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MIGRATION BY GALAPAGOS GIANT TORTOISES REQUIRES LANDSCAPE-SCALE CONSERVATION EFFORTS

STEPHEN BLAKE, CHARLES B. YACKULIC, MARTIN WIKELSKI, WASHINGTON TAPIA, JAMES P. GIBBS, SHARON DEEM, FREDY VILLAMAR AND FREDY CABRERA

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Migration by Galapagos giant tortoises requires landscape-scale conservation efforts

Stephen Blake[1,2,3,4,5,6], Charles B. Yackulic[7], Martin Wikelski[1], Washington Tapia[8], James P. Gibbs[4,5], Sharon Deem[6], Fredy Villamar[5] and Fredy Cabrera[5]

[1]Max Planck Institute for Ornithology, [2]Whitney Harris World Ecology Center, University of Missouri-St. Louis, [3]Department of Biology, Washington University, [4]State University of New York, College of Environmental Science and Forestry, [5]Charles Darwin Foundation, [6]Institute for Conservation Medicine, [7]Grand Canyon Monitoring and Research Center, [8]Galapagos National Park Directorate

Galapagos tortoises (*Chelonoidis spp.*) are among the most iconic animals on Earth, inspiring wonder at the natural world among people everywhere. Ecologically, they play an important role in the ecosystem through seed dispersal, herbivory, trampling, and trail construction (Blake *et al.*, 2013; Gibbs *et al.*, 2008; Gibbs *et al.*, 2010). They are also a major attraction for tourists to the Galapagos Islands, making them a cornerstone of the local economy (Watkins & Oxford, 2009). Effective conservation of these animals is therefore important on many levels for the sustainability of Galapagos.

Galapagos tortoises on Santa Cruz Island undergo long distance seasonal migration (Blake *et al.*, 2013), during which individuals may travel many kilometers between the coast and upland farmland. Around the world, long-distance migrations are disappearing rapidly (Berger, 2004; Wilcove & Wikelski, 2008) because of overhunting and habitat loss due to agriculture expansion, fencing, and other barriers (Harris *et al.*, 2009). The disruption of migration can be catastrophic to migratory species, which often display little behavioral and ecological flexibility with which to cope with changing landscape dynamics (Holdo *et al.*, 2011a; Shuter *et al.*, 2012).

Conserving migratory species in the face of human impacts is often more difficult than for sedentary species due to the scale of their geographic requirements and their evident lack of behavioral flexibility to adapt to change (Milner-Gulland *et al.*, 2011). Disruption of migration can have catastrophic consequences for migratory species and ecosystems (Holdo *et al.*, 2011b; Wilcove & Wikelski, 2008). Most Galapagos tortoise populations are no longer threatened by overhunting (Márquez *et al.*, 2007), but tortoise persistence on the major islands will depend on maintaining connectivity for tortoise migration as intensification of land use in Galapagos moves forward. Here we briefly describe the salient features of the Galapagos tortoise migration on Santa Cruz Island and provide practical management recommendations that can be implemented immediately. We anticipate management and science evolving together closely over the next decade as we continue to gather better information on the geography, ecology. and extent of tortoise migration, and the corresponding impacts of human activity.

Methodology

To understand tortoise migration patterns, we fitted GPS tags (Figure 1) to 25 adult tortoises from two populations on Santa Cruz Island (*Chelonoidis porteri*). The largest population occurs in the Tortoise Reserve (La Reserva) to the southwest, while a second, smaller population, which is likely a different species, is found near Cerro Fatal on the eastern flank of the Island (Figure 2). Twelve tracking tags (made by e-obs GmbH, Munich, Germany) were deployed in Cerro Fatal (seven females and five males) and 13 in La Reserva (six females and seven males). The tags record a tortoise's location every hour. Results presented here are from tortoises with over one year of data.

