

Integration of palaeontological, historical, and geographical data on the extinction of koa-finches

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ABSTRACT

Identifying the root causes of extinction or endangerment requires long chronological records that begin before a population started to decline and extend until its extinction or functional extinction. We present a case study of the koa-finches, genus *Rhodacanthis*, an extinct group of Hawaiian honeycreepers that was specialized to feed on green pods and seeds of the koa tree or other leguminous plants. Six island populations of koa-finches are known; four in the Holocene fossil record and two that survived until the 1890s. We document the palaeoecological context of the fossils and identify constraints on the age span of the specimen record for each population using stratigraphic contexts, associated radiometric determinations, and museum specimen data. We estimate the potential geographical range of koa-finches at the time of human arrival using two methods: assessment of their historical and palaeohabitats, and geographical information system mapping of the pre-human distribution of the koa plant (*Acacia koa*) and its sister species, the koai'a plant (*Acacia koaia*). After integrating the foregoing data with chronological records and distributional maps of the potential forcing agents of extinction, we conclude that at least two extinctions of island populations were due to ecological change in the lowlands in the prehistorical and perhaps the early historical periods. In the same time frame, the koa-finch populations on Hawai'i Island became rare and restricted to upland refugia, making them vulnerable to the upland forest harvesting and degradation that was accelerating in the 1890s. Neither climatic variation nor mosquito-vectoring diseases are likely to have caused the observed extinctions. This study illustrates an approach that can be applied to many other extinct and endangered island species to better understand the causes of high extinction rates in the human era.

Keywords

Drepanidini, extinction risk, Hawaiian finches, Hawaiian honeycreepers, human impacts, geographical range.

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INTRODUCTION

The high extinction risk that modern island species face is often attributed to a synergy of multiple factors associated with human presence. The implication is that extinction would not occur without the interaction of several forcing agents (i.e. habitat loss, disease, predation, competition with invasive species, trophic cascades, genetic bottlenecks, and climate change), which may operate simultaneously or in a time series (Pimm, 1996; LoGiudice, 2006). Yet, the presence of multiple interacting factors does not necessarily imply that they are required to produce population decline and extinction. Experimental approaches to studying the effects of the different forcing agents on extinction outcomes are impractical. Consequently, deep chronological records that specify the timing of a species' decline

and extinction in relation to the timing of potential forcing agents can be particularly valuable for understanding extinction risk.

Such records can be recovered by closely scrutinizing palaeoecological, biogeographical, and historical records for individual island populations of extinct and endangered species. We apply this approach to birds from the Hawaiian Islands, where the Holocene extinction of roughly 65 species of land birds has been attributed somewhat vaguely to ecological change associated with human presence in the islands (James & Olson, 1991; Olson & James, 1991). Our premise is that the deeper history of Holocene extinctions can help us understand risk levels for currently threatened species; essentially the converse of Diamond's (1984) Rosetta Stone analogy.

Taking the extinct genus of koa-finches as an example, we integrate stratigraphic, radiometric, palaeobotanical, taphonomic,

and biogeographical information from fossil sites; museum specimen records and ethnographic evidence of historical distributions; and historical and archaeological evidence on the timing of potential forcing agents of extinction. We use two means of estimating the potential prior range of koa-finches: (1) their observed distribution, with evaluation of their historical and palaeo-habitats, and (2) geographical information system (GIS) mapping of the late Holocene distribution of the plants that provided their primary food resource. We are then able to compare the estimated original range with the regions most strongly affected by prehistorical farming, invasive cattle and diseases, and other forces of ecological change through time.

BACKGROUND

Koa-finches are an extinct genus of the Hawaiian finches or honeycreepers (Fringillidae: Drepanidini: *Rhodacanthis*), with four known species. Two species survived long enough to overlap with 19th century ornithological collectors, who discovered them in 1891 but were unable to collect any further specimens after 1896 (Banko, 1986; Olson, 1999). These birds were striking in appearance, large in body size with thick finch-like bills, with the adult males mantled in vibrant orange (greater koa-finch, *Rhodacanthis palmeri*) or yellow (lesser koa-finch, *R. flaviceps*) plumage. During their brief historical existence, they occurred together in upland mesic koa (*Acacia koa*) forest on the island of Hawai'i. Both species fed primarily the green pods and seeds of the koa, an endemic leguminous plant that is currently distributed on all of the main islands except the two smallest (Ni'ihau and Kaho'olawe), and is often a dominant tree in dry to wet upland forest (Wagner *et al.*, 1990). Koa has a sister species, koai'a (*Acacia koaia*), which has similar pods and occurs in drier regions that are usually lower in elevation.

During the period of intensive ornithological survey of the island of Hawai'i in the 1890s, collectors observed hundreds of the birds and preserved 67 museum specimens of them (Banko, 1986). The birds were confined to upland forest dominated by tall koa trees, and were apparently absent from nearby wetter forests, where koa is less abundant. The birds were most abundant in the upland region between Hualalai and Mauna Kea volcanoes, where they fed in small flocks (mostly of *R. palmeri*) that were concentrated at different elevations in different years. The most recent unverified site records of koa-finches date to 1937 on the island of Hawai'i and 1961 on Maui (Banko, 1986).

The extinctions of koa-finches on Hawai'i Island were only the tail end of a series of extinctions in what had been a broadly distributed Hawaiian genus. Quaternary fossils representing two additional species of *Rhodacanthis* occur on the islands of Maui, O'ahu, and Kaua'i (Olson & James, 1982; James *et al.*, 1987; James, 1987; James & Olson, 1991; Olson, 1999; Burney *et al.*, 2001). All told, a minimum of six island populations of koa-finches became extinct in the Holocene (James & Olson, 2005). Undoubtedly the real number is higher than this, as the fossil and historical records are incomplete.

