



Technical Report HCSU-046A

PALILA RESTORATION RESEARCH, 1996–2012
SUMMARY AND MANAGEMENT
IMPLICATIONS

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September 2014



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Citation: Banko, P. C., and C. Farmer, editors. 2014. Palila restoration research, 1996–2012: summary and management implications. Hawai'i Cooperative Studies Unit Technical Report HCSU-046A. University of Hawai'i at Hilo. 70 pages.

This product was prepared under Cooperative Agreements CA03WRAG0036-3036WS0012, CA03WRAG0036-3036WS0032, and CAG09AC00041 for the Pacific Island Ecosystems Research Center of the U.S. Geological Survey.

This article has been peer reviewed and approved for publication consistent with USGS Fundamental Science Practices (<http://pubs.usgs.gov/circ/1367/>). Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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PALILA RESTORATION RESEARCH, 1996–2012

INTRODUCTION

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The Palila Restoration Project was initiated in 1996 by the U.S. Geological Survey to assist government agencies mitigate the effects of realigning Saddle Road (Highway 200) through Palila Critical Habitat (U.S. Fish and Wildlife Service 1998, Federal Highway Administration 1999). Ecological research on the palila (*Loxioides bailleui*), an endangered Hawaiian forest bird, carried out by the U.S. Geological Survey (formerly organized as the Research Division of U.S. Fish and Wildlife Service) since 1987 and research conducted by the Palila Restoration Project provided the scientific bases for developing a recovery strategy (U.S. Fish and Wildlife Service 2006) and its adaptive implementation.

The main objectives of the Palila Restoration Project were to develop techniques for reintroducing the palila to a portion of its former range, investigate the biological threats to the palila and its habitat, and synthesize the existing body of ecological knowledge concerning the palila. Five broad study themes formed the research framework:

1. Population reintroduction and restoration
2. Demography and breeding ecology
3. Habitat use and food ecology
4. Vegetation ecology
5. Predator ecology and management

An element that was not included in the research program of the project was the ecology and management of introduced ungulates, which has historically constituted the single greatest threat to Palila Critical Habitat (Banko *et al.* 2009). The absence of ungulate studies should not be interpreted to mean that we believe ungulates no longer damage palila habitat. Other research has already established that removing alien browsers and grazers from Mauna Kea is essential for the recovery of the subalpine forest on which palila now depend (Scowcroft and Giffin 1983; Scowcroft and Sakai 1983; Scowcroft and Conrad 1988, 1992; Hess *et al.* 1999). Moreover, the Federal District Court of Hawai'i has ordered the State of Hawai'i to remove browsing ungulates from Palila Critical Habitat (Banko *et al.* 2009, Hess and Banko 2011).

This final report summarizes results of Palila Restoration Project research from December 1996 to December 2012. Even though some results contained in this report have been published in scientific journals and other technical reports (Appendix I), they are included here to provide a comprehensive chronicle of all project activities.

Synopsis of Palila Biology and Conservation

Palila occurred prehistorically at low elevation on O'ahu and Kaua'i (Olson and James 1982, Burney *et al.* 2001), but historically they were found only on Hawai'i Island where they were restricted to the slopes of Mauna Kea and portions of Hualālai and Mauna Loa (Banko *et al.* 2002a). Due mainly to habitat loss from ungulate browsing, palila have declined in abundance

and distribution and are now only found in about 5% of their historical range on the upper slopes of Mauna Kea (Scott *et al.* 1986, Banko *et al.* 2013). Here, the relatively dry, subalpine forest of māmane (*Sophora chrysophylla*) and naio (*Myoporum sandwicense*) supports a small and annually fluctuating population, which at its peak during 1998–2012 was estimated to be 6,463 individuals in 2003 (Camp and Banko 2012).

The population has increasingly become restricted to the western slope of Mauna Kea (Jacobi *et al.* 1996, Camp and Banko 2012). Like most other endangered Hawaiian forest birds, palila are found today only in the upper limit of their former range where habitat conditions may always have been marginal. Annual fluctuations in numbers and the concentration of nesting within about 10 km² of habitat make palila highly vulnerable to extinction. Palila show strong site fidelity (Fancy *et al.* 1993), and individual palila nest in the same general location year after year (Banko *et al.* 2002a).

Palila depend on māmane trees for immature seeds, flowers, leaf buds, and insects (Banko *et al.* 2002a). Annual variation in māmane seed pod production affects palila survival, and palila attempt fewer nests and produce fewer chicks in years of relatively low māmane pod production (Lindsey *et al.* 1995, Banko *et al.* 2002a). Māmane is heavily browsed by feral sheep (*Ovis aries*) and European mouflon sheep (*O. gmelini musimon*), but the culling of these populations by hunters and Hawai'i Division of Forestry and Wildlife has allowed some māmane regeneration (Hess *et al.* 1999).

Palila habitat has also been invaded by introduced annual grasses and other weeds, resulting in the accumulation of fire fuels in some areas. The threat of fire has been a longstanding concern for the survival of the palila.

In some areas of Palila Critical Habitat, such as on the eastern slope of Mauna Kea, the belt of māmane forest has been narrowed by long-term cattle ranching and feral ungulate browsing. Because the timing of seed set varies with elevation, the seasonal availability of māmane seeds has shortened as forest width has narrowed (Banko *et al.* 2002b). Although narrow bands of forest may support palila populations during years when seed crops are large, there are few alternate food resources available when seed crops are small. Therefore, the width of the forest belt and the density of trees are important considerations when planning reintroduction and recovery programs.

Predation by feral cats (*Felis catus*) reduces palila nesting success and survival (Banko *et al.* 2002a, Hess *et al.* 2004). Rats (*Rattus rattus*), which are more abundant where naio trees are co-dominant with māmane (Amarasekare 1994), also destroy some palila nests (Banko *et al.* 2002a). Even low rates of predation by small mammals, in combination with high nest and roost site fidelity by palila, might reduce the persistence and productivity of small populations. Therefore, reducing predation may be important when enhancing or re-establishing palila outside the core breeding area.

The palila is an appropriate candidate for which to develop and apply restoration techniques because: (1) the species probably cannot be recovered without active and timely management (Banko *et al.* 2009); (2) adequate information on palila ecology exists to guide management efforts (van Riper *et al.* 1978; van Riper 1980a, 1980b; Pletschet and Kelly 1990; Fancy *et al.* 1993; Jeffrey *et al.* 1993; Lindsey *et al.* 1995; Jacobi *et al.* 1996; Fancy *et al.* 1997; Banko 2009); and (3) techniques developed for palila recovery may be applicable to recovering other Hawaiian forest birds. Another advantage to working with palila is that they can carry radio

transmitters large enough to permit monitoring for up to eight weeks, which can facilitate the evaluation of management activities. In addition, avian malaria and pox are essentially absent in the palila population and are not likely to complicate the interpretation of management treatments. Finally, it is possible to develop management techniques when levels of inbreeding are low and unlikely to impede population restoration (Fleischer *et al.* 1994).

Personnel

The project team (Appendix II) consisted of the project leader and technical and administrative staff employed through the University of Hawai'i at Mānoa (Pacific Cooperative Studies Unit) or the University of Hawai'i at Hilo (Hawai'i Cooperative Studies Unit). In addition to salaried staff, hundreds of interns assisted with field and laboratory investigations. Groups of interns consisted of university students or recent graduates. In return, they received professional training and experience.

Study Areas

We studied eight relatively dry, montane to subalpine woodland sites where palila studies had been conducted since 1987 or where palila might eventually be reintroduced (Figure I.1). These study sites are referred to in most chapters of this report, often without reprinting a map. Sites on the western slope of Mauna Kea where palila were most abundant and nested most frequently were Pu'u Lā'au Mauka (PL Mauka) and Pu'u Lā'au Makai (PL Makai). Manao and Ahumoa were sites on western Mauna Kea where palila were less abundant and nested less frequently. Three potential reintroduction sites on Mauna Kea where palila were absent or rare were North, South, and Pōhakuloa Flats (PFlats). Another possible reintroduction site was located on Mauna Loa (Kīpuka 'Alalā). Pōhakuloa Flats (also known as Training Areas 1 and 2) and Kīpuka 'Alalā (also known as Training Area 23) were located within the U.S. Army's Pōhakuloa Training Area. The other sites were located on state lands managed as forest reserve or game management areas by the Hawai'i Division of Forestry and Wildlife. Research was conducted within a grid of transects at each of the western slope study sites (Figure I.2). At proposed reintroduction sites, we initially worked along one or two transects which paralleled roads. In 1998, we established a grid system of transects at the northern site to facilitate translocation and predator control and research (Figure I.3).

The study sites encompassed a wide range of elevation, extending from 1,701–2,835 m (5,580–9,300 ft; Table I.1). Annual rainfall averaged 500–1,000 mm at all sites. Annual rainfall averaged 511 mm (58-year record) at PL Mauka and PL Makai and surrounding areas (Juvik *et al.* 1993). North potentially was the wettest site; followed closely by the other reintroduction sites. There was a distinct rainfall gradient at PFlats, which resulted in about 35% more precipitation in the eastern portion compared to the western portion. All sites were dominated by native trees, generally less than 3–10 m tall, and shrubs (Hess *et al.* 1999). Native grasses were present in all areas, but alien grasses generally dominated.

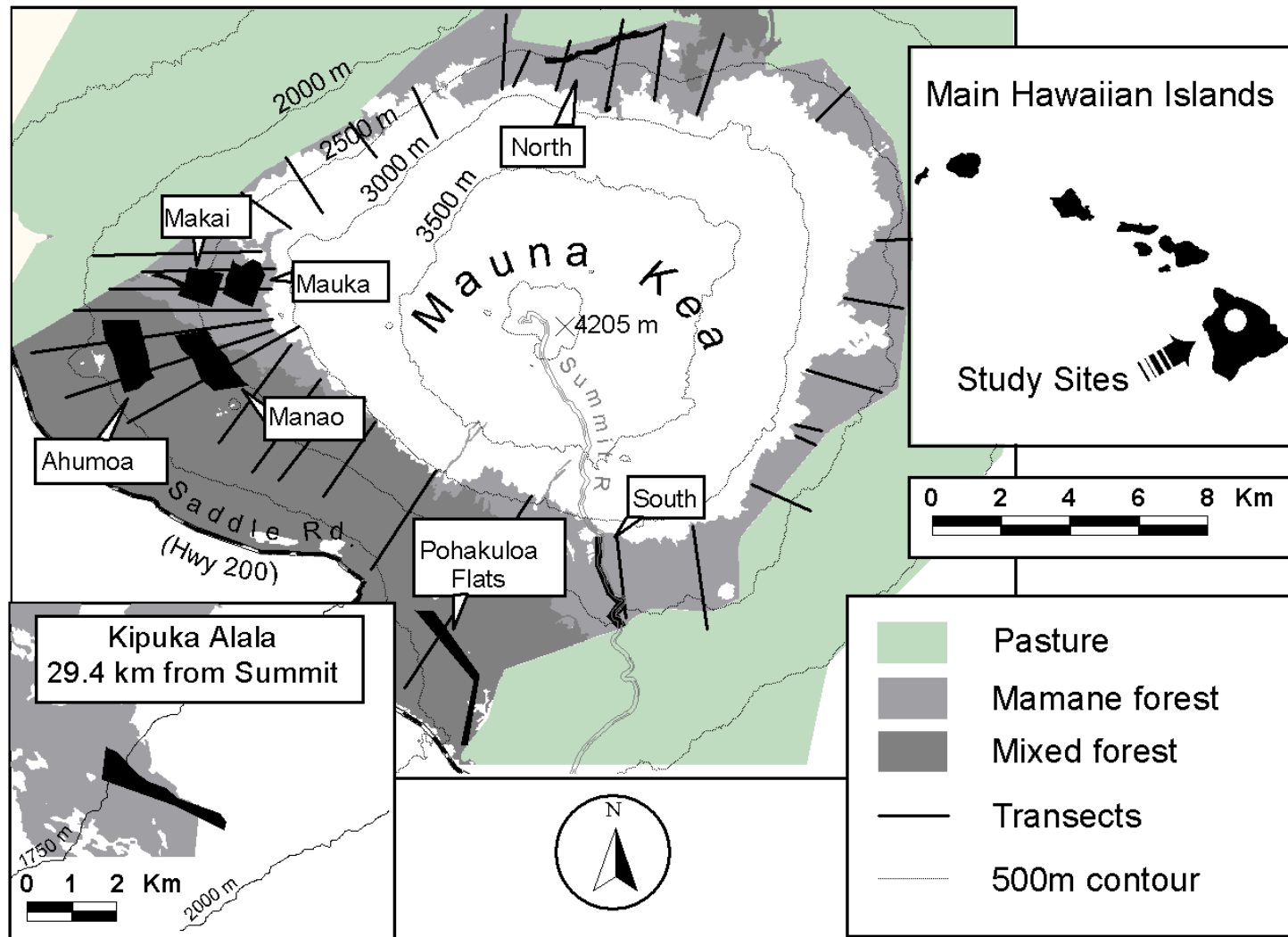


Figure I.1. Locations of eight study sites and 32 transects on Mauna Kea and Mauna Loa. Mauna Kea study sites were located within Palila Critical Habitat in Mauna Kea Forest Reserve (MKFR) and Ka'ohē Game Management Area (Ahumoa). Kīpuka 'Alalā was situated on Mauna Loa within Pōhakuloa Training Area (PTA) and Pōhakuloa Flats was within MKFR and PTA.