Tortoises from both populations displayed long-distance seasonal migration up and down the flanks of the island. In La Reserva, tortoises migrated over an elevation range between sea level and 400 m, whereas in Cerro Fatal they ranged between 63-429 m. Nineteen (76%) tagged tortoises completed altitudinal migrations of over 150 m in elevation (Figure 2). The migrations in La Reserva were longer, up to >10 km, and more linear that those at Cerro Fatal. Six individuals (24%) were sedentary, occupying consistent elevations year round, five in the lowlands and one in the highlands.

The pattern of migration is largely driven by forage quality (Figure 3). During the dry or garúa season, the highlands

Figure 1. An adult male Galapagos tortoise from the La Reserva population on Santa Cruz Island, fitted with a GPS tag made by e-obs GmbH, Munich, Germany.

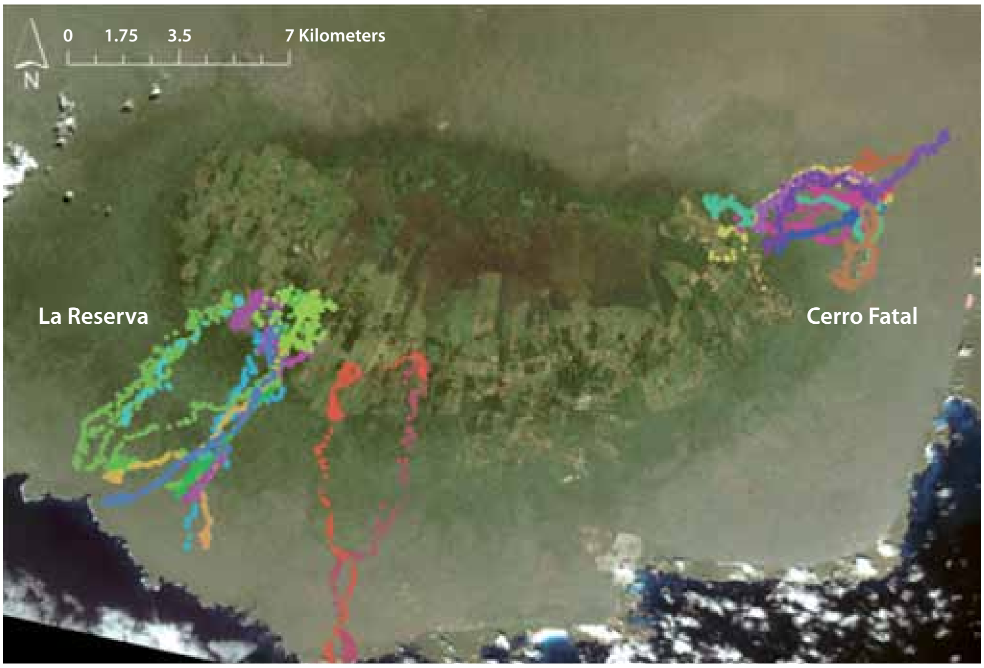

Figure 2. Movement tracks of giant tortoises on Santa Cruz Island.

remain humid due to prolonged periods of fine mist (garúa), while the arid lowlands become progressively drier. Therefore, vegetation productivity is relatively consistent year round in the highlands, compared to the highly variable lowlands. During the garúa season, tortoises occur predominantly in the highlands where they take advantage of abundant vegetation. As rainfall increases in January, the lowlands "green up" [as measured by a NASA satellite in the form of Normalized Difference Vegetation Index (NDVI), a measure of greenness and a proxy for vegetation productivity]. Tortoises then migrate downslope as lowland productivity peaks, and remain in the lowlands until productivity declines to low levels whereupon they migrate back to the highlands. Tortoises are likely drawn to lowland vegetation during the wet season because the rapid new plant growth means that food quantity is higher and more easily digestible than older growth upland vegetation.