The historical observations that koa-finches fed mainly on koa pods are supported by the evidence of their distribution, cranial

anatomy, and stomach contents. Koa-finches have a narrow parasphenoidal rostrum and their bills have blade-like tomial and palatal crests. James & Olson (2005) interpret these characters as part of an adaptive complex in the bill and skeletomuscular system that enabled the birds to cut into green leguminous pods using a slicing motion of the mandibles. Stomach contents were mainly large pieces of green koa pods and seeds, with a limited number of smaller seeds, particularly of a common shrub or small tree, *Dodonea viscosa* ('a'ali'i) (Munro, 1944). Caterpillars were also consumed.

METHODS

Locality, stratigraphic provenance, and associated radiocarbon or other chronological data were documented for each koa-finch fossil. Radiocarbon ages were calibrated to calendar years using the program Calib 5.01 and the calibration curve IntCal0 4.14c (Reimer *et al.*, 2004; Stuiver *et al.*, 2005). Radiocarbon ages are reported in conventional radiocarbon years before present (years BP $\pm 1 \sigma$), and as 95% (2σ) confidence ranges after calibration to calendar years (cal years BP).

The fossils were examined for taphonomic signatures of ecological and behavioural traits, such as evidence of predation and the prevalence of immature individuals in the fossil sample. Taphonomic observations contributed to our inferences about the former distribution of koa-finches in different habitats. The habitats that existed at the fossil localities at the time of deposition were inferred, in order of preference, from contemporaneous palaeobotanical records, evaluation of the faunal assemblage, and extrapolation from modern vegetation and climate. The habitats in which koa-finches occurred historically were summarized from published observations and specimen records (Banko, 1986; Olson, 1999).

For comparison with data on the distribution of the finches, we estimated the distribution of forests containing significant presence of koa and koai'a at human contact, using GIS mapping of contemporary and historical data on distributions of forest types. We estimate that koa was an important component in forests with dry and especially with mesic moisture from approximately sea level to 2200 m. Koai'a is more problematic because it occurs in dry low elevation habitats that have been greatly altered, and thus it is now reduced to scattered populations (Wagner *et al.*, 1990). Considering its local abundance in relict patches of lowland forest, we estimate that koai'a was an important component in forests with dry to mesic moisture, on all the islands, from sea level to approximately 1200 m. We also assumed that young lava substrates were not primary koa-finch habitat. We applied these assumptions to the methodology developed by Price *et al.* (in press), which incorporates environmental GIS layers corresponding to elevation, moisture availability, and substrate age. Using ArcInfo (ESRI 2005), we selected those areas with appropriate environmental characteristics, reflecting the approximate extent of plant communities expected to contain significant amounts of koa and koai'a based on the known range of elevation and moisture tolerances of those species.

Chronological data from museum specimen labels, historical records of ornithological expeditions, and dates of arrival in the Hawaiian Islands of humans and associated invasive taxa, were compared with the estimated age distributions of each island population of *Rhodacanthis* to constrain the window of time when extinction occurred and to shed light on its possible causes. Finally, the regions of the islands that experienced the greatest ecological changes in the human era were mapped in relation to the potential prior ranges of koa-finches.

Our taxonomic nomenclature follows Wagner *et al.* (1990, 1999) for plants, Olson & James (1991) and James & Olson (2005) for extinct birds, and Sibley & Monroe (1990) for living birds. Museum and laboratory acronyms are explained in the acknowledgements.

RESULTS

Summary of fossil record

The fossil sample of *Rhodacanthis* identified in James & Olson (2005) consists of eight cranial bones from four sites on Maui, O'ahu, and Kaua'i. Locality and provenance data for each fossil are given in Table 1; fossil localities and the general locations where living birds were collected or observed are mapped in Figs 1 and 2. The taphonomic context and associated fauna and flora for the sites that produced the fossils are briefly reviewed below.

Makauwahi Cave and Sinkhole Complex, Kaua'i

Fossil birds are primarily from lake and wetland sediments in the large central sinkhole of the cave complex, located near sea level along the south-eastern shore of the island (Burney *et al.*, 2001). Over 40 species of native seabirds, water birds, and land birds

occur in the assemblage, about half of them songbirds. *Rhodacanthis forfex* is represented by two individuals. Bones of two native avian predators, a hawk *Buteo cf. solitarius* and an extinct owl *Grallistrix auceps*, are common. Pollen, spores, and plant macrofossils preserved in the bone-rich sediments indicate that nearby plant communities included a diverse mixed lowland forest with xeric to mesic adapted plants, as well as typical strand vegetation.

Barber's Point coral cavity, O'ahu

Bishop Museum Archaeological Site 50-Oa-B6-22. This large sinkhole on the 'Ewa Plain of south-western O'ahu has preserved the richest Holocene assemblage of fossil birds known from the island (Olson & James, 1982), with more than 30 species of native birds, notably including six songbird species with finch-like bills. *Rhodacanthis litotes* is represented by a single maxilla. Avian predators in the assemblage include the extinct O'ahu owl *Grallistrix orion*, a small harrier *Circus dosseus*, and an eagle (*Haliaeetus cf. albicilla*). Pollen spectra from a core of a former lake on the 'Ewa Plain record the presence of a mixed dry native forest with abundant pollen of *Pritchardia* (native palm), *Dodonaea* (native shrub), and *Kanaloa* (native leguminous shrub) in the second millennium BP, and a shift towards more open habitat during the first millennium BP (Athens *et al.*, 2002). Pollen of koa is present, though not abundant, until roughly 500 years ago (estimated by interpolation).