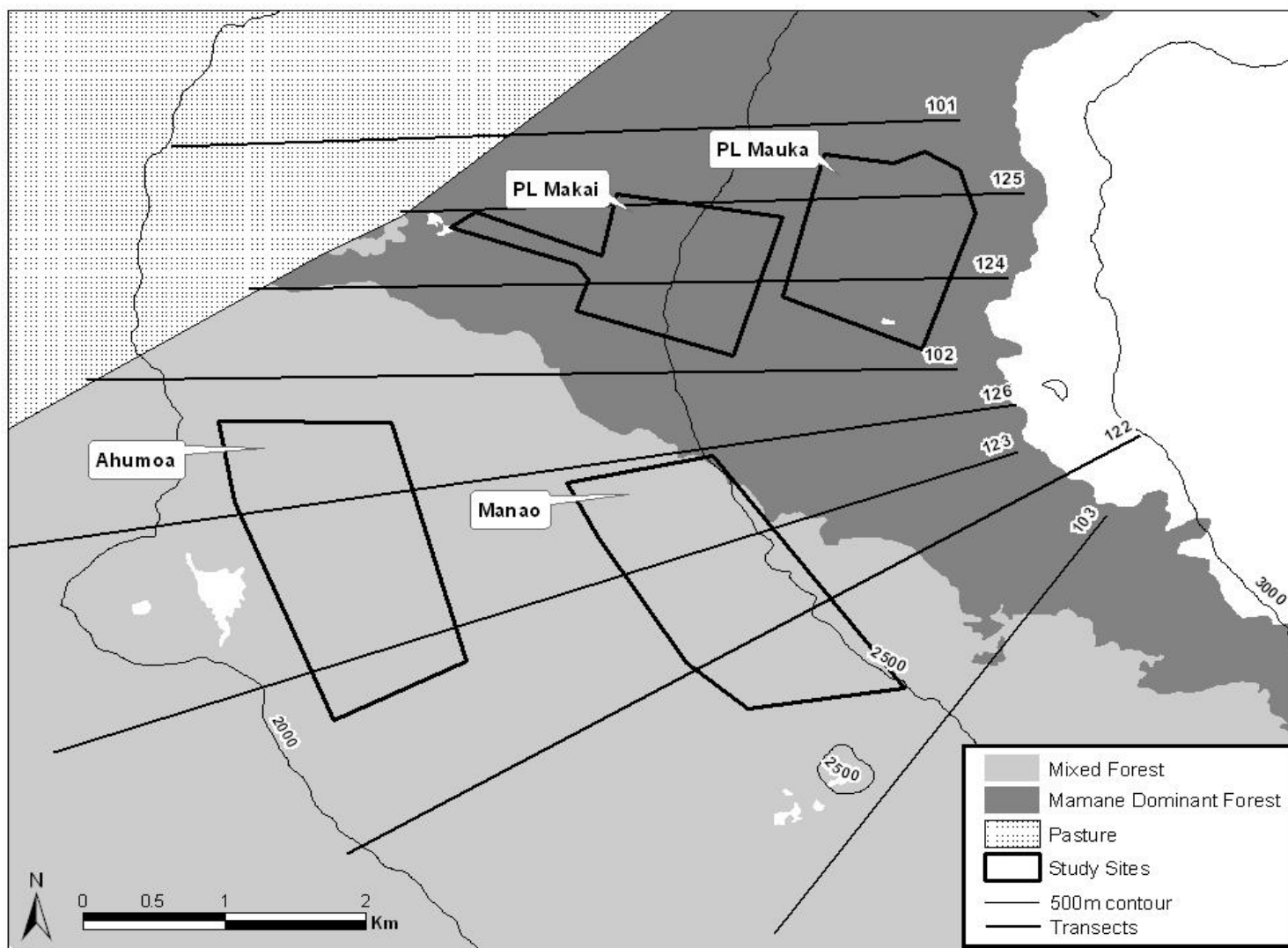


Figure I.2. Study sites and transects on the western slope of Mauna Kea. Transects 101–103 were established by the Hawai'i Forest Bird Survey (Scott *et al.* 1986), and transects 122–126 were established by the Palila Restoration Project in 1998.

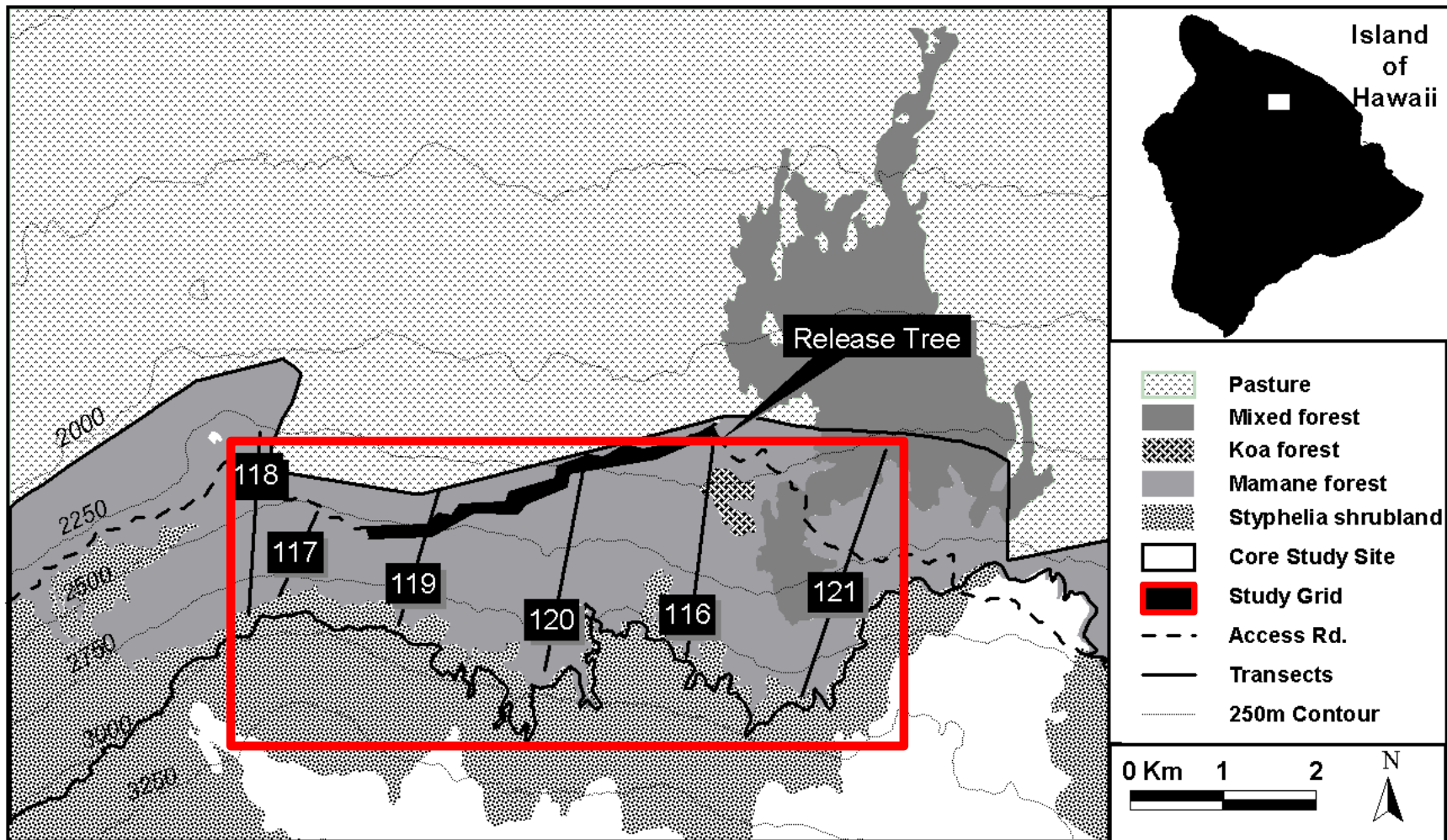


Figure I.3. Transects and habitat where translocated palila were released on the northern slope of Mauna Kea, Hawai'i, 1997–2006. Transects 116–117 were established by the Hawai'i Forest Bird Survey (Scott *et al.* 1986), and transects 118–121 were established by the Palila Restoration Project in 1998. *Styphelia* now is *Leptocophylla*.

Table I.1. Elevation and palila population status at study sites.

| Study site | Range of elevation | Palila population status |
|------------------|---------------------------------|--------------------------|
| Pu'u Lā'au Mauka | 8,500–9,200 ft 2,591–2,804 m | High |
| Pu'u Lā'au Makai | 7,500–8,500 ft 2,286–2,591 m | High |
| Manao | 7,500–8,300 ft 2,286–2,530 m | Intermediate – low |
| Ahumoa | 6,800–7,360 ft 2,073–2,243 m | Intermediate – low |
| North | 6,900–8,400 ft 2,103–2,560 m | Absent since 1970s |
| South | 8,080–9,300 ft 2,463–2,835 m | Very low |
| Pōhakuloa Flats | 6,580–6,650 ft 2,006–2,027 m | Absent since 1970s |
| Kīpuka 'Alalā | 5,580–6,270 ft 1,701–1,911 m | Absent since 1950s |

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Presentations at Conferences and Symposia

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2. Banko, P. C., L. Johnson, S. Dougill, C. Kuehler, A. Lieberman, M. Kuhn, J. Kuhn, P. Conry, J. Giffin, A. Char, B. Miura, and K. Rosa. 1996. Palila restoration and habitat management on Mauna Kea. Pp. 235–245 *in* Proceedings of the Seventy-sixth Western Association of Fish & Wildlife Agencies Conference, 22–26 July 1996, Honolulu, HI. (also Oral)