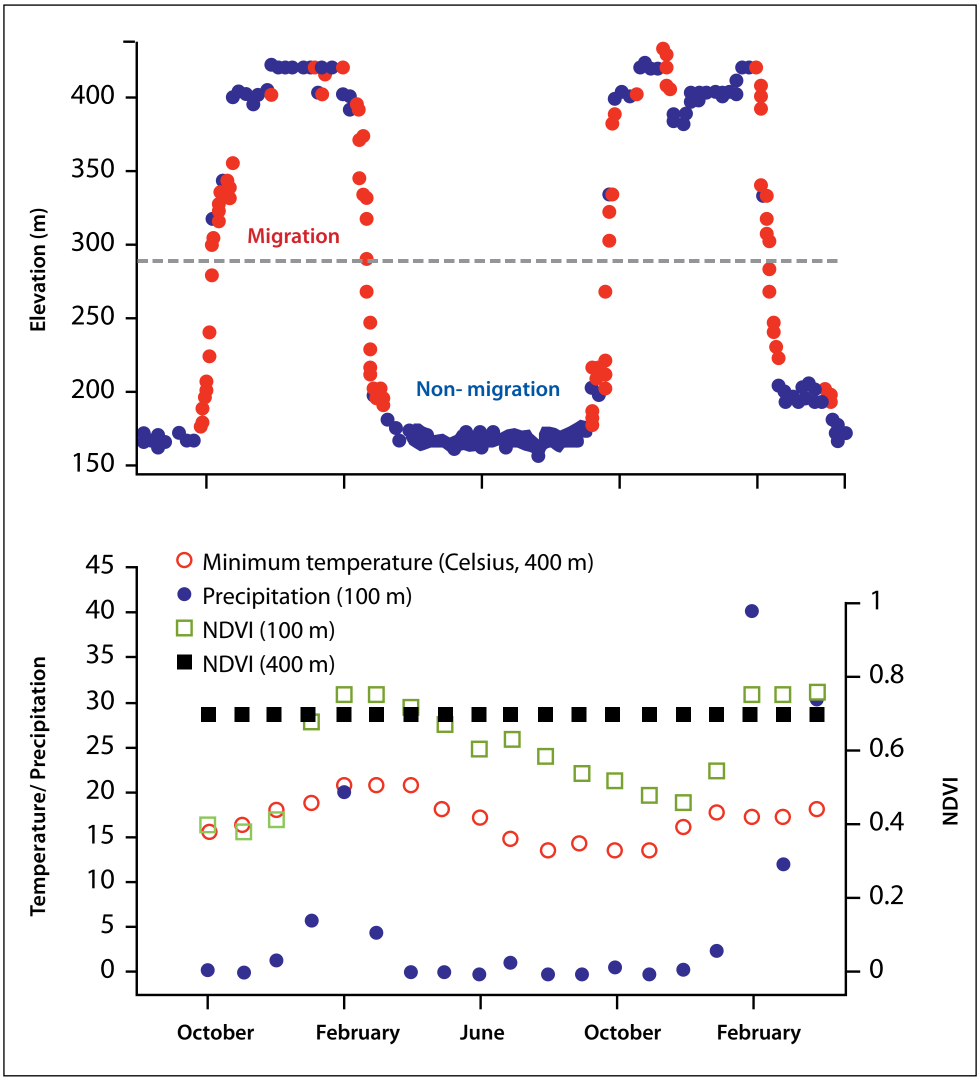

Figure 3. An example of the migration (using the tortoise Helber's tracks) in relation to environmental variables, including elevation, precipitation, temperature, and vegetation productivity (NDVI, the Normalized Difference Vegetation Index, derived from satellite data).

That food quantity and quality alone drive tortoise migration is certainly an over-simplification of what is happening and more work is needed. For example, reproduction is critical to population dynamics, and female tortoises nest only in the arid lowlands, which may help explain the timing of migration and sedentary behavior.

Tortoise migration and landscape management

Tortoise migration links important seasonal habitats for these animals: feeding/nesting grounds in the lowlands and foraging areas in the highlands. Tortoise migration patterns evolved over millennia, long before humans arrived on Galapagos and transformed natural highland habitats into farmland filled with introduced and invasive species, traversed by roads and fences, and dotted with habitations. The natural migration patterns result in many tortoises moving high into the agriculture zone of Santa Cruz. Tagged tortoises in La Reserva spend 33% of their total time in the agriculture zone, where they feed overwhelmingly on leaves and fruits of introduced species (Figure 4). Preliminary data indicate that tortoises do well on this diet based on body condition indices calculated in late 2013, using a formula modified from Flint *et al.* (2009). Condition index was calculated as weight ÷ length^2.89; Flint *et al.* (2009) used an exponent of 3, whereas our exponent of 2.89 is based on the slope of the relationship between log-curved carapace length vs log-mass, calculated from a sample of 100 Santa Cruz tortoises. Red blood cell counts and total protein content of blood were all higher for tortoises in the highlands than in the lowlands. Large areas of the agriculture zone