Ulupau Head lacustrine deposits, O'ahu

A rich Middle Pleistocene assemblage of fossil birds from ancient lake sediments in the crater of a tuff cone, on the Mokapu Peninsula of south-eastern O'ahu, includes more than 26 species

Table 1 Provenances of koa-finch fossils.

Species	Island	Specimen	Fossil site (elevation above modern sea level)	Excavation data	Site description
<i>R. forfex</i>	Maui	USNM 445792	Pu'u Naio Cave (393 m)	Grid W-13, unit IV, subunit C/D, 70–80 cm below surface of sediment	James <i>et al.</i> (1987), James & Burney (1997)
	Kaua'i	USNM 524870	Makauwahi Cave and Sinkhole Complex (4 m)	East pit, near grid LL 49, unit IV, approximately 340 cm below ground surface	Burney <i>et al.</i> (2001)
		USNM 524871	Ditto	East pit, grids JJ 46 and KK 46, unit V, approximately 310 cm below ground surface	Ditto
<i>R. litotes</i>	Maui	USNM 445793	Pu'u Naio Cave	Grid W-13, unit IV, subunit C/D, 70–80 and 80–90 cm below surface of sediment (two pieces of same bone)	James <i>et al.</i> (1987), James & Burney (1997)
		USNM 445794	Ditto	Missing label	Ditto
		USNM 445796	Ditto	14.0–15.0 m from the entrance to the upper branch, near the west wall of the cave, unit IV, subunit C/D (three pieces of same bone)	Ditto
	O'ahu	USNM 445795	Ulupau Head (3 m)	Unit IV	James (1987), Hearty <i>et al.</i> (2005)
		BPBM 158861	Coral cave near Barber's Point, Bishop Museum site 50-Oa-B6-22 (15 m)	Grid P3, layer 1	Olson & James (1982)

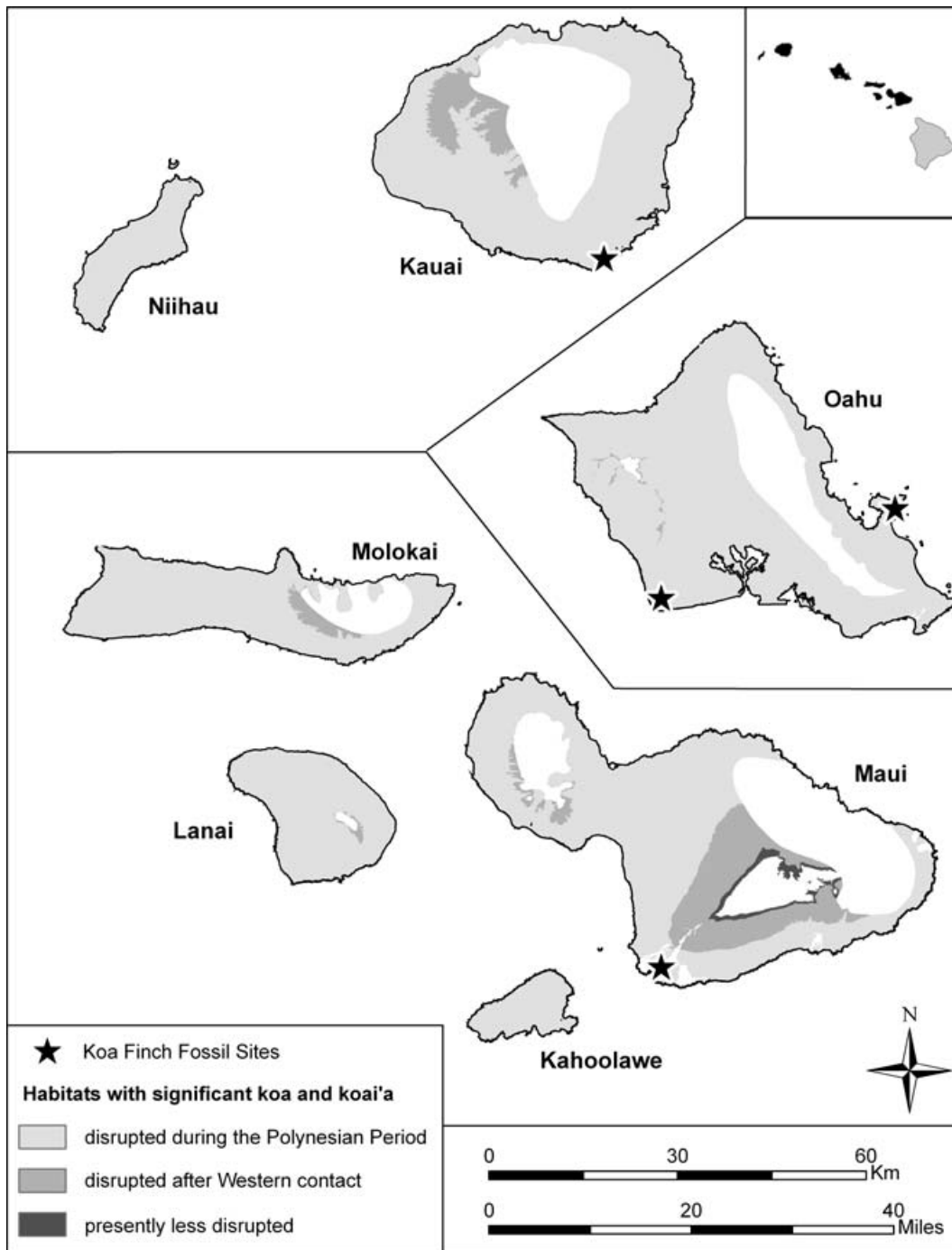


Figure 1 Fossil localities and the estimated potential habitat for koa-finches, Niʻihau through Maui. Potential habitat is based on (1) the modelled distribution of plant communities expected to have significant amounts of koa and koai'a, and (2) areas expected to be less disturbed by human activity and introduced species. This distribution is estimated for three time periods (1) before human arrival c. 1300 years ago, (2) during the prehistorical Polynesian era, and (3) at present.