3. Hess, S. C., P. C. Banko, G. J. Brenner, and J. D. Jacobi. 1996. Tree densities in subalpine woodland on Mauna Kea, Hawai'i. Pp. 225–234 *in* Proceedings of the Seventy-sixth Western Association of Fish & Wildlife Agencies Conference, 22–26 July 1996, Honolulu, HI. (also Oral)
4. Banko, P. C. 1997. Progress of terrestrial Hawaiian bird recovery programs. *In* symposium: Conservation and management of Pacific landbirds and endangered ecosystems. Cooper Ornithological Society, 67th Annual Meeting, 30 April–4 May 1997, Hilo, HI. (Oral)
5. Johnson, L., S. J. Dougill, P. C. Banko, J. G. Massey, T. Work, S. C. Hess, and L. P. Laniawe. 1997. Reintroducing a population of palila to recovering habitat on Mauna Kea, Hawai'i. Cooper Ornithological Society, 67th Annual Meeting, 30 April–4 May 1997, Hilo, HI. (Oral)
6. Hess, S. C., P. C. Banko, M. H. Reynolds, G. J. Brenner, L. P. Laniawe, and J. D. Jacobi. 1997. Seasonal changes in food resource availability and drepanidine densities in subalpine woodland on Mauna Kea, Hawai'i. Cooper Ornithological Society, 67th Annual Meeting, 30 April–4 May 1997, Hilo, HI. (Oral)
7. Johnson, L., S. Dougill, and P. Banko. 1998. Renesting behavior of the palila in response to clutch removal for captive propagation. The Wildlife Society, Western Section, Annual Meeting, 11–14 February 1998, Sacramento, CA. (Oral)
8. Hess, S., P. Banko, G. Brenner, L. Laniawe, and J. Jacobi. 1998. Habitat selection and food preference of the endangered palila on Mauna Kea, Hawaii. The Wildlife Society, Western Section, Annual Meeting, 11–14 February 1998, Sacramento, CA. (Oral)
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12. Banko, P. C., E. G. Gray, S. Dougill, D. Goltz, L. Johnson, P. Oboyski, J. Semones, and M. Wiley. 1998. Developing techniques for restoring palila (*Loxioides bailleui*). International Ornithological Congress, 22nd Meeting, 16–22 August 1998, Durban, South Africa. (Poster)
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15. Wiley, M. R., E. M. Gray, P. C. Banko, S. D. Dougill, L. M. Johnson, and J. D. Semones. 1999. Roost site selection and behavior of a Hawaiian finch. Animal Behavior Society, 36th Annual Meeting, 26–30 June 1999, Lewisburg, PA. (Poster)
16. Laut, M. E., P. C. Banko, E. M. Gray, and L. P. Laniawe. 1999. Time allocation of nesting palila: a video study. American Ornithologists' Union, 117th Annual Meeting, 8–14 August 1999, Ithaca, NY. (Poster)
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18. Banko, P. C., S. Dougill, D. Goltz, E. Gray, L. Johnson, and P. Oboyski. 2000. Advances in restoring the endangered palila and its habitat. The Wildlife Society, Western Section, Annual Meeting, 26–29 January 2000, Riverside, CA. (Oral)
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20. Banko, P. C., S. Dougill, L. Gold, D. Goltz, L. Johnson, P. Oboyski, and J. Slotterback. 2001. Removing a diverse suite of invasive threats to recover an endangered Hawaiian bird species and its dry forest habitat. Conference on the Eradication of Island Invasives: Practical Actions and Results Achieved, University of Auckland and Invasive Species Specialist Group of the International Union for the Conservation of Nature (IUCN) Species Survival Commission, 19–23 February 2001, Auckland, New Zealand. (Poster)
21. Banko, P. C., S. Dougill, D. Goltz, L. Johnson, and P. Oboyski. 2001. Hawaiian bird recovery: removing invasive threats, restoring habitat, and reestablishing populations. Society for Conservation Biology, 15th Annual Meeting, 29 July–1 August 2001, Hilo, HI. (Oral)
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43. Neal, R., K. Brinck, P. Banko, M. Cipollini, and G. Breton. 2005. Intraspecific variation in quinolizidine alkaloids of mamane (*Sophora chrysophylla*) seed embryos: relevance to specialist seed predation by palila (*Loxioides bailleui*) and *Cydia* spp. Association of Southeastern Biologists, 66th Annual Meeting, 13–15 April 2005, Florence, AL. (Oral)
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45. Farmer, C., and P. C. Banko. 2005. Translocation of an endangered passerine, the palila. American Ornithologists' Union, 123rd Annual Meeting, 23–27 August 2005, Santa Barbara, CA. (Oral)
46. Farmer, C., P. Banko, R. Stephens, K. Brinck, B. Frederick, and C. Snow. 2006. Status of translocated palila. 2006 Hawai'i Conservation Conference, 26–28 July 2006, Honolulu, HI. (Poster)

47. Schwarzfeld, M., C. Farmer, P. Banko, D. Pollock, and P. Oboyski. 2006. Changes in distribution of alien ants on Mauna Kea, Hawai'i. 2006 Hawai'i Conservation Conference, 26–28 July 2006, Honolulu, HI. (Poster)
48. Banko, P., J. Price, C. Farmer, K. Brinck, and K. Rapozo. 2007. Ecology of dryland forest birds. Ka'ahahui 'O Ka Nāhelehele, Dryland Forest Working Group, Nahelehele Dryland Forest Symposium, 23 February 2007, Kailua-Kona, HI. (Oral)
49. Farmer, C., K. Brinck, P. Banko, D. Goltz, R. Danner, and S. Hess. 2007. Extremely low black rat (*R. rattus*) capture rates on western Mauna Kea, Hawai'i. Rats, Humans, & Their Impacts on Islands: An Interdisciplinary Conference, University of Hawai'i at Mānoa, 27–31 March 2007, Honolulu, HI. (Oral)
50. Banko, P., J. Burgett, S. Conant, R. David, and D. Leonard. 2007. Population restoration: a panel discussion of case studies and major issues. Cooper Ornithological Society, 77th Annual Meeting, 19–23 June 2007, Moscow, ID. (Oral)
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52. Farmer, C., P. Banko, K. Brinck, J. Morris, and C. Snow. 2007. Demography of a reintroduced colony of palila. 2007 Hawai'i Conservation Conference, 25–27 July 2007, Honolulu, HI. (Poster)
53. Hess, S. C., H. Hansen, and P. C. Banko. 2007. Ecology of an invasive predator in Hawai'i. USDA National Wildlife Research Center, Managing Vertebrate Invasive Species Symposium, 7–9 August 2007, Fort Collins, CO. (Oral)
54. Farmer, C., K. W. Brinck, and P. C. Banko. 2008. Fifteen-year nesting study of a Hawaiian honeycreeper. 2008 Hawai'i Conservation Conference, 29–31 July 2008, Honolulu, HI. (Oral)
55. Farmer, C., K. W. Brinck, and P. C. Banko. 2008. Forest structure and composition on Mauna Kea, Hawai'i. 2008 Hawai'i Conservation Conference, 29–31 July 2008, Honolulu, HI. (Poster)
56. Leonard, D. L., Jr., P. C. Banko, K. W. Brinck, C. Farmer, R. J. Camp, and J. Nelson. 2008. Palila population plummets. 2008 Hawai'i Conservation Conference, 29–31 July 2008, Honolulu, HI. (Poster)
57. Banko, P. C., C. Farmer, K. W. Brinck, S. J. Dougill, D. L. Leonard, and J. Nelson. 2008. Recent palila population decline relative to vegetation structure and browsing threats. Combined annual meeting of American Ornithologists' Union, Cooper Ornithological Society, and Canadian Society of Ornithologists, 4–8 August 2008, Portland, OR. (Oral)
58. Farmer, C., K. W. Brinck, and P. C. Banko. 2008. Fifteen-year nesting study of a Hawaiian honeycreeper. Combined annual meeting of American Ornithologists' Union, Cooper Ornithological Society, and Canadian Society of Ornithologists, 4–8 August 2008, Portland, OR. (Poster)

59. Banko, P. C., C. Farmer, and K. W. Brinck. 2009. Translocation as a tool for recovering an endangered Hawaiian forest bird. The Wildlife Society, 16th Annual Meeting, 19–23 September 2009, Monterey, CA. (Oral)
60. Banko, P. C., C. Farmer, and K. W. Brinck. 2010. Palila restoration: is counting sheep resulting in a 30-year nightmare? Combined annual meeting of American Ornithologists' Union, Cooper Ornithological Society, and Canadian Society of Ornithologists, 7–11 February 2010, San Diego, CA. (Oral)
61. Watkins, W., R. Neal, K. Brinck, P. Banko, and M. Cipollini. 2010. Intraspecific developmental variation in quinolizidine alkaloids of mamane (*Sophora chrysophylla*) seed embryos: relevance to specialist seed predation by palila (*Loxioides bailleui*). Association of Southeastern Biologists, 71st Annual Meeting, 7–10 April 2010, Asheville, NC. (Oral)
62. Brinck, K., R. Camp, M. Gorresen, P. Banko, and D. Leonard. 2010. Techniques to identify trends in the population of the endangered palila. 2010 Hawai'i Conservation Conference, 4–6 August 2010, Honolulu, HI. (Poster)
63. LaPointe, D. A., C. T. Atkinson, P. C. Banko, R. J. Camp, P. M. Gorresen, J. D. Jacobi, T. K. Pratt, and M. D. Samuel. 2011. Hawaiian forest birds: the past, present and future status of an endangered avifauna. Pacific Climate (PACLIM) Workshop, USDA Forest Service, 6–9 March 2011, Pacific Grove, CA. (Invited)
64. Banko, P. C., C. Farmer, and K. Brinck. 2011. Long-term studies of threats to the palila, an endangered forest bird on Mauna Kea, Hawai'i. 2011 Meeting of the Pacific Branch of the Entomological Society of America, 27–30 March 2011, Waikoloa, HI. (Oral)
65. Banko, P. C. 2011. Feeding specialization and the vulnerability of Hawaiian forest birds to food web disruption and environmental change. Symposium on Evolution of Life on Pacific Islands and Reefs: Past, Present, and Future. Smithsonian Institution and National Tropical Botanical Garden, 26–30 May 2011, Honolulu, HI. (Oral)
66. Banko, P. C., R. W. Peck, and W. E. Banko. 2011. The evolution of feeding specialization in Hawaiian forest birds and its ecological consequences. The Wildlife Society, 18th Annual Meeting, 5–10 November 2011, Waikoloa, HI. (Invited)
67. Banko, P. C., C. Farmer, K. W. Brinck, D. L. Leonard, and R. M. Stephens. 2011. Reintroduction of an endangered Hawaiian forest bird and prospects for its recovery. International Congress for Conservation Biology, 5–9 December 2011, Auckland, New Zealand. (Abstract)
68. Banko, P. C., R. J. Camp, C. Farmer, K. W. Brinck, D. L. Leonard, and R. M. Stephens. 2012. Response of a Hawaiian subalpine, dry forest bird community to prolonged drought and habitat degradation by feral ungulates. 2012 Hawai'i Conservation Conference, 31 July–2 August 2012, Honolulu, HI. (Invited Oral)
69. Banko, P., J. Juvik, S. Juvik, J. Jacobi, P. Scowcroft, C. Farmer, K. Brinck, R. Camp, D. Leonard, and R. Stephens. 2012. Mauna Kea and the myth of multiple use, revisited. Vulnerable Islands in the Sky: Science and Management of Tropical Island Alpine and

Sub-Alpine Ecosystems International Symposium, 4–7 August 2012, Waimea, HI.
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70. Banko, P. C., R. J. Camp, C. Farmer, K. W. Brinck, D. L. Leonard, and R. M. Stephens. 2012. Response of a subalpine Hawaiian forest bird community to prolonged drought and habitat degradation by feral ungulates. North American Ornithological Conference V, 14–18 August 2012, Vancouver, Canada.

Fact Sheets

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2. Banko, P., and C. Farmer. 2006. Palila restoration: lessons from long-term research. USGS Fact Sheet #2006-3104. Available at: <http://www.usgs.gov/ecosystems/pierc/files/factsheets/Palila.pdf> accessed March 2013.

