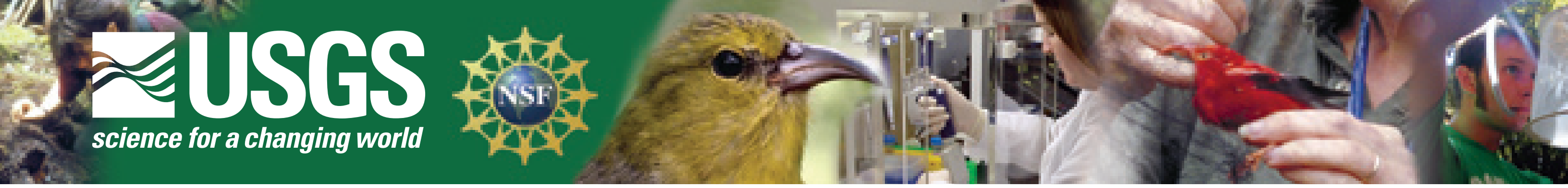

Biocomplexity of Introduced Avian Diseases in Hawai‘i: Threats to Biodiversity of Native Forest Ecosystems

By Bethany L. Woodworth, Carter T. Atkinson, Michael D. Samuel, Dennis A. LaPointe, Paul C. Banko, and Jorge A. Ahumada

Emergent Diseases on the Rise. The past quarter century has seen an unprecedented increase in the number of new and re-emerging diseases throughout the world, with serious implications for humans, domestic animals, and wildlife. The rise in emergent diseases is attributed to many factors, including human alteration of habitats, accelerated transportation of vectors and pathogens, and anthropogenic climate change. Climate change, in particular, can lead to geographic range shifts and large changes in prevalence of vector-borne diseases because temperature can affect vector distribution, as well as parasite development and transmission rates.

Hawaiian Ecosystem in Crisis. Hawaiian forest birds (Figure 1) evolved as an important vertebrate component in native Hawaiian rainforests, performing key ecosystem processes such as pollination, seed dispersal and nutrient cycling. Sadly, since the arrival of humans, over half of the honeycreepers have become extinct and those remaining are in danger of extinction. The loss of these endemic birds may have helped to initiate cascading extinctions among associated plants and invertebrates and the loss of biodiversity in Hawaiian ecosystems. Introduced mosquito-transmitted diseases, avian malaria and avian pox, are thought to be one of the main factors driving loss of native forest birds.

Figure 1. Native Hawaiian honeycreepers, such as the *‘i‘iwi* (*Vestiaria coccinea*), suffer mortality rates of 65 to 90 percent from avian malaria (Photo © Jack Jeffrey, USFWS; used with permission).

Model Ecosystem for Disease Ecology and Evolution. The diversity and topography of Hawai‘i provides an ideal system for investigating the interactions of vector-borne avian malaria, climate, and biotic factors on native bird populations. Because of its isolation, Hawai‘i has a simplified host, vector, and pathogen system (Figure 2), interacting over a gradient of climate and habitat conditions from coastal scrub to wet montane forest above 1,500 meters.