of water birds, land birds, shore birds, and seabirds (James, 1987). Among 10 species of songbirds, *R. litotes* is represented by a single maxilla. A hawk possibly allied with *B. solitarius* is abundant in the assemblage, and *Grallistrix orion* is common. A palaeoecological reconstruction based on habitat preferences of the birds in the assemblage suggests that, at the time of fossil deposition, the lake was surrounded by mixed lowland forest and

scrubland with perhaps some areas of more open habitat such as herb land and grassland (Hearty *et al.*, 2005).

Pu'u Naio Cave, Maui

This lava cave is the only fossil locality for koa-finches that is significantly above current sea level (James *et al.*, 1987). The

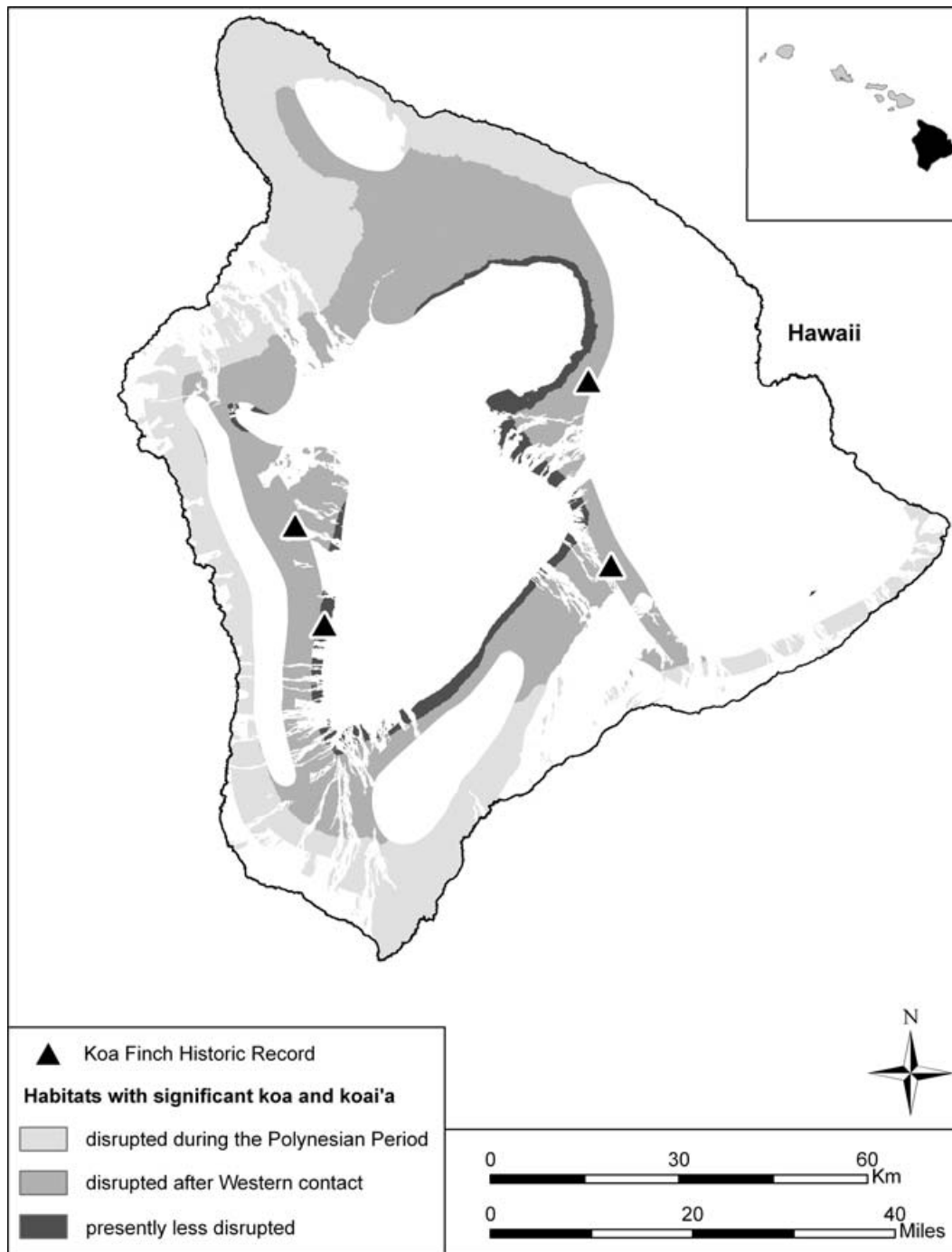


Figure 2 The historical distribution of koa-finches (Banko, 1986), and their estimated potential habitat on Hawai'i Island. Potential habitat is based on (1) the modelled distribution of plant communities expected to have significant amounts of koa and koai'a, and (2) areas expected to be less disturbed by human activity and introduced species. This distribution is estimated for three time periods (1) before human arrival c. 1300 years ago, (2) during the prehistoric Polynesian era, and (3) at present.

assemblage includes 29 species of native birds, of which 20 are songbirds and six have finch-like bills. The four fossils identified as *Rhodacanthis* represent a minimum of two individuals of *R. litotes* and one individual of *R. forfex*. The only native avian predator found in the stratigraphic units that produced *Rhodacanthis* is the extinct endemic owl, *Grallistrix erdmani*. Most of the songbird remains in the deposit were apparently first

deposited in owl pellet accumulations near the cave entrance, and then washed into the passage during floods.