Appendix II: Project Staff Roster

Project Management:

- 1996–2012 **Paul Banko**, PhD. Project leader. Research planning, interpretation, management, and coordination.
- 1999–2004 **Julie Leialoha**. Project coordinator. Interagency coordination and planning; community outreach; supervision of vegetation research.
- 2002–2003 **Steven Hess**, PhD. Project manager. Field research planning and management; data analysis and interpretation; report preparation; GIS.
- 2004–2009 **Chris Farmer**, PhD. Project manager. Field research planning and management; data analysis and interpretation; report preparation; geographic information system (GIS).

Data Management and Analysis:

- 1998–1999 **Elizabeth Gray**, PhD. Quantitative ecologist. Supervision of data management, analysis, and interpretation.
- 1998–2001 **Megan Laut**, MSc. Data technician. Data entry and management; report preparation.
- 1998 –2005 **Barbara Muffler**. Data technician. Data entry and management; literature management; administration.
- 1999–2000 **Heather Weddle**. Data clerk. Data entry; literature entry; administration.
- 2002–2009 **Kevin Brinck**, MSc. Quantitative ecologist. Statistical analysis and interpretation of data; research design; geographic information system (GIS).
- 2003–2005 **Kelly Kozar**. Data technician. Data entry and management; report preparation; geographic information system (GIS).
- 2004–2007 **Sarah Nash**, MSc. Data technician. Data entry and management; report preparation; geographic information system (GIS); administration.

Bird Studies (translocation; nesting biology; banding and radio-tracking; population monitoring):

- 1996–2001 **Luanne Johnson**. Field leader. Supervision of ornithological research; logistical planning; data collection, analysis, and management; field safety.
- 1997–1999 **John David Semones**. Ornithologist. Data collection, analysis, and management; intern supervision.
- 1997–2000 **Michael Wiley**. Ornithologist. Data collection, analysis, and management; intern supervision.
- 1999 **Kendy Radasky**. Ornithologist. Data collection; intern supervision.

- 1999–2000 **Rachael Rounds**. Ornithologist. Data collection; intern supervision.
- 2000–2002 **David Cerasale**. Ornithologist. Data collection; intern supervision.
- 1999–2004 **Colleen (Murray) Cole**. Field leader. Supervision of ornithological research; logistical planning; data collection, analysis, and management; field safety. Data and administrative clerk. Data entry and management; report preparation; administration.
- 2001–2003 **Susan Marshall**. Ornithologist. Data collection; intern supervision.
- 2002–2003 **Brittany Cline**. Ornithologist. Data collection; intern supervision.
- 2002–2004 **Andrea Lindo**. Ornithologist. Data collection; intern supervision.
- 2003–2005 **Emily Severson**. Ornithologist. Data collection; intern supervision.
- 2003–2004 **Grant Beauprez**, MSc. Field leader. Supervision of ornithological research; logistical planning; data collection, analysis, and management; field safety.
- 2003–2005 **Julie (Castner) Danner**. Ornithologist. Data collection; intern supervision.
- 2003–2004 **Corinna Hanson**. Field technician (temporary hire).
- 2004–2006 **Bobby Hsu**. Ornithologist. Data collection; intern supervision.
- 2005–2006 **Robert Stephens**, MSc. Field leader. Supervision of ornithological research; logistical planning; data collection, analysis, and management; field safety.
- 2005–2006 **Bridget Frederick**. Ornithologist. Data collection; intern supervision.
- 2006–2007 **Carter Snow**. Ornithologist. Data collection; intern supervision.
- 2006–2007 **Jeremy Morris**. Ornithologist. Data collection; intern supervision.

Insect Studies (avian diet composition; distribution and life history of māmane moths; biology of caterpillar parasitoids; distribution and impacts of yellowjackets and ants):

- 1996–2001 **Peter Oboyski**, MSc. Field leader. Supervision of entomological research in field and laboratory; research and logistical planning; data collection, analysis, and management; field safety.
- 1998 **Mathew Kveskin**. Entomologist. Data collection, management, and analysis; intern supervision.
- 1999–2002 **John Slotterback**. Entomologist. Data collection, management, and analysis; intern supervision.
- 2000–2002 **Aaron Gregor**. Entomologist. Data collection, management, and analysis; intern supervision.

- 2002–2005 **David Pollock**, MSc. Field leader. Supervision of entomological research in field and laboratory; research and logistical planning; data collection, analysis, and management; field safety.
- 2004–2006 **Marla Schwarzfeld**. Entomologist. Data collection, management, and analysis; intern supervision.
- 2005 **Katherine Kieler**. Entomologist. (temporary hire)

Predator Studies (biology and impacts of small mammals and raptors; control of alien predators):

- 1997–2003 **Dan Goltz**, MSc. Field leader. Supervision of predator research and control; data collection, analysis, and management.
- 1999–2000 **Chris Murray**. Wildlife biologist. Data collection, analysis, and management; intern supervision.
- 2000–2002 **Alison (Agnes) Polanski**. Wildlife biologist. Data collection, analysis, and management; intern supervision.
- 2002–2005 **Raymond Danner**. Field leader. Supervision of predator research and control; logistical planning; data collection, analysis, and management.
- 2004 **George Parish**. Field technician. (temporary hire)
- 2004–2005 **Daniel Nelson**. Field leader. Supervision of predator research and control; logistical planning; data collection, analysis, and management; field safety.
- 2004–2005 **Jacob Scheidler**. Field technician. (temporary hire)

Vegetation Studies (composition and structure of subalpine vegetation; distribution and impacts of weeds; habitat requirements of birds):

- 1996–2002 **Steve Dougill**. Botanist. Supervision of vegetation research; logistical planning; data collection, analysis, and management; geographical information system (GIS).
- 1999 **Traci (Rogers) Semones**. Botanist. Data collection, analysis, and management; intern supervision.
- 1999–2001 **Laurie Gold**. Botanist. Data collection, analysis, and management; intern supervision.
- 2004–2009 **Kalei Rapozo**. Botanist. Phenology coordinator; data collection, analysis, and management.
- 2004–2005 **Jennifer (Crummer) Higashino**. Botanist. Forest restoration coordinator; supervision of vegetation research; community outreach.
- 2008 **Jennifer Tietjen**. (temporary hire)

SUMMARY

The Palila Restoration Project was initiated in 1996 by the U.S. Geological Survey to assist government agencies mitigate the effects of realigning Saddle Road (Highway 200) through Palila Critical Habitat. The palila (*Loxioides bailleui*) is an endangered Hawaiian forest bird found only on the upper slopes of Mauna Kea Volcano.

The objectives of the Palila Restoration Project were to develop techniques for reintroducing the palila to a portion of its former range, investigate the biological threats to the palila and its habitat, and synthesize the existing body of ecological knowledge concerning the palila. Five broad study themes formed the research framework:

1. Population reintroduction and restoration
2. Demography and breeding ecology
3. Habitat use and food ecology
4. Vegetation ecology
5. Predator ecology and management

Population Reintroduction and Restoration

We evaluated four sites (three on Mauna Kea and one on Mauna Loa) by comparing their assets and liabilities to those of four sites on western Mauna Kea, where most of the palila population was located. We assessed habitat quality in terms of environmental gradients, vegetation structure, species composition, and recruitment of māmane (*Sophora chrysophylla*). We also evaluated the availability of food, particularly māmane pods but also caterpillars and other insect prey, and threats from predators, diseases, wildland fire, and human disturbance. We identified the northern slope of Mauna Kea as having the best characteristics for reintroducing palila mainly because of the opportunity to restore habitat along a substantial gradient of elevation.

We translocated 188 palila from the western slope of Mauna Kea to an area near Pu'u Mali on the northern slope during six trials from 1997–1998 and 2003–2006. The methods we developed resulted in a relatively high survival rate of birds and the establishment of a small, breeding colony. About 19 first-generation (F1) palila and at least one second-generation (F2) palila were produced near Pu'u Mali. We determined that some translocated birds periodically moved between the reintroduction and source sites, and unbanded birds regularly were detected on the northern slope. Movement between slopes would be an important means of connecting the populations and might eventually lead to palila moving between habitats according to the condition of the vegetation, availability of food, and other environmental factors.

Although some palila remained for over a year near Pu'u Mali, many returned to the western slope within two months. We were unable to predict which individuals were likely to remain and breed in the reintroduction area. The return of translocated birds to the source area was partially offset by palila that moved between the northern and western slopes. Ultimately, in the grip of a severe drought and with insufficient resources for augmenting the colony with additional birds, the reintroduced colony disappeared. We were unable to determine whether birds that had bred on the northern slope eventually returned to the western slope or died.

Palila that were fledged on the northern slope generally remained there longer than their parents, based on sightings of birds in the years following the last translocation in 2006. Severe drought conditions prevailed during most of the study, and its effect on the translocation results are not clear. Nevertheless, the effects of drought on māmane trees seemed somewhat less severe on the northern slope than they were on the western slope, suggesting that additional translocation efforts coupled with increased habitat restoration could result in a more enduring population.

Patterns of habitat use by the translocated birds revealed that large areas on the northern slope were of marginal value to palila. Translocated birds concentrated in relatively few, small areas where the size and density of māmane trees were highest. This information can be used to target habitat restoration efforts to improve the carrying capacity for palila. As habitat restoration continues and expands within historical habitat, the persistence of palila at future reintroduction sites would be expected to increase.

Protecting translocated palila from predators was important in reducing mortality in the reintroduction area. Palila were selective about the location and species of tree they used for roosting after being translocated. This, in addition to their initial unfamiliarity with the new area, may have increased their vulnerability to predation from introduced mammals and native raptors. Predation of even a few individuals would have a disproportional impact on the overall survival and productivity of a small, incipient population.

In addition to translocation, we investigated other methods for reintroducing and bolstering palila populations. As a precursor to rear-and-release and long-term captive propagation, we harvested eggs from wild pairs and monitored the effect of egg harvest on their subsequent reproduction. Harvesting wild eggs did not suppress re-nesting, and the hatchability of wild eggs was high in captivity. In support of a separately funded program, we monitored the survival and behavior of captive-reared palila that were released near Pu'u Mali. Captive-reared females did not produce nestlings, but captive-reared males nested successfully with wild, translocated females. Relatively few captive-reared palila were released to the wild due to the low level of productivity of the captive flock.

Demography and Breeding Ecology

Annual population surveys revealed that the palila population declined significantly after 2003, due primarily to severe drought conditions and continued habitat degradation by browsing ungulates. Drought strongly depressed māmane pod production, which in turn affected palila survival and reproduction. Between 1998 and 2012, the population estimate reached a maximum of 6,463 in 2003 and a minimum of 1,495 in 2011 for an average loss of over 500 birds annually. The rate of decline was 57% over the 15-year period. During this time, the range of the palila also contracted, increasing the vulnerability of the species to environmental disturbance and invasive species threats.

Determining the sex ratio and how it may change between age classes is important for calculating survival rates, conducting population viability analyses, and planning conservation strategies for endangered species. We compared genetic (PCR) and plumage techniques for sexing palila and found a significant difference in sex ratios among age classes. In the adult age class (after second year, ASY), males outnumbered females by $\geq 50\%$ using both sampling methods. The sex ratio changed, even at the embryo and nestling stages, to a male bias after individuals began breeding. Both methods of sex determination indicated parallel shifts in sex ratios from hatch year (HY; tendency towards more males) to second year (SY; female bias) to

ASY (male bias). We found that sexing SY birds using the plumage-based technique alone was subject to a high error rate, but even when corrected the results were female-biased. As the palila population declines, the effects of the male-biased sex ratio may become increasingly problematic due to increased demographic stochasticity and competition for mates.