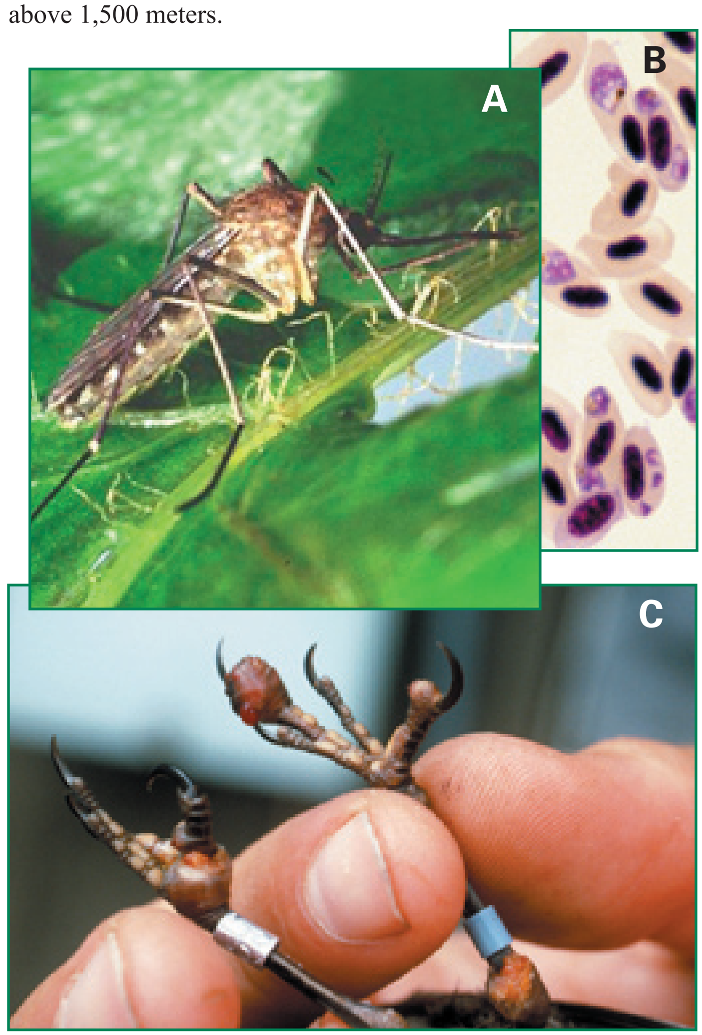

Figure 2. Because both avian malaria and avian pox have been introduced to Hawai‘i within the last 100 years, their continued virulence is typical of emergent diseases. The non-native mosquito *Culex quinquefasciatus* (**A**) is the primary vector of avian malaria and pox. Avian Malaria, *Plasmodium relictum*, can be detected in infected blood smears (**B**) while pox virus forms swollen lesions (**C**) at inoculation sites.