The site falls in the modern dry forest and shrubland zone, thought to have been particularly rich in native tree and shrub species before human-era disturbance. Koa'i'a is one of the characteristic native trees of the region (Medeiros *et al.*, 1986), and we project that the lower limit of the koa belt at first human

contact reached nearly this elevation. The inferred age of the koa-finch fossils in Pu'u Naio Cave suggests that they were deposited during the middle Holocene wet period reported by Burney *et al.* (1995). Koa may have been relatively abundant near the site at that time.

Radiometric data

Radiocarbon dating has not been performed directly on koa-finch fossils, but has been determined on other materials from the deposits. We report four new radiocarbon dates (those with laboratory numbers) and cite previously published dates that bracket the strata containing *Rhodacanthis* bones.

Rhodacanthis forfex, Kaua'i

A series of dates was determined on seeds, sediments, and bones of other species from the same stratigraphic units in Makauwahi Cave that produced the *Rhodacanthis* bones (Burney *et al.*, 2001: Table 1). Eight determinations from unit IV of the east pit range from 5120 ± 50 to 4310 ± 60 years BP. Four determinations from unit V of the east pit range from 3670 ± 60 to 822 ± 60 years BP. Calibrated to calendar years, the entire series of dates ranges from 5987 to 667 cal years BP based on 95% confidence ranges of the individual dates.

Rhodacanthis forfex and *R. litotes*, Maui

The koa-finch fossils are bracketed stratigraphically by two radiocarbon ages from the Pu'u Naio Cave deposit (James & Burney, 1997). From the bottom of unit III (subunit I, grid W14.75–15.00), a bone of an extinct flightless anatid (*Thambetochen chauliodous*) dated to 3858 ± 30 years BP (4157–4410 cal years BP, NZA 25637). From the bottom of unit IV in grid W-13, 98 cm below the sediment surface, a bone of an extinct flightless ibis (*Apteribis* sp.) dated to 8220 ± 140 years BP (8773–9515 cal years BP, AA-3090). Field notes for the specimen without provenance data indicate that it, too, originated in the stratigraphic layers that are bracketed by these dates.

Rhodacanthis litotes, O'ahu

The fossil from Ulupau Head is Pleistocene in age (James, 1987). It is bracketed by K/Ar age determinations on underlying lava from a neighbouring vent (450 ± 70 and 420 ± 45 kyr), and U-series ages on calcareous algae ($240 \pm 10/15$ kyr) and corals (131.2 ± 0.4 – 115.4 ± 1.2 kyr) from overlying strata in the local section (Hearty *et al.*, 2005).

The fossil from the 'Ewa Plain is almost certainly Holocene in age. Four radiocarbon dates on bones from the site range from 3140 ± 60 years BP (3178–3310 cal years BP, AA-2975/87) for a moa-nalo bone (*Thambetochen xanion*), to modern (150 ± 50 years BP, AA-2974/87) for a bone of the Hawaiian short-eared owl (*Asio flammeus*). Twenty-three dates on extinct land bird bones from other, similar sites on the 'Ewa Plain range from 8840 to 1058 cal years BP (Athens *et al.*, 2002).

Taphonomic observations

Relative abundance

The sample consists of eight fossils representing a minimum of seven individuals, with one to three individuals per site. The sites where they occur have been among the most productive in the islands for fossils of songbirds. An inventory of passerine bones has been completed for two of the sites, and in both cases the most common passerine is a native thrush, genus *Myadestes*. The Makauwahi Cave collection (units IV and V) contains 32 identified specimens of *M. palmeri* compared with two of *R. forfex*, while the Pu'u Naio Cave collection (unit IV) contains 56 identified specimens of *M. cf. lanaiensis* compared with one of *R. forfex* and three of *R. litotes*. *Rhodacanthis* is thus an uncommon fossil everywhere it occurs, and it only occurs in sites that tend to concentrate the remains of small forest birds.

Age at death of fossil individuals

The four fossils from Pu'u Naio Cave are from juvenile birds as evidenced by pitted or striated bone surfaces. These bones represent three of the minimum of seven individuals in the fossil record. The juvenile individuals have attained or nearly attained adult size and shape (James & Olson, 2005), indicating that they may have already fledged at the time of death rather than being young nestlings or embryos.

Predation

The condition of preservation of the skull from Makauwahi Cave provides evidence that at least one of the adult individuals was deposited in the fossil site by an avian predator. The skull has had the back of the braincase neatly removed to gain access to the brain (Fig. 3). The damaged skull and the missing piece of the braincase were found in the same area of the excavation, indicating that the bird was eaten or regurgitated at the site and dropped into the shallow lake, where it was preserved. Two predators

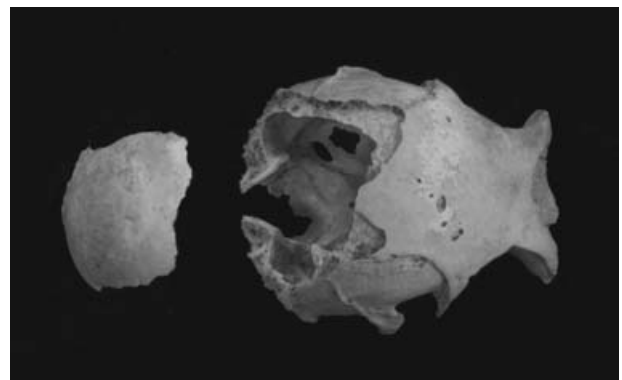


Figure 3 Evidence of predation on a fossil koa-finch from Makauwahi Cave, Kaua'i (USNM 524870). The predator has removed the back of the braincase to gain access to the brain.