We surveyed for avian malaria, pox virus, and *Mycoplasma* bacteria to assess potential disease threats where introduced mosquitoes have not yet invaded. Our results indicated that avian malaria is unlikely to affect the existing palila population or future reintroduced populations in subalpine Mauna Kea. We rarely observed lesions caused by avian pox virus in palila, although lesions were encountered more frequently in bird species that seasonally vacated the lower-elevation, wetter forests of windward Mauna Kea to feed on māmane flowers within the palila's range. Despite proximity to pox- and malaria-infected birds, the lack of an effective vector protects the palila in the near-term. Although changes in climate could eventually increase the exposure of palila to disease vectors, the recent trend towards drier conditions in subalpine Mauna Kea is not likely to favor mosquitoes. Nevertheless, additional screening for avian diseases and vectors is warranted within Pōhakuloa Training Area and other potential reintroduction sites at relatively low elevations. The effects of bacterial diseases and other pathogens are of concern to palila management because of their possible implication in the deaths of captive chicks. *Mycoplasma* bacteria were not cultured from wild palila or other honeycreepers within Palila Critical Habitat (PCH).

We conducted intensive studies of breeding to identify factors limiting reproduction. Although palila may first breed at one and two years of age (females and males, respectively) and may continue breeding to at least 17 years of age, we found that the mean breeding age varied annually between 4.2 and 6.1 years; almost 20% of nesting adults were older than 6 years, and a few adults older than 10 years were breeding each year. Breeding palila were significantly older than birds not associated with nests, due mainly to a greater proportion of 9–10-year-old birds in the breeding population. Although we did not determine whether older parents had higher fledgling success rates, experienced adults likely formed a larger proportion of the breeding population in years when food availability was marginal. Our genetic studies indicated that males may gain nesting experience by helping at the nests of parents or close relatives, which likely increases nesting success and reduces the overall costs of nesting. Nest helping by males may increase if the sex ratio becomes increasingly male-biased.

Although palila tended to nest in the same general area from year to year, the timing and number of pairs breeding varied considerably, presumably in response to food availability. We found a positive correlation between the number of active nests during the breeding season and the number of māmane pods available. Nest density was usually higher in māmane-dominated forest than it was in forest dominated by naio (*Myoporum sandwicense*), although the naio habitat encompassed a large area of the western slope and supported many nesting pairs in some years. Nesting activity is likely to increase in habitats now dominated by naio, because studies show that, following the culling of introduced ungulates, māmane is regenerating faster than naio.

The availability of food during the breeding season may also affect nest success, although further research is needed to understand the underlying mechanisms and interactions among variables. We found that 33–67% of palila nests were successful annually during 1996–2004 (excluding 2001, when only 2 of 11 nests fledged chicks). Feral cats (*Felis catus*) were responsible for many nest failures annually, but intensive trapping resulted in increased nesting

success. Nevertheless, some nests were depredated by native raptors, specifically pueo (*Asio flammeus sandwichensis*).

Palila nested primarily in māmane trees, but about 10% of nests were placed in other trees or shrubs, and one was placed in a grass clump. Additionally, the amount of canopy overlap with neighboring trees was negatively associated with nest success, possibly because branches of neighboring trees increase the number of routes available to mammalian nest predators. Even so, we found that nest success also decreased as distance to nearest neighboring trees increased, suggesting that adjacent trees can provide additional cover from adverse weather and may help hide nests from aerial predators, such as owls. Our results suggest that reducing the risk of predation would result in palila nesting more frequently in denser tree cover, and tree cover will increase after introduced ungulate browsers are eliminated.

We modeled the relationship between vegetation characteristics and palila nest site selection and success. Palila selected larger trees for nesting, and large māmane will become more common on Mauna Kea as the young cohort of trees continues to grow in response to the elimination of browsers. Our model also identified the native mint, *Stenogyne microphylla*, as an important factor. The additional foliage of *S. microphylla*, which is browsed by introduced ungulates may have added important protection to nests, especially when māmane foliage may have been sparse due to drought. Palila also eat the buds, flowers, and young leaves of *S. microphylla*, which may have been important alternate foods in years of low māmane pod production.

Our study of palila nesting behavior indicated that during the pre-fledgling stages, female palila were most attentive during the egg stage. This was presumably due to the embryo's greater sensitivity to changes in temperature than that of nestlings and the male's ability to provision the female more frequently before eggs hatch. Nest attendance decreased during the nestling period with break length increasing greatly over time as chicks became more covered with feathers and capable of thermoregulation. We observed no evidence of heat stress in the behavior of females or nestlings. The need to simultaneously brood chicks and supply food explained why females recessed more frequently but for shorter periods during the early nestling period. The long nesting period of palila makes them especially vulnerable to introduced mammalian predators, and video surveillance revealed that feral cats contributed substantially to nest failure.

Habitat Use and Food Ecology

We conducted a variety of studies to identify patterns of habitat use, foraging behavior and diet, and threats to critical foods. Although we found no significant differences between the home range sizes of translocated and non-translocated birds, translocated birds' daily movements were smaller than non-translocated birds. This suggests that there are differences between the quantity and quality of habitats on the northern and western slopes of Mauna Kea that influence palila habitat use. Mature māmane stands and mixed māmane-naio woodlands were less abundant on the northern slope, possibly influencing the persistence time of translocated palila. The habitat selected for nighttime roost sites differed from that of daytime use areas. Mixed māmane-naio woodlands were important to palila for night roosting, probably because the dense canopy provided abundant cover.

Previously, palila were not known to move far around Mauna Kea, but we found that palila were more mobile than previously suspected. We observed that translocated palila travelled between the northern and western slopes over a distance of up to 16 km. We also found that palila

translocated to the northern slope used two distinct patches of māmane habitat that were separated by about 3 km of shrub habitat. These results suggest that focusing resources on restoring and enlarging patches of current habitat might allow palila to persist among multiple sites until habitat can be restored across the wider landscape.

Palila habitat use was strongly influenced by the distribution and phenology of māmane, the seeds of which composed the main portion of the diet. Palila consumed reproductive parts and foliage of māmane, but took a higher proportion of māmane seeds than other māmane food items relative to their availability. Palila spent proportionally more time in māmane trees and ate māmane foods in much greater proportion to their availability compared to other foods. In mixed naio-māmane woodland, where naio density was greater than māmane density, palila spent more than twice as much time in māmane trees. Palila densities were related to pod availability and were higher in māmane woodland than in mixed woodland where māmane density was lower. Palila demonstrated limited ability to exploit alternate food resources, using naio fruits only occasionally and when māmane resources were scarce. Although palila consumed more flowers than pods in mixed woodland, they spent more time foraging on pods than other food items in both woodland types. Caterpillars were also consumed by palila and were taken mainly from inside māmane pods.

Our analyses of fecal samples demonstrated that the palila diet consists overwhelmingly of green (unhardened) māmane seeds. We found no difference in the diets of adults between the breeding and non-breeding seasons, when nutritional requirements might be expected to shift to high-protein foods, such as insects. Caterpillars were an important supplementary food throughout the year in the diets of adult palila, and they were especially important in the diets of nestlings. *Cydia* caterpillars, which feed within the seeds of māmane pods where they spend their larval life, were the main insect prey in our samples. *Cydia* fragments were found in the feces of virtually all palila nestlings but in less than two-thirds of adult birds. Of all age classes, second-year palila consumed *Cydia* least frequently, suggesting that experience is needed to forage effectively for caterpillars within māmane pods. Auxiliary foods, such as flower stamens, grass seeds, and arthropods other than *Cydia* (e.g., *Scotorythra* spp.), were found more often in feces of nestlings, suggesting that other age groups relied more on māmane seeds.

We showed that the green māmane embryos eaten by palila (palila do not feed on the orange, hardened seeds found in brown, dry pods), contain relatively low levels of fiber and high levels of carbohydrate, lipid, and protein (a ratio of about 1:2:2), as well as relatively balanced profiles of essential amino acids and minerals (Banko *et al.* 2002c). Based on our estimate of daily seed consumption, the amount of nitrogen and protein consumed by palila is likely to meet their requirements for daily activities. Although we did not assay minor organic constituents, such as vitamins, māmane embryos seem particularly well-balanced nutritionally, which largely explains the heavy reliance of palila on this food for their daily diet and for rearing offspring. We showed that embryos contained high levels of several different alkaloids, including the highly toxic quinolizidine cytisine, which exceeded 1.5% of seed dry mass. Our data suggest that *Cydia* caterpillars are relatively non-toxic sources of lipid, protein, and other nutrients, and thus represent occasional, relatively high-quality resources.

The timing of flowering and seed set in māmane varied with elevation with flowers first appearing at higher elevations then moving down the mountain slope. Therefore, trees distributed along a large elevation gradient can provide māmane pods, flowers, and *Cydia* caterpillars throughout the year. Palila densities were positively correlated with the number of

māmane pods at different elevations. Although māmane pods were available around Mauna Kea throughout the year, the actual abundance varied seasonally. Māmane seeds were most available during the palila nesting season (March–September). The abundance of *Cydia* caterpillars was episodic in all areas of Mauna Kea. The number of *Cydia* per pod peaked in November when pods were relatively uncommon. Presumably as pods become less abundant, *Cydia* become more concentrated in the remaining pods. Nevertheless, the overall availability of caterpillars per tree was highest in June when pods were abundant and many palila were breeding.

Insect surveys revealed that caterpillars found on māmane foliage were generally uncommon in the subalpine forests of Mauna Kea. *Scotorythra artemidora* was the most abundant caterpillar collected in both years of the study, but it was collected most frequently in 1999. Possible explanations for these trends are small sample sizes, differences in microhabitats, variation in rainfall, and uneven timing of sampling during the year. Virtually all caterpillars collected in this study were early instars, suggesting that our daytime sampling was likely biased against older, larger caterpillars, which typically would be expected to spend daylight hours in seclusion while feeding at night. Even so, our sampling took place during the hours when birds would be most actively foraging, which realistically reflected food availability for palila and other birds.

Although many invasive arthropod threats, including ants, predacious wasps, and parasitoid wasps, were identified in surveys of the Pu'u Mali mitigation parcel, we did find two moth species formerly thought to be extinct and one undescribed moth species. Additionally, we collected caterpillars of *Uresiphita polygonalis*, which were observed historically feeding heavily on māmane leaves and being eaten by palila.

We reared *Cydia* and other caterpillar species to determine rates of attack by parasitoid wasps. Despite feeding inside māmane pods, *Cydia* were parasitized by four, widespread generalist wasp species, one of which is an indigenous species, one alien, and two of uncertain origins although likely native. Parasitism rates by different wasp species varied with elevation, but overall parasitism (about 40%) decreased with increasing elevation. Five parasitoid species were reared from caterpillars collected from the foliage of three common host trees and shrubs within PCH. The overall rate of parasitism on the most common caterpillar, *S. artemidora*, collected from māmane was 26%, representing the cumulative impacts of four parasitoid species. *Peridroma albiorbis*, collected from māmane, was also parasitized at a frequency of 26% by three species. Parasitism rates reached 47% in *P. albiorbis* at 2,650 m elevation, indicating the potential of parasitoids for limiting the availability of this common caterpillar to foraging birds.

We also conducted surveys for social Hymenoptera, including yellowjackets (*Vespula pensylvanica*) and ants, which might threaten caterpillars of importance to palila. The abundance of yellowjackets on Mauna Kea varied depending on the slope, year, and elevation. The only consistent pattern was the seasonal cycle of occurrence. Yellowjacket abundance tended to be lowest on the western slope of Mauna Kea, where the palila population is concentrated. Below PCH or at its lower edges, we collected seven ant species in five surveys over six years, including three species not previously reported in this region. Our results indicated a significant increase in the range of three species, especially *Cardiocondyla kagutsuchi*. Distributional patterns of the three most common species in our survey area differed, suggesting that each species' invasion had a different series of interactions with local habitat conditions or arthropod communities. Argentine ants (*Linepithema humile*) were

distributed in two concentrated populations whose boundaries shifted through time, and big-headed ants (*Pheidole megacephala*) ranged within one relatively fixed area, whereas *C. kagutsuchi* was found scattered over the survey area.