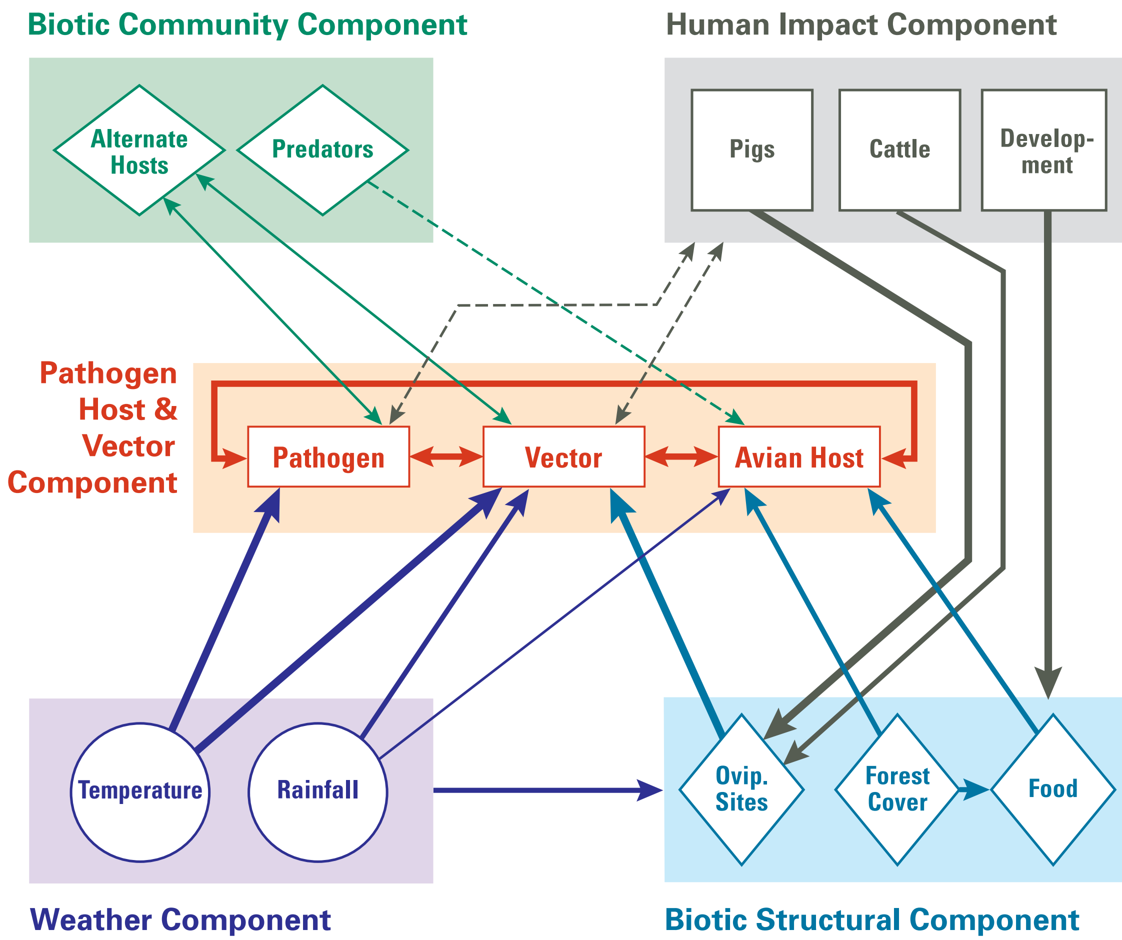

Figure 3. Conceptual model of the malaria-pox Hawai'i disease system. Unidirectional arrows from component "A" to "B" denote "A influences B." Bi-directional arrows refer to reciprocal interactions between components. Solid arrows are hypothesized relationships between components; broken arrows are tentative relationships. The thickness of the arrows represents the importance assigned to the relationship between system components.

Avian Conservation Strategies and Future Threats. Scientific studies integrating field efforts, laboratory experiments, and modeling will provide a better understanding of avian disease in Hawai'i and reveal weak links that can be targeted by management actions to protect native Hawaiian forest birds (Figure 3). The outcomes of vector control, habitat management, translocations, and other strategies can all be investigated and evaluated in the model before valuable resources are invested on the ground. The model can also be used to predict the future stability or instability of Hawaiian forest bird populations as the current disease system evolves or is altered by manmade change. For example,

- What will happen when new diseases or mosquito vectors are introduced into the system, e.g. West Nile Virus or *Aedes japonicus*?
- How do changing land use patterns and habitat fragmentation affect disease transmission across large landscapes?
- How will climate change affect long term patterns of disease transmission?
- What causes epidemics in vector transmitted pathogens? How do these differ from outbreaks in directly transmitted pathogens?
- Does the presence of exotic hosts influence disease transmission rates to native species? What role does avian biodiversity at different altitudes play in buffering or amplifying disease outbreaks?
- Which management strategies hold potential for interrupting the disease transmission cycles and encouraging recovery of Hawaiian forest birds?
- How can we best manage habitats and populations to minimize impact of disease on wildlife, domestic livestock and ultimately human populations?

Interdisciplinary Research at Multiple Scales. Our research covers 1,100 km^2 on the eastern flank of Mauna Loa on the island of Hawai'i, encompassing major portions of Hawai'i Volcanoes National Park, State Natural Area and Forest Reserves, small towns, and rural agricultural areas. Data on bird, mosquito, and disease dynamics are collected at nine 1-km^2 study plots located in *'ohi'a* (*Metrosideros polymorpha*) forests ranging from sea level to 1,800 meters. Evolutionary and epidemiological research begins at the genome level of the pathogens, vectors, and hosts to explore population structure and evolutionary trends in disease virulence and host resistance. Complementary laboratory experiments examine the specific interactions between organisms in controlled environments, while field studies document community composition, disease prevalence, and transmission dynamics across the complex landscape. Modeling and numerical simulation are used to integrate across scientific disciplines and guide research on key system parameters, understand complex interactions, and reveal nonlinear behavior. Modeling provides analytical tools and computer simulations that allow us to evaluate management strategies for disease control and forest bird conservation. These can be used to identify similar threats to biodiversity in other disease systems, and to predict the consequences of introducing new vectors or diseases.

Interdisciplinary Team. Supported by a Biocomplexity grant from the National Science Foundation (DEB-0083944) and USGS funding, a research team consisting of molecular biologists, ornithologists, mathematical modelers, entomologists, parasitologists, ecologists, and a climatologist/geographer from three federal and three academic institutions provides the expertise to investigate this system from the molecular to the landscape level, from the ecological to the epidemiological, and from the evolutionary past into the predicted future. Three postdoctoral positions and two graduate assistantships have been funded by this project, and over 200 internships have been provided to train undergraduate, post-baccalaureate and graduate students of field ecology (Figure 4).

Important Interim Findings and Potential Conservation Strategies

Effects of weather on disease dynamics. Rainfall and temperature vary considerably with season and elevation having direct effects on the physiology and development rates of the mosquito vectors and the malaria parasite; climate thereby drives vector and disease dynamics. At higher elevations, environmental conditions are unsuitable for completion of the mosquito life-cycle and development of the malaria parasite, so transmission is rare. In mid-elevation forests, transmission occurs primarily during the fall and early winter, when temperature and rainfall conditions are suitable for the growth and survivorship of mosquito populations and development of malaria parasites. Annual variation in malaria infection sets the stage for periodic epizootics that can infect nearly 100 percent of susceptible birds. In contrast, temperature and rainfall conditions are consistently favorable at lower elevations and disease transmission occurs at high rates throughout the year, with only minor seasonal fluctuations. Thus disease becomes endemic in low elevation bird communities and coevolutionary processes are intensified.