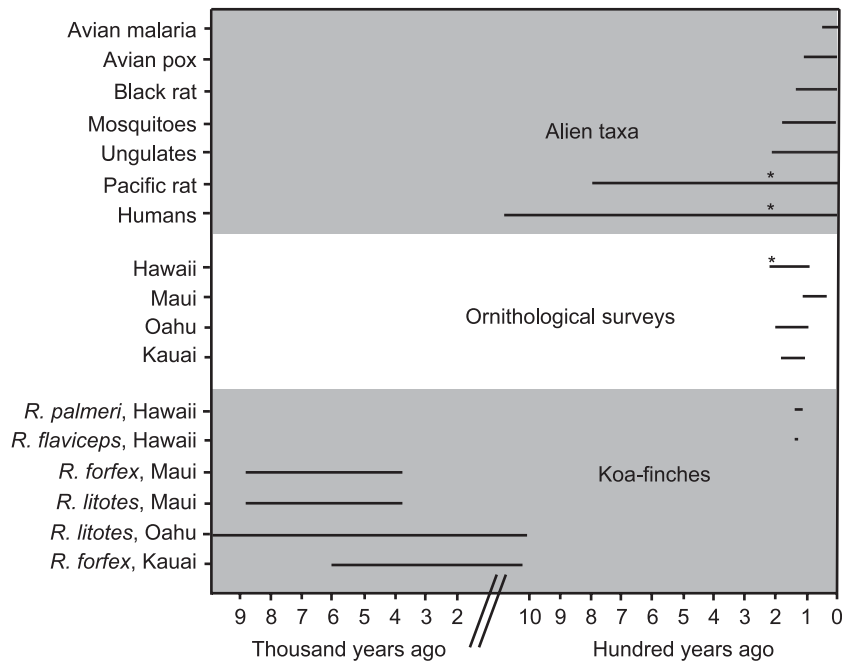


Figure 4 Temporal constraints on koa-finch extinction. The mid-Pleistocene range of *Rhodacanthus litotes* on O’ahu is not shown. We assumed the fossil from south-west O’ahu to be no younger than the most recent date on an extinct, terrestrial vertebrate from the ‘Ewa Plain (about one millennium old). *Date of Captain Cook’s visit to Hawai’i.

that might have performed the act are the extinct endemic owl *Grallistrix auceps* and hawk *Buteo* sp., both of which are common in the fossil deposit (Burney *et al.*, 2001). The *Buteo* of Kauai’i is osteologically indistinguishable from the Hawaiian hawk (*Buteo solitarius*) of Hawai’i Island, a species that has been observed to take off the back of the braincase of birds to eat the brain (Olson & James, 1997; Clarkson & Laniawe, 2000). Whether the extinct owls of the genus *Grallistrix* did the same is unknown.

Spatial distributions

All fossil localities for koa-finches are lower in elevation than the historical range of koa-finches (Figs 1 and 2). The historical records fall between about 1000–2000 m a.s.l., vs. 0–390 m for the fossils. Average solar radiation and temperature are higher at the fossil localities and thus average daily energy requirements for the finches would have been lower there (Porter *et al.*, 2006). Of course, local climatic conditions may have been somewhat different when the fossils were deposited. We consequently relied mainly on the contemporaneous palaeobotanical data and historical observations to assess prior habitat use by koa-finches (see Discussion).

Figures 1 and 2 show the estimated distribution of primary koa-finch habitat at the time of human arrival, based on our assumptions about their food plants. We also estimated the portion of that distribution that remained after the prehistorical Polynesian period, based on a published estimate that the vegetation of all regions of the main islands below 750 m a.s.l. (2500 ft), and receiving more than 500 mm precipitation per year, was altered prehistorically by humans (Kirch, 1982). We then estimated the amount of habitat suitable for koa-finches that remains at present. This estimate was based on the assumption that invasive species and forest clearance has degraded all remaining habitat

below 2000 m in elevation. This assumption may be too optimistic because the high elevation koa forests on Hawai’i Island proved not to provide effective refuge for the two species that became extinct in the 1890s. One possible explanation is that koa-finches eat a low-energy diet that does not meet their energetic requirements for life above 2000 m, where freezing temperatures are frequent. Another is that the finches at those elevations could not thrive unless they could move down slope at times.

The distribution of mosquitoes is an important variable because the invasive southern house mosquito, *Culex quinquefasciatus*, is thought to be the principal vector of blood-borne diseases in Hawaiian forest birds. The elevation above which *Culex* mosquitoes become rare has been moving upslope, but was reported to be 600 ± 150 m in the 1960s (Warner, 1968). The 750-m line in Figs 1 and 2 thus roughly delimits the probable upper limit of mosquitoes in the 19th century. Mosquitoes were absent from the islands before the 19th century.

Chronology of extinction

Radiometric and other historical data that constrain the window of time when each island population became extinct are graphed in Fig. 4. The potential age range of the fossil sample for each population is indicated by the maximum and minimum radiocarbon ages (calibrated 2 σ ranges) that bracket the fossils stratigraphically. For the two species of koa-finches that survived into historical times on Hawai’i Island, the range of collecting dates of museum specimens is graphed (*R. palmeri*, AD September 1891 to March 1896; *R. flaviceps*, AD 30 September to 16 October 1891; see Olson, 1999).