Suspecting that an introduced, generalist arthropod predator, such as the carabid beetle *Laemostenus complanatus*, might prey on palila food resources, we conducted surveys within PCH. During daylight these beetles were found under rocks, plants, and the loose bark of trees, but at night we observed them moving on the ground or in māmane and naio trees. Although capture rates of *L. complanatus* dropped markedly between 1992 and 2002, suggesting an overall decrease in abundance of the beetle, the beetle's range expanded. Range expansion and the occasional abundance at which we observed it suggest that it could add to the overall impacts of other invasive arthropod predators on food webs and trophic interactions of importance to the palila.

Vegetation Ecology

We combined data obtained from satellite imagery with aerial photographs and intensive field surveys to create a detailed thematic vegetation classification for exploring ecological relationships between the palila and its environment. Our classification revealed the effects of feral ungulates in PCH, populations of which have been culled annually since 1980, and provided a means for predicting changes in forest structure and composition as culling efforts continue. We expect that the most dramatic change may occur in the mixed shrub community where māmane regeneration was very high. The density of māmane is likely to continue to increase if feral sheep (*Ovis aries*), European mouflon sheep (*O. gmelini musimon*), and their hybrids are eliminated or maintained at very low levels. Recovery of this habitat would provide a habitat corridor between woodland on the western and northern slopes of Mauna Kea. Māmane regeneration was also high in bare regions, where long-term browsing has been especially severe at the tree line. Regeneration near tree line was mostly confined to rocky ridges and was lacking in large expanses of cinder and ash, possibly because rocky cracks create microclimates where young trees can become established. In addition to the recovery of māmane-dominated woodlands, māmane will likely also increase in the mixed woodlands at lower elevations due to a higher rate of regeneration following culling of sheep.

Some areas of heavily browsed habitat were shown to be recovering slowly, if at all. Tree mortality was high and māmane regeneration was poor in grassy māmane-dominated woodland. In the pasture grasslands that have a recent history of cattle grazing, standing dead trees were more common than live ones and regeneration was extremely low.

We identified 180 plant species in our extensive survey of vegetation in PCH. Over two-thirds of the species were alien, including several species that had not been recorded previously on Hawai'i Island. Although most herbaceous and grass species were alien, most of the trees, shrubs, and ferns were native.

Although trees were widely distributed in PCH, tree cover was generally patchy and sparse except on the southwestern slope, where naio and māmane were relatively abundant and where palila were concentrated. Māmane was the most broadly distributed tree species, but māmane cover was likely too low to support palila in most areas around Mauna Kea. Nevertheless, a small but relatively dense patch of māmane forest on the northern slope was extensively used by palila translocated there.

Māmane trees in PCH were small, averaging 3.7 m in height. Nearly two-thirds of māmane trees were less than 4 m tall, indicating widespread regeneration within the preceding 25 years, based on growth models. Although māmane saplings (less than 2 m height) were found in 91% of survey plots, only 38% of plots contained densities equivalent to at least one sapling per 100 m². These results suggest that the condition of the forest is improving due to the annual culling of ungulates, but habitat recovery has not been sufficient to prevent steep declines in palila numbers during drought.

We found evidence of sheep and other ungulates on a majority of plots on the southwestern slope, indicating their attraction to māmane as a food source and indicating that māmane will increase once browsing is eliminated. We encountered many dead and dying māmane trees on vegetation plots throughout PCH. We did not identify causes of mortality, but contributing factors likely include fungal root rot, browsing, alien weeds, and drought.

Surveys on Pu'u Mali and Ka'ohe, lands that were removed from cattle grazing as part of the mitigation for realigning Saddle Road through PCH, established the baseline conditions of the vegetation. Five individuals of *Bidens campylotheca campylotheca*, a species of concern, were discovered on the Pu'u Mali parcel. The five tree species that were recorded at Pu'u Mali represent the majority of the native tree species expected in this region. This suggests that existing seeds and scattered trees could promote forest regeneration at a local level, if not at a landscape scale. Individual trees were concentrated in localized patches within the 'a'ā flow at Pu'u Mali, whereas Ka'ohe supported fewer tree species and they were generally more scattered and less abundant. Tree density was lowest on a portion of Ka'ohe, suggesting that planting and other management will be needed to accelerate habitat restoration.

Invasive plants may impede native species recovery in both mitigation parcels. Although both areas have been invaded or are imminently threatened by relatively few habitat-modifying weeds, Kikuyu grass (*Cenchrus clandestinus*) is of particular concern because it forms large, nearly impenetrable mats of vegetation that hinder germination of native shrubs and trees. Other alien species, such as cape ivy (*Delairea odorata*), gorse (*Ulex europaeus*), and banana poka (*Passiflora tarminiana*), which are common on Mauna Kea in places outside of PCH, could also hinder restoration efforts if they are allowed to become established or spread.

We surveyed PCH for 15 species of invasive weeds representing the greatest potential for increasing fire hazard, competing with native plants, and facilitating pest arthropods. Nevertheless, the effects of many of these weeds on regional hydrological processes, nutrient cycling, and other ecosystem processes are not well known. In addition to target species, we noted localized populations of other weeds that posed potential threats and warranted monitoring. Despite a large source population of fountain grass (*Cenchrus setaceus*) on the lower southern and southwestern slopes of Mauna Kea, generally below PCH, the abundance of this serious fire hazard increased only slightly in the 20 years following earlier surveys. Fountain grass was found mostly in small, disturbed sites, suggesting that native vegetation may replace it once disturbance from ungulates has been eliminated. Cape ivy increased modestly in the mixed naio-māmane forest, although it remained concentrated on the lower western slope of Mauna Kea. Invading PCH much more rapidly was fireweed (*Senecio madagascariensis*), which by 2007 occupied 86% of stations ($n = 381$) and had spread to tree line around Mauna Kea.

The threat of fire in PCH is a major concern for palila recovery due to the dramatic spread of fireweed and the longstanding, dense beds of fine fuels formed by invasive grasses, including the six species targeted in our survey. Although widespread on Mauna Kea, orchard grass

(*Dactylis glomerata*), velvet grass (*Holcus lanatus*), sweet vernal grass (*Anthoxanthum odoratum*), and Kentucky blue grass (*Poa pratensis*) were rare or absent on the southwestern slope, which was largely dominated by dense naio stands at higher elevations and naio-`a`ali`i (*Dodonaea viscosa*) shrubland at lower elevations. Nevertheless, fountain grass was widespread on the southwestern slope, indicating the potential for the creation of a grass/fire cycle that would be difficult to break. The native bunchgrass, *Eragrostis atropioides*, also was common on the arid southwestern slope and flourished after wildfires in 1991 and 1995 that started along the road skirting the lower edge of the forest. Grass density, and therefore fire hazard, was high over several extensive areas of the mountain: 1) middle elevations on the western and eastern slopes where orchard grass, velvet grass, sweet vernal grass, and Kentucky blue grass dominate, 2) lower elevations of the western slope where Natal redbtop (*Melinis repens*), perennial ryegrass (*Lolium perenne*), and smutgrass (*Sporobolus africanus*) were common, and 3) low elevations on the southern slope close to Mauna Kea State Park, where needlegrass (*Stipa cernua*), purple veldtgrass (*Ehrharta calycina*), and fountain grass were abundant. Although gorse was concentrated in alien-dominated pasture below PCH on the eastern slope, it has the potential to spread higher and into PCH, increasing the risk of fire.

To evaluate weed threats to PCH from areas immediately below, we surveyed the lower slopes of southwestern Mauna Kea in 1999. We searched for three particularly noxious weed species: fountain grass, cape ivy, and prickly pear cactus (*Opuntia ficus-indica*).

Fountain grass was recorded at about one-third of all stations, but it was distributed patchily and in low densities (often as individuals or small clumps). Most plants were associated with disturbance or gullies that could act as dispersal corridors. Our survey revealed isolated patches of cape ivy outside the main concentration on the western slope. One patch of cape ivy was growing in a very dry `a`ali`i shrubland with scattered short trees, suggesting that the potential for invasion in many parts of Mauna Kea is high. Although we encountered only one prickly pear cactus during our survey, small patches were identified on Pu`u Ahumoa on the western slope and upslope of Bradshaw Airfield within Pōhakuloa Training Area on the southern slope.

We investigated the effects of the 1999 Pu`u Loa fire on the subalpine vegetation in wooded pastureland and adjacent ungrazed forest on the eastern slope of Mauna Kea. Ten months after the fire, we inspected all trees within the burn to evaluate mortality and regeneration of ground and epicormic (growing from underneath the bark of a trunk, stem, or branch) sprouts. These data were compared to trees within an adjacent unburned control area 20–100 m outside the edge of the burn. We also assessed vegetation structure and composition within plots. Alien grass species were more common in burned plots than they were in forest control plots, suggesting that fine fuel loading increases following fire. The forested area also harbored species that did not recover from the fire, supporting the idea that fire is rare in this and other native communities in Hawai`i. The fire burned with its highest intensity within the forested area, where the density of māmane and fine grass fuels were higher. Grazing by cattle reduced the grass biomass in the pasture, which resulted in a short sward and lower fire intensity.

Although two-thirds of the trees in the burned forest were defoliated, many of these were producing suckers close to their bases. This trend was even more dramatic in the pasture, where a tenfold increase in suckers was observed in the burned area compared to control plots. In addition, the proportion of ground suckers near live trees was twice as high for scorched trees as it was for unburned trees in the pasture, suggesting that low intensity fire can stimulate root suckers. Nevertheless, at high intensities, as was observed in the forest, fire

reduced the amount of māmane regeneration. Māmane saplings were more abundant in the burned pasture plots compared to the unburned plots. This may have resulted from decreased competition from the temporary reduction of grass and increased input of nutrients from burned plants rather than the direct effects of heat on seed germination. Māmane trees showed little phenological response to fire, suggesting that they did not evolve in a community shaped by frequent fires.

Predator Ecology and Management

We conducted studies to determine the behavior, ecology, and impact of introduced mammalian predators on palila. We also developed methods for controlling predators. We found feral cats to be very active during daylight hours, but their activity peaked at night between 2000–2200 hours, which may have been the most favorable time to forage for rats and roosting birds. The period of lowest cat activity (0400–0600 hours) coincided with the lowest diurnal temperatures at the study site. Radio signals often became weak or non-receivable during this period, suggesting that cats may have been entering dens or sheltered areas to avoid colder temperatures. The mongoose (*Herpestes auropunctatus*) was diurnal, as has been reported in other studies. A mongoose that we tracked occupied a large home range (at least 1 km²), which was consistent with home range sizes reported by others.

We discovered that rats were active from sunset to about 0300 hours. They spent most of their time foraging on naio fruit in the upper canopy of trees. We located three rat dens in naio trees, two in māmane, and another underneath a pile of lava rocks. A female rat occupied a home range of 1,179 m². When she was re-tagged seven weeks later, she had moved to a new territory 2,500 m away and occupied a home range of about 650 m². A male rat occupied a home range of 2,772 m².

Mean home ranges of feral cats on Mauna Kea were the largest reported among seven other studies from the Pacific region for females (772 ha) and the second largest for males (1,418 ha). We found that home ranges of male feral cats on Mauna Kea were 60% larger and those of females were 71% larger than those reported from Hakalau Forest National Wildlife Refuge, which is located on the eastern slope of Mauna Kea approximately 25 km in distance from our study site.

