive pathogens as threats to island species. *Ecology and Society* 9: 5.