Evolution of disease resistance in a Hawaiian honeycreeper. The project has identified thriving populations of *Hawai'i 'amakihi* (*Hemignathus virens*; Figure 5) in low-elevation Hawaiian forests, despite extremely high local transmission and prevalence of avian malaria. Molecular and experimental studies suggest these lowland populations are genetically distinct from high elevation populations and have higher resistance to avian malaria. Such examples of evolution and coevolution of vertebrate hosts and pathogens occurring within a few hundred generations are extremely rare and may provide important insight into factors facilitating the evolution of disease resistance. Discovery of healthy native bird populations at low-elevations also indicates the importance of low-elevation forests in the long-term recovery and conservation of Hawaiian forest birds.

Interactions between avian pox and malaria. Interactions between avian pox and malaria make this system particularly relevant to areas of the world where multiple diseases cycle in animal and human populations. Experimental studies with *Hawai'i 'amakihi* indicate the two diseases interact; new pox infections increase mortality in birds with chronic malarial infections and increase the transmissibility of malaria from chronically infected birds to mosquito vectors.

Reservoirs of avian disease. Although malaria was introduced to Hawai'i via non-native species, it is the highly-susceptible native species which act as the primary reservoir for disease. Native species are readily fed upon by mosquitoes, suffer prolonged periods with high levels of parasites circulating in their blood, and surviving birds remain infective to mosquitoes for years. These factors make native birds ideal disease reservoirs, able to initiate disease outbreaks between years or to carry infections into new areas. In contrast, most exotic species have defensive behaviors which reduce mosquito feeding success, and once infected, have only brief periods with circulating parasites.

Roles of exotic species and human habitation in mosquito abundance. A major

Figure 4. The project has provided over 200 internships to undergraduate, post-baccalaureate and graduate students of field ecology, as well as training graduate students, post-masters and post-doctoral professionals in molecular ecology, population ecology, parasitology, and mathematical ecology (Photo second from top © University of Hawai'i-Hilo; used with permission).

Figure 5. Selection on *Hawai'i 'amakihi* in lowland southeast Hawai'i, where disease transmission is intense and year-round, has led to the evolution of disease-resistant subpopulations (Photo © Dennis LaPointe, USGS; used with permission).

finding is the existence of restricted gene flow (movement) of mosquitoes between locations on Mauna Loa, which has important implications for landscape-scale vector dynamics. In forests located on young lava substrates, naturally occurring larval mosquito habitat is limited to the surface pitting or depressions in exposed basalt. In forests on older substrates, tree fern cavities created by feral pigs appear to be the most important habitat available to larval mosquitoes. Removal of feral pigs appears to reduce mosquito numbers, and studies underway should elucidate whether local disease transmission is successfully reduced as a result. We are exploring how human habitations alter vector numbers, transmission dynamics, and bird population dynamics in surrounding areas.

Evaluation of future conservation strategies. A range of conservation strategies will need to be considered to protect or restore native Hawaiian forest bird populations threatened by avian malaria and pox. These include the protection, restoration, and expansion of high elevation forest bird habitat to buffer the effects of global climate change, intensive management and restoration of mid-elevation habitats where epizootics can dramatically impact susceptible forest bird populations, and protection of low elevation native forest habitats as a source of disease-resistant populations and as a crucible for continued evolution of disease resistance in some native species. Specific efforts that focus on forest bird restoration could include translocating disease-resistant honeycreepers to areas of suitable habitat that have lost endemic species because of disease transmission. Vector control strategies could include management to reduce larval mosquito habitat in forests and adjacent agricultural or human housing areas. Computer models developed in this project can help resource managers evaluate alternative management strategies in areas with different rainfall, forest cover and forest bird communities. For example, these models may help guide decisions about fence locations and feral ungulate control, the size and location of management units for vector control, the optimal timing and goals for control actions, and the potential outcomes of management programs that integrate multiple control strategies.

See our website for additional information:
www.uhh.hawaii.edu/~biocomp/

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