We found some evidence that the spatial arrangement and low density of feral cats on Mauna Kea was tied to social organization. There were strong differences between sexes in home range size, which we attributed primarily to mate-seeking behavior in males and denning behavior in females. Although females on Mauna Kea occupied large areas relative to other study locations, their overall mean home ranges were only 54% as large as males. Nevertheless, their core activity areas were larger than those of males indicating they use smaller areas more intensively while males use larger areas more extensively. Male cat home ranges overlapped extensively. There was no overall seasonal pattern to home range overlap, although the range of one male extended to lower elevation primarily during March–August 2001 and then was subsequently centered in higher elevations. Evidence for territorial encounters among males on Mauna Kea comes from the prevalence of feline immunodeficiency virus (FIV), which is primarily transmitted by biting and scratching. While 17% of 39 males from Mauna Kea tested positive for FIV, all 29 females were negative. Overall female home ranges on Mauna Kea overlapped only slightly, and core activity areas did not overlap.

We documented average daily movements of about 82 m/day and some much greater maximum movements. Because mean daily movements on Mauna Kea did not differ between

sexes, males apparently did not always return to the same location on a daily basis, given their larger home ranges, whereas females may have been tied to a central location, such as a den. Trap spacing should account for minimum daily movements and differences between sexes in home range. The radius of a circular area equivalent to the home range of female feral cats on Mauna Kea is 1,568 m and males is 2,125 m. Cats may be expected to encounter traps when traps are spaced at shorter distances, but daily movements may be used to guide minimum spacing between transects during short-term (two-to-three-day) trapping sessions. Most subjects moved more than 100 m per day. The implications of large home ranges in male cats are that large trapping areas are needed to confine immigration to buffer zones on the perimeter of endangered species habitat in this environment in Hawai'i.

We identified bird remains in 79% of cat and 47% of mongoose stomachs, indicating a higher incidence of bird predation compared to other studies on Mauna Kea and elsewhere on Hawai'i Island. Insects and rodents also were eaten. Much of the discrepancy in reported occurrences of prey types probably arises from differences in methodology. We expect that examining stomach contents produces more identifiable remains than examining scat, in which contents pass through the entire digestive system. We could often distinguish between gallinaceous and passerine bird fragments in predator stomachs, but we could not distinguish between native and alien passerine fragments. Nevertheless, our findings indicate that the exceptionally high rate of predation on passerine birds by feral cats in PCH poses a significant threat to palila.

We conducted 10 rodent surveys for one month biannually during winter (January and February) and summer (June and July), during 2000–2005 on the western slope of Mauna Kea to better understand the threats posed to palila and other native birds. We also examined rodent habitat use patterns, morphology, age, sex ratios, and pregnancy rates during selected surveys. We determined rodent arboreal activity in a single, separate, and independent trapping session.

Mice inhabited the māmane, mixed, and naio forests in similar abundances, but rarely utilized pasture, where the grass cover was continuous. The scarcity of mice in the pasture may have been due to increased exposure to predators or to the scarcity of grass seed resulting from Kikuyu grass, a species that spreads vegetatively, dominating the pasture. Cattle grazing may also have kept grass seed availability low. Mouse abundance did not vary significantly in relation to elevation on the western slope. There was a positive, but non-significant, relationship between mouse abundance and six-month median precipitation.

The changes in mouse abundance over all 10 surveys did not seem directly dependent on season (winter or summer), but there might have been a subtle non-seasonal population cycle. Mouse and rat capture rates were high throughout the winter 2005 survey, indicating an intense population irruption.

The scarcity of rats on the western slope was consistent with results of previous studies and may be attributable to factors associated with high elevation, such as low temperatures or lack of water or possibly depredation by carnivores. Although we were unable to determine the relationship of rats to habitat type due to low capture rates, the frequency with which they were trapped near 'iliahi (*Santalum paniculatum*) trees suggests some level of attraction. Our finding that both mice and rats exhibit arboreal activity agrees with results from other studies.

To help identify mammalian predators of palila whose carcasses were found in the wild, we initiated a study to help recognize diagnostic clues left by different species. Our method was to

observe predators feeding on the carcass of a small bird in a controlled setting to determine whether the predator could be identified solely on clues observed on the carcass. We observed predator feeding habits, videotaped their behavior, and described and cataloged the remains. We used this information to develop methods and skills for identifying species responsible for nest destruction and bird mortality.

Using our methods, the remains of dead palila sometimes provided clues to the identity of the predator that killed them. Nevertheless, scavengers usually could not be distinguished from predators. Scat, hair, and tracks provided important evidence in determining predator and scavenger identity.

We monitored nests of all bird species on two 500 x 500 m grids in māmane forest and mixed māmane-naio forest on the western slope of Mauna Kea in 1999 to determine the impact of introduced mammalian predators. Predation at nests on both study grids occurred at similarly high levels (56.2% in māmane and 57.1% in mixed forest). However, fledgling production was higher on the māmane grid, where 43.8% of nests fledged at least one chick, than on the mixed forest grid, where 21.4% of nests fledged a chick. Three nests in the mixed forest grid were abandoned possibly due to prolonged rain and cold weather in late February 1999.

Our failure to capture rats in 2,360 trap-nights on the two study grids supports other findings of low rat density on the western slope. The lack of trapping success could reflect seasonal or annual variation in rat population levels or a decline in rat densities due to drought conditions that prevailed during the study.

We tested techniques for removing predators on the northern and western slopes of Mauna Kea during 1998–2005. Methods for reducing feral cat and mongoose numbers focused on the effectiveness of different spatial and temporal distributions of live traps during nine sessions. Research into reducing rat threats consisted of varying the placement and duration of poison baits. The ultimate response variable of interest for both rats and carnivores was the effect of different treatments on the depredation of palila. Nevertheless, due to personnel limitations, we used predator abundance as a proxy for depredation rate.

Overall capture rates for feral cats during our study were similar to capture rates recorded during other studies on Mauna Kea, although our capture rates ranged between 0.64–7.42 per session. The wide range in capture rates may partly reflect environmental variability in subalpine Mauna Kea over six to eight years of trapping effort. Additionally, changes in the cat population through removal (by trapping), reproduction, and environmental factors such as prey availability, may have affected capture rates among sessions.

We found that controlling the feral cat population on Mauna Kea may not require continual, high-intensity trapping as we found that many cats were removed during the initial 1,000 trap-nights. Feral cat capture rates declined significantly during some sessions. After decreasing, the capture rates during the longer trapping sessions stabilized at a lower level, suggesting continued low-level immigration from surrounding areas after the removal of all resident cats. Nevertheless, cat capture rates increased significantly in one session. The beginning of another trapping session coincided with a rodent irruption on Mauna Kea, and the overabundance of prey may have made our baits less attractive. Moreover, the abundance of food may have increased cat survival, reproduction, and immigration, potentially increasing the number of cats available to be trapped later in the session. Interruptions between and during our trapping

sessions suggest that breaks of up to two months did not affect the subsequent cat capture rate. On the other hand, long breaks in trapping were followed by higher capture rates.

Carnivore trap arrays were spaced according to cat movement data, and our results suggest that closer trap spacing might have been more effective for mongoose control. In addition, very young mongooses were able to escape from our live traps. The lack of mongoose captures where diphacinone bait was applied to control rodents suggested that poison bait was effective for mongoose management.

Rats and mice entered diphacinone bait boxes and consumed bait. Mice depleted diphacinone baits quickly, making it necessary to continually stock bait stations with diphacinone to remove rats. Although we did not evaluate changes in rodent populations before and after distributing diphacinone, we observed dead mice at the bait stations.

Palila experienced less predation when measures were taken to reduce populations of small introduced mammals. During the 1999–2001 palila nesting seasons, when there was no predator control on the western slope, feral cats depredated 8–11% of active nests annually. In contrast, we observed no nest predation by cats during the 2002 breeding season, when we trapped intensively. Additionally, we did not control small mammal numbers during the second translocation trial, and we implicated rats in the deaths of two palila and the deaths or scavenging of three others. Predation decreased markedly during the third, fourth, and fifth translocation trials.

ACKNOWLEDGEMENTS

This research was made possible in part thanks to support from the U.S. Army Garrison, Hawai'i, under the administration of the U.S. Army Corps of Engineers through 2001, the Federal Highway Administration since 2002, and the U.S. Geological Survey (USGS) Wildlife Program and Invasive Species Program throughout the project.

We thank the dozens of staff (see Appendix II of Introduction) and hundreds of local, national, and international research interns who provided invaluable assistance in gathering and processing data. The project was successful because of their skillful and dedicated efforts.

Thierry Work (DVM, USGS, National Wildlife Health Center, Hawai'i Field Station, Honolulu) and Greg Massey (DVM/DABVP, School of Veterinary Medicine, University of California, Davis) conducted necropsies of palila that died. Dr. Massey also provided extensive training and advice on avian first-aid and health. The San Diego Zoological Institute for Conservation Research and The Peregrine Fund maintained and bred palila in captivity at Keauhou Bird Conservation Center, Volcano, Hawai'i. Hawai'i Division of Forestry and Wildlife (DOFAW) removed predators from the western slope of Mauna Kea during 1996. Francis Benevides (FB Engineering, Hilo) designed our remote video camera surveillance system and provided other technical assistance and ideas. Greg Brenner (Pacific Cooperative Studies Unit [PCSU], University of Hawai'i at Mānoa) provided initial guidance with studies of *Cydia* and their parasitoids and assisted with the design of caterpillar surveys. The late Jack Beardsley (Bishop Museum, Honolulu) and Bernarr Kumashiro (Hawai'i State Department of Agriculture, Honolulu) identified species of parasitoid wasps. Linda Pratt (Emeritus, USGS, Pacific Island Ecosystems Research Center [PIERC]), Thomas Belfield (Hawai'i Volcanoes National Park), and Rick Warshauer (PCSU) helped to identify plant species. Jim Jacobi (USGS, PIERC) provided technical and other assistance to map the area burned by the Pu'u Loa fire.

Special thanks go to Reggie David of Rana Biological Consulting, Inc., David Gedeon, Jodi Chew, Michael Vanderhoof, and Michael Will of Federal Highway Administration, Beth Miura (U.S. Army Corps of Engineers), and Alvin Char (U.S. Army Garrison, Hawai'i) for administrative assistance and guidance. Administrative assistance was also provided by Sharon Ziegler-Chong (Hawai'i Cooperative Studies Unit [HCSU], University of Hawai'i, Hilo), David Duffy (PCSU), and William Steiner, David Helweg, Dirk Van Dyk, Loyal Mehrhoff, Gordon Tribble, and Debbie Cobb (all USGS, PIERC). We are especially thankful to Diane Butler (HCSU), Helene Love (USGS, PIERC), and Lorna Young (USGS, PIERC) for their administrative assistance at Kīlauea Field Station. We thank Nick Shema (USGS, PIERC) for providing safety training, construction, and logistical support. U.S. Fish & Wildlife Service and DOFAW provided permits and other support. For access to public and private lands, we thank representatives of KK Ranch, Parker Ranch, Hawai'i DOFAW, and Pōhakuloa Training Area.

We are grateful to Michelle Wilcox and Sarah Nash (HCSU) for assistance in editing and formatting the report. We are profoundly thankful to the reviewers who provided insightful, thoughtful comments and suggestions to improve the report: Sheila Conant for her review of the entire report; Jay Nelson for his review of two sections; and David Foote, Eben Paxton, Linda Pratt, and George Wallace for their reviews of individual sections.

IMPLICATIONS OF RESEARCH FOR PALILA RESTORATION

Paul C. Banko, Chris Farmer

Introduction

The history of research into the conservation biology of the endangered palila (*Loxioides bailleui*) extends over four decades with many biologists dedicating years of effort to understanding this species. As a result, more is known about the palila's ecology and its conservation needs than any other Hawaiian bird. It is especially important, therefore, to apply this rich and extensive ecological knowledge of the species to its recovery. In the following, we highlight information that is most relevant to palila recovery.