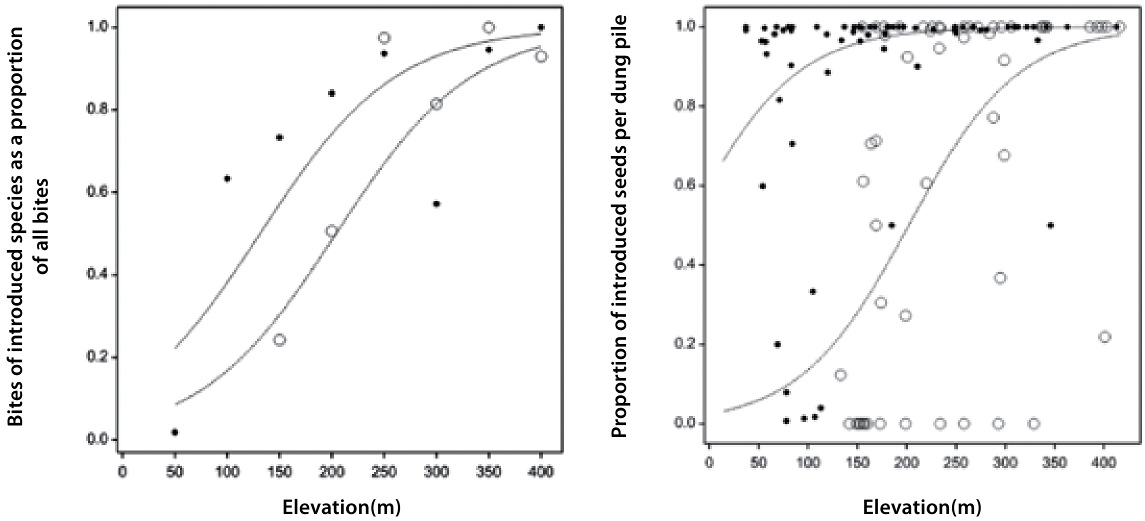

Figure 4. The effect of elevation on giant tortoise diets in terms of (a) the proportion of bites on invasive species and (b) the proportion of seeds of invasive fruit species in tortoise scat (open circles represent data from Cerro Fatal and closed circles from La Reserva).

contain species that were introduced specifically for their high nutritional value for livestock, such as the grass *Paspalum conjugatum*, and for human consumption, such as *Psidium guajava* and *Passiflora edulis*, the fruits of which are attractive to tortoises.

A serious problem facing Santa Cruz tortoises lies in maintaining access to and the quality of their critical seasonal habitats in the face of the increasing expansion of invasive species and infrastructure development. Two particularly aggressive introduced plant species, *Rubus niveus* (blackberry) and *Pennisetum purpureum* (elephant grass), grow in extensive, dense thickets in which they out-compete and eliminate tortoise food species, inhibit tortoise movements, and block migration routes.

In other cases, farmers construct dense fences of tightly spaced trees spanned by barbed wire to keep tortoises off their cattle pastures (Figure 5). Small fenced areas that protect vegetables and fruit may not be detrimental for tortoises, but if large areas of upland habitat are blocked by fences, the tortoises' ability to find food and maintain good body condition in their upland phase will be compromised. In 2011, a tortoise called Sebastian (Figure 5), who had migrated in the previous year, entered a fenced farm. Sebastian remained in the farm for most of the following year and did not migrate. Eventually Sebastian found a way out of the farm in time to migrate as he had previously. While we cannot be sure that Sebastian was unable to find his way out of the farm, there are very few gaps in the fence, and we surmise he was accidentally held captive by fencing.