Radiocarbon ages help constrain the earliest date when koa-finches could have become extinct on each island, while

historical avifaunal surveys help establish the latest date. The time span for ornithological survey of each island extends from the date the first museum specimen was collected to the date the last living native species was found on the island (Olson & James, 1991; Olson & James, 1994). Those spans are, for Kaua'i, AD 1836–1897; for O'ahu, AD 1786–1902; for Maui, AD 1879–1973; and for Hawai'i, AD 1779–1904.

The first human (Polynesian) settlements in the Hawaiian Islands may have been established as recently as 1000–1200 years ago (Athens, 1997; Tuggle & Spriggs, 2000; Burney & Burney, 2003). The lower koa belt became the most intensively farmed and settled habitat type in the islands prehistorically (Cuddihy & Stone, 1990; Kirch, 1994). Pacific rats (*Rattus exulans*) were transported to the islands prehistorically in Polynesian sailing canoes, and became the first rodents to invade the Hawaiian ecosystem. The rats are thought to be capable of driving small ground-nesting birds to extinction via nest predation and causing forest collapse via predation on seeds and seedlings (Holdaway, 1999; Athens *et al.*, 2002). Athens *et al.* argue that the initial transformation of native lowland vegetation in the islands was primarily due to Pacific rats rather than to habitat conversion by humans. Radiocarbon dates on Pacific rat bones tend to confirm the late arrival of humans in the archipelago, the oldest date being 1058–790 cal years BP (Athens *et al.*, 2002).

The voyage of Captain James Cook made first European contact with the islanders in AD 1778 and 1779. Cattle, goats, sheep, and European domesticated pigs were quickly introduced to the islands and allowed to become feral. These animals, particularly cattle, caused much damage to the koa forests and other native habitats. Between 1815 and 1826, sandalwood was extensively harvested in low to mid-elevation mesic forests. Ecological impacts due to ranching and logging in upland koa forests intensified from about 1850 onwards (Cuddihy & Stone, 1990). Vast areas of upland koa forest on Hawai'i and Maui were converted to pasture in this era. Habitat conversion for plantation agriculture began at about the same time in the lowlands of all the main islands except the two smallest.

Epizootics of avian pox (*Poxvirus avium*) and avian malaria (*Plasmodium relictum*) caused mortality of Hawaiian forest birds beginning sometime after mosquitoes were introduced to Maui in 1826 (Warner, 1968). It has been assumed that the pox epizootic began shortly after mosquitoes arrived (Van Riper *et al.*, 2002), although the first occurrence of pox-like lesions on museum specimens of endemic Hawaiian birds, as far as we have ascertained, is on a specimen of 'O'u (*Psittirostra psittacea*) collected by Scott Wilson on the island of Hawai'i in AD 1888 (BM 1925.2.16.82 at the Natural History Museum, Tring). A study currently underway of *Plasmodium* DNA in museum specimens of Hawaiian birds has not confirmed avian malaria in native forest species before about 1940 (R.C. Fleischer, pers. comm.).

The invasion of black rats (*Rattus rattus*) probably took place between 1870 and 1890 (Atkinson, 1977). Black rats are nest predators of forest birds and also girdle the trunks of young koa trees, potentially inhibiting regeneration (Scowcroft & Sakai, 1984).

By the 1960s, regions of koa woodlands were fragmented and limited to high elevations, although mixed 'ohi'a (*Metrosideros polymorpha*) and koa forest was still the most widespread and important habitat type for native forest birds in the islands (Whitesell, 1964; Freed, 1999).

DISCUSSION

Fossil koa-finches have been found only where other fossil passerines are abundant, which suggests that predator accumulations were their main mode of deposition. Consistent with this inference are the high proportion of first-year birds in the fossil sample, the compelling evidence of predation on the fossil skull from Kaua'i, and the presence of extirpated avian predators in the fossil assemblage of each of the sites. Koa-finch fossil sites are distributed on the fringes of, and in one case outside, the reconstructed range of koa and koai'a forest. However, rich predator accumulations have not been found within that range, so that the fossil evidence does not contradict the historical and anatomical evidence that these birds had their densest populations where *Acacia* pods were abundant.

Palaeoecological records show that the former distribution of the genus included dry, seasonal lowlands where koa was uncommon historically. Reconstructions of the contemporaneous vegetation from pollen records at two of the sites that are near sea level indicate mixed dry forest and scrub at Makauwahi Cave, and an extirpated dry forest community, with pollen spectra dominated by *Pritchardia* palms and the shrubby legume kanaloa, on the 'Ewa Plain. Koa was uncommon in the 'Ewa Plain pollen record and absent in the Makauwahi Cave record (although absence from the pollen record does not necessarily mean the tree was absent from the local community). Considering that home ranges of the Hawaiian hawk have a maximum observed diameter of about 2.6 km (Clarkson & Laniawe, 2000), it is reasonable to assume that koa-finches could have been captured up to a few kilometres from their fossil sites. We estimate that koa/koai'a habitat extended close enough to the Kaua'i site, but was distant from the 'Ewa Plains site on south-west O'ahu. These lowland fossil records confirm that the genus *Rhodacanthis* had a broader range of habitat than is indicated by the historical observations on Hawai'i Island. Likely alternative foods for koa-finches in the drier lowlands include kanaloa pods (*Kanaloa* sp.), 'a'ali'i berries (*Dodonaea viscosa*), and caterpillars. The last two were recorded as a minor component of the diet of *R. palmeri* historically (Olson, 1999).

Taking into consideration the fossil and historical evidence, and the projected pre-human distribution of food plants, we conclude that koa-finches were widely distributed on each island at human contact. Populations were probably concentrated in the mesic and dry moisture zones, where we expect that, before human disturbance, plant communities contained significant amounts of koa and koai'a.