Similarly, there is little doubt that the main road from Puerto Ayora to Baltra is a formidable barrier to tortoise movement (Figure 6a). By contrast, dirt tracks are used frequently by tortoises, though they often have barriers along much of their length, which prevent tortoises from moving off the road into surrounding vegetation (Figure 6b).

Conclusions and recommendations

Effective management of tortoises requires better knowledge of their seasonal distribution and abundance, the identification of migration corridors, a quantitative

Figure 5. An adult male tortoise called Sebastian, who was apparently trapped inside an upland farm for a year by nearly impregnable fencing and was thus unable to complete his seasonal migration to the lowlands.

Figure 6. Contrasting impacts of roads on tortoises: (a) the main road bisecting Santa Cruz is likely a formidable barrier for tortoises, (b) small tracks can be conduits for movement.

assessment of the geography and severity of current threats, and an analysis of likely future problems and opportunities. An important step forward on Santa Cruz would be a quantitative census and mapping exercise across the range of tortoises to: (a) provide accurate estimates of tortoise abundance, which are currently unavailable; (b) identify the seasonal distribution of tortoises by habitat type including natural versus farmed areas and proximity to infrastructure, and (c) map harmful invasive species and assess their effectiveness as barriers. In addition, tortoise researchers and managers should work with land use planning departments to determine likely development scenarios and their potential impacts on tortoises in order to plan mitigation measures.

Pending the results of such an assessment and more detailed analysis of tortoise movements on Santa Cruz, Alcedo, and Española currently underway, the following actions are recommended:

1. Removal and/or reduction of barriers to migration

Cattle farmers who attempt to protect their farms from tortoises should be encouraged to make their pasture lands available to tortoises, which have relied on such areas for millennia. This can be achieved by maintaining multiple openings within otherwise dense fences through which tortoises can pass, but which are too small to allow the passage of cattle.

No successful methods exist for the eradication of either blackberry or elephant grass, which represent two significant barriers to tortoise movement that are also catastrophic to native species. In lieu of effective eradication, pathways should be made through extensive thickets of these species in known tortoise migration areas.

2. **Mitigation of impacts due to roads.**

   We are unaware of current plans for road development in the Santa Cruz highlands, but as the economy continues to grow infrastructure development becomes more likely. Ideally, further road construction should be avoided due to the myriad negative ecological impacts (Trombulak & Frissell, 2000), not just on tortoise migrations. If road developments occur, planning should include mitigation measures for tortoises focusing on: (a) highland to lowland orientation; (b) ensuring that roadside vegetation is permeable to tortoises; (c) developing and enforcing strict rules on minimal urbanization in areas of tortoise use; (d) controlling traffic, and (e) considering the establishment of tortoise overpasses or underpasses at critical intersections where major roads cross tortoise migration routes.

3. **Maintenance of high quality habitat at both ends of the migration**

   Tortoises may be incompatible with production of low stature vegetable and fruit crops, given that failure to protect these crops in areas with large numbers of tortoises will lead to damage and economic losses. However, these crops tend to require small areas with high degrees of input for which fencing should not represent a major additional cost. Fruit and nut trees are compatible with tortoises as long as understory plants are maintained. Applied research is necessary to explore production options compatible with tortoise conservation, potentially involving a matrix of pasture and native/semi-native open woodland. Other crops such as coffee, the production of which is expanding rapidly on Santa Cruz, may require protection in the establishment phase, so careful consideration of how to protect large areas under cultivation without creating major barriers to tortoise movement is needed.

In summary, the tortoises of Santa Cruz are of enormous ecological, cultural, and socioeconomic benefit to Galapagos. The fact that tortoises migrate render them vulnerable to habitat modification at the landscape scale. Failure to maintain critical habitats and connectivity for migration could result in serious negative consequences for both tortoise populations on Santa Cruz. Careful land use planning, refinement of our recommendations through discussions among farmers, citizens, professionals, and scientists, and implementation in the short term of simple, effective ways to help tortoises continue to do what they have done for millennia, are solid, practical, and compassionate first steps.

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