Pollen records from mid- to high elevation bogs show temporal shifts in the local abundance of koa during the late Pleistocene and Holocene (Selling, 1948; Burney *et al.*, 1995; Hotchkiss & Juvik, 1999), raising the possibility that climate change caused

the extinctions. The fossil evidence, however, argues against this explanation. The population of *R. litotes* on O'ahu apparently survived at least two full glacial cycles before becoming extinct in the mid- to late Holocene (James & Olson, 2005). If koa-finch populations could survive the Pleistocene they are unlikely to have succumbed to relatively minor Holocene climate changes. The palaeontological evidence thus points to human-induced ecological changes as the cause of the extinctions.

Historical and ethnographic records offer little reason to think that koa-finches were widespread during in the early historical period, particularly in lowland areas frequented by humans. The lowland koa belt was densely populated by humans and extensively converted to agricultural lands in prehistorical times (Cuddihy & Stone, 1990; Kirch, 1994). Yet these brilliantly plumaged birds were unfamiliar to the most knowledgeable native informants when they were discovered in the 1890s (Perkins, 1903), and were never reported to exist on the other islands historically. In addition, *Rhodacanthis* feathers have not been identified in the many surviving examples of Hawaiian feather art from this time period (Conant, 2005). The feather objects include 30 obtained by the Cook Expedition in 1778 and 1779, mostly from Kealakekua Bay, which lies down slope of the primary historical range of koa-finches. It is also relevant that 80% of the endemic species of Hawaiian birds had already been described scientifically by the time Rothschild (1892) introduced the genus *Rhodacanthis* (Olson & James, 1991: Table 1). Taken together, these lines of evidence suggest that koa-finches existed mainly at higher elevations, and at population levels too low for easy human detection in the 19th century.

The integration of the evidence discussed above suggests the following explanation of koa-finch extinction. Lowland koa and koai'a habitats, although outside the historical range of the genus, were important if not essential to the maintenance of healthy populations of the finches. The finches were largely extirpated from this part of their range before or shortly after the time of western contact, causing koa-finch extinction on all islands that lacked extensive upland refugia (all islands except Maui and Hawai'i). On Maui and Hawai'i, the birds became largely restricted to less productive upland habitat, resulting in population decline until the finches were hard to find in the 19th century. On Hawai'i Island, the birds persisted at least through the latter half of the 19th century, when their upland refugium was degraded by logging, ranching, and intensified predation (i.e. by the black rat). The two populations on Maui may well have survived in an upland refugium at least this long, although the only verified records of them are from fossils at a lower elevation.

Our reconstruction of prior koa-finch ranges is consistent with a pattern in endangered mammals, in which a species' range collapses as it is extirpated from areas of greatest human disturbance, including the centre of the range where population densities may have been highest (Lomolino & Channell, 1995). The loss of lowland range could have taken place in the early historical period between about 1790 and 1850, although it is more likely to have been prehistorical considering the absence of any historical or ethnographic trace of the six known populations in the lowlands. Mosquito-vectored diseases apparently were not

important factors in the ultimate extinction of koa-finches because the mosquitoes and diseases were restricted to lower elevations, and arrived after koa-finches were restricted to the uplands. The expansion of ranching, logging, and invasive predators into montane regions no doubt hastened the extinction of koa-finches on the island of Hawai'i; however, those populations may already have been in terminal decline due to prior loss of lowland range.

Predation on plants and birds by the Pacific rat has become a popular explanation for prehistorical transformation of plant communities and forest bird extinction in the Pacific. However, koa forest was still extensive in the islands in the early historical period, at least five centuries after the rats arrived. Either the rats were rare or absent from higher elevation koa forest (Tomich, 1986), or their effects on koa forest were not devastating. Direct predation on koa-finches by Pacific rats could explain the early loss of their lowland range, although the only recorded observation of nest-building behaviour in koa-finches was of a male of *R. palmeri* that appeared to be constructing a nest high in the canopy (Perkins, 1903). Canopy nesters are thought to have been relatively protected from Pacific rat predation even though the rat does climb (McCartney, 1970; Atkinson, 1977; Holdaway, 1999). Clearly, there is a need for further study of the prehistorical distribution and ecological role of the rat, particularly in relation to the vulnerabilities of different plant communities and avian species to rat predation.

Koa-finches comprise a small fraction of the avian species lost during the human era in the Hawaiian and other island groups. By reconstructing the ecological history of these species' decline, we may gain insight into the causes of high extinction risk in island species and the actions needed to ensure long-term recovery for endangered island biota. In the case of koa-finches, the integrated record tends to place the extinctions or functional extinctions earlier than the time when some of the most potent modern forcing agents of extinction came into play. If we are correct about the importance of lowland range, other Hawaiian species that are currently restricted to uplands may be in decline for the same reason. Establishing reserves and restoring habitats within the modern ranges of such species may be insufficient action for their long-term conservation.

ACKNOWLEDGEMENTS

We thank Storrs Olson for long-term collaboration on Hawaiian fossil birds, and the curators who lent specimens from the Bernice P. Bishop Museum (BPBM), American Museum of Natural History (AMNH), and University Museum of Zoology, Cambridge (UMCZ). Radiocarbon ages were determined at the University of Arizona/NSF Accelerator Facility (AA) and the Rafter Radiocarbon Laboratory (NZA). Photography is by John Steiner of Smithsonian Photographic Services. We thank Donald Drake and Arthur Medeiros for helpful discussion, and Sheila Conant, Storrs Olson, and David Steadman for comments on a previous draft. This research was supported by a Department of Defense Legacy grant and the Radiocarbon and Wetmore Funds of the Smithsonian Institution.

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