Population Reintroduction and Restoration

Evaluating Sites for Reintroduction

As indicated in the most recent recovery plan for Hawaiian forest birds (U.S. Fish and Wildlife Service 2006), palila are at risk of extinction primarily because they are concentrated in a small area of māmane (*Sophora chrysophylla*) forest on the western slope of Mauna Kea. The plan identified habitat degradation due to browsing by introduced ungulates and the high risk of fire as key factors threatening the palila. In addition to protecting the existing population, the plan highlighted the need to reestablish palila in multiple locations within its historical range. With this goal in mind, we evaluated three sites on Mauna Kea and one site on Mauna Loa for their potential to support an experimental reintroduction of palila.

Our surveys revealed extensive habitat damage by browsing ungulates and the widespread distribution of fire-promoting alien grasses and other fine fuels. Nevertheless, we also discovered that māmane has been recovering to a limited degree on Mauna Kea due to annual culling of ungulate populations by public hunting and aerial shooting since 1980. On Mauna Loa at Kīpuka 'Alalā in Pōhakuloa Training Area, we found little recruitment of māmane, although naio (*Myoporum sandwicense*) and 'a'ali'i (*Dodonaea viscosa*) were thriving despite the presence of ungulates. Casual inspection of the Kīpuka 'Alalā study site indicated substantial māmane regeneration following the removal of ungulates, suggesting that habitat conditions might eventually improve sufficiently to allow the reintroduction of palila.

Māmane food resources were available throughout the year where the habitat was distributed along a broad elevation gradient. Moreover, the large expanse of māmane forest extending along a broad elevation gradient on the western slope of Mauna Kea was a key factor contributing to the concentration of palila there (Scott *et al.* 1984, Banko *et al.* 2002a). Palila populations can be reestablished more readily where there is high potential for expanding māmane forest size, density, and altitudinal range following the removal of browsing ungulates.

Our surveys indicated that the southern slope of Mauna Kea had high potential for supporting palila due to its relatively high density of māmane trees and saplings. The southern slope and the adjacent Pōhakuloa Flats area together composed a large expanse of forest and supported substantial gradients of elevation and rainfall, which potentially would provide food to palila throughout the year. Nevertheless, ongoing military activity and highway development could impede palila recovery in the southern portion of Palila Critical Habitat (PCH), where palila have become extremely rare.

Alternatively, we found that the northern slope offered a suitable and immediate option for reintroducing palila. The main attraction of the northern slope was the potential, now underway, for eliminating ungulates and restoring māmane forests on pasturelands below PCH. Extending the gradient of elevation over which palila can track māmane pods while improving habitat quality throughout the area would provide support for a critical second population in the event of a catastrophe within the core habitat of the palila on the western slope.

Despite the limited range of elevation and size of the forest at Kīpuka `Alalā (1200 ha), habitat restoration there could be accelerated by planting seedlings or scattering seeds of māmane, as is being done on the northern slope of Mauna Kea by the Mauna Kea Forest Restoration Project (R. Stephens, personal communication) and in montane habitat on Mauna Loa in Hawai'i Volcanoes National Park (S. McDaniel, personal communication). By itself, Kīpuka `Alalā may never support many palila without intensive management, but it could play an important role in recovery if palila are eventually reintroduced to the western slope of Mauna Loa (Banko *et al.* 2009).

Translocating Wild Palila

From our six translocation trials, we developed methods that resulted in the high survival of birds and the establishment of a small, breeding colony. The highlight of the project was the production of many first-generation palila and at least one second-generation palila at the site. Another milestone was discovering that some translocated birds periodically moved between the reintroduction site on the northern slope of Mauna Kea and the source site on the western slope, and unbanded birds regularly were detected on the northern slope. Movement between slopes would be an important means of connecting the populations and might eventually lead to palila moving between habitats according to the condition of the vegetation, availability of food, and other environmental factors.

The greatest problem we encountered was the low persistence rate of birds at the reintroduction site. Although some birds remained for over a year, many returned to their point of origin on the western slope within two months. We were unable to predict which individuals were likely to remain and breed in the reintroduction area. The return of translocated birds to the source area was partially offset by palila that moved between the northern and western slopes.

Ultimately, the reintroduced colony disappeared due to severe drought conditions and the lack of sufficient resources for augmenting the colony with additional birds. We were unable to determine whether birds that had bred on the northern slope eventually returned to the western slope or died. Palila that were fledged on the northern slope generally remained there longer than their parents, based on sightings of birds in the years following the last translocation in 2006. Severe drought conditions prevailed during most of the study, and its effect on the translocation results are not clear. Nevertheless, the effects of drought on māmane trees seemed somewhat less severe on the northern slope than they were on the western slope, suggesting that additional translocation efforts coupled with increased habitat restoration could result in a more enduring population.

Despite the relatively high potential of the northern slope for reestablishing a palila population, patterns of habitat use by the translocated birds revealed the marginal value of large areas of habitat where māmane cover was sparse. Translocated birds concentrated in two habitat patches where the size and density of māmane trees were highest and spent relatively little time elsewhere. Therefore, habitat restoration to improve the carrying capacity for palila is

necessary for reestablishing a population on the northern slope. The most effective methods of promoting habitat recovery are to remove ungulates permanently from PCH and increase māmane cover through planting and other means where natural regeneration is poor.

Protecting translocated palila from predators was important to reduce mortality in the reintroduction area. Palila were selective about the location and species of tree they used for roosting after being translocated. This, in addition to their initial lack of familiarity with the new area, may have increased their vulnerability to predation from introduced mammals and native raptors. Predation of even a few individuals would have a disproportional impact on the overall survival and productivity of a small population.

Harvesting Wild Eggs and Supplementing Food at Nests

A potential tool for bolstering wild populations is rear-and-release, which involves harvesting wild eggs for propagation in captivity and releasing the young birds to the wild (Lieberman and Kuehler 2009). This method of producing birds to augment or reintroduce populations in the wild might be feasible, even if with substantial effort, because wild palila nests are not particularly cryptic or difficult to access compared with nests in taller, denser forests. Moreover, we found that palila readily re-nested after their eggs were removed for artificial incubation. Nevertheless, in years of severe drought, which have occurred frequently in recent years, relatively few palila nested due to the scarcity of māmane pods (Banko *et al.* 2013). Although rear-and-release might be practical only in years when conditions were favorable for breeding by wild pairs, our work suggests it may be ineffective to release captive-reared birds or translocate wild birds under harsh environmental conditions, when poor survival would be expected.

We attempted to supplement the diet of wild palila nestlings but found it to be logistically impractical. Opportunities to directly supplement the diet of nestlings were infrequent because females were away from the nest on only a few occasions each hour, and recesses generally lasted fewer than 10 minutes. We also failed to attract nesting adults to supplemental foods. Pairs ignored food items placed near the nest, probably because they seldom or never foraged in the nest tree during chick rearing. Placing supplemental food away from nest trees in areas where adults frequently forage may yield more promising results. Supplemental feeding trials might also be more productive in naio-dominant forest, where māmane food resources are less available. Given that much more work is needed, supplemental feeding as a management tool for sustaining palila during nesting or times of food shortage does not seem promising in the near-term. Before investing more effort in developing supplemental feeding techniques, it would be helpful to evaluate the effects of diet augmentation and the effect of different diets on the growth of palila nestlings. Nevertheless, improving habitat quality throughout PCH would undoubtedly increase palila survival and reproduction.

Release and Monitoring of Captive-Reared Palila

The staff at Keauhou Bird Conservation Center was successful in propagating and releasing a limited number of palila on the northern slope of Mauna Kea (Lieberman and Kuehler 2009). Although many birds disappeared within two months, one captive-reared male survived on the northern slope of Mauna Kea for seven years. Captive-reared females were not known to have produced chicks, but at least two males nested successfully with translocated females or their progeny.

We noticed differences in foraging behavior and song structure between some captive-reared and wild palila. Measures to reduce behavioral differences through conditioning or parent-

rearing might result in increased survival and breeding after release to the wild. Even so, difficulties in producing larger numbers of palila in captivity will need to be overcome before captive propagation is likely to play a significant role in reintroducing palila to former range or bolstering the existing population. Neither wild birds that were brought into captivity nor birds that were reared in captivity from wild-harvested eggs have bred readily.

Demography and Breeding Ecology

Population Trends and Response to Environmental Factors

Annual population surveys revealed that the palila population declined significantly after 2003, primarily due to severe drought conditions and continued habitat degradation by browsing ungulates (Banko *et al.* 2013). Between 1998 and 2012, the population estimate reached a maximum of 6,463 in 2003 and a minimum of 1,495 in 2011 for an average loss of over 500 birds annually. The rate of decline was 57% over the 15-year period (Camp and Banko 2012). During this time, the range of the palila also contracted, increasing the vulnerability of the species to environmental disturbance and invasive species threats (Banko *et al.* 2013).

Drought was largely responsible for the decline in palila numbers and range because of its strong effect on māmane pod production, which in turn affects palila survival and reproduction (Banko *et al.* 2013). Despite the effects of drought on pod production, habitat carrying capacity could be substantially improved for palila by eliminating browsing ungulates, planting māmane and other native trees and shrubs in areas with sparse regeneration, and possibly reducing the cover of invasive grasses and other weeds that may compete with native plants (Banko *et al.* 2013).

Given the magnitude of the palila's decline, it is important to continue to improve the annual population survey. One method for improving the precision of the annual counts is to sample the survey stations more than once, thereby increasing the numbers of detections, reducing the total uncertainty in the abundance estimates, and improving the overall power to detect population changes (Camp and Banko 2012). In addition, repeat surveys allow for state-space modeling, which can be used to identify observation and process error in the population estimates. Process error is the inherent uncertainty in estimating the population due to temporal and spatial variability and natural population fluctuations. Observation error is associated with sampling, detecting birds, and population modeling. Reducing observation error will allow a more precise accounting of the process error (noise) in the population estimates.

Sex Ratio

Both genetic (PCR) and plumage techniques for sexing palila indicated a significant difference in sex ratios among age classes. There was a strong tendency towards males in the adult age class (after second year or ASY) where males outnumbered females by 50% or more in both sample types. The sex ratio changed to a male bias after individuals began breeding. Both methods of sex determination indicated parallel shifts in sex ratios from hatch year (HY; tendency towards more males) to second year (SY; female bias) to ASY (male bias) as Lindsey *et al.* (1995) reported. We found that sexing SY birds using the plumage-based technique alone was subject to a high error rate; but even when corrected the results were female-biased.

Determining the sex ratio and how it may change between age classes is important for calculating survival rates, conducting population viability analyses, and planning conservation strategies for endangered species. As the palila population declines, the effects of the male-

biased sex ratio may become increasingly problematic due to increased demographic stochasticity and competition for mates.

Disease

Avian malaria is unlikely to affect the existing palila population or future reintroduced populations in subalpine Mauna Kea, where mosquitoes and other vectors are absent or rare (Banko *et al.* 2009). We rarely observed lesions caused by avian pox virus in palila, although lesions were encountered more frequently in bird species that seasonally vacated the lower-elevation, wetter forests of windward Mauna Kea to feed on māmane flowers within the palila's range (Hess *et al.* 2001). Despite proximity to pox- and malaria-infected birds, the lack of an effective vector protects the palila in the near-term. Although changes in climate could eventually increase the exposure of palila to disease vectors, the recent trend towards drier conditions in subalpine Mauna Kea (Banko *et al.* 2013) is not likely to favor mosquitoes. Nevertheless, additional screening for avian diseases and vectors is warranted within Pōhakuloa Training Area (see Figure I.1) and other potential reintroduction sites at relatively low elevations. The occurrence of mosquitoes within PCH could be detected and managed with periodic monitoring. The effects of bacterial diseases and other pathogens are of concern to palila management because of their possible implication in the deaths of captive chicks. *Mycoplasma* bacteria have not been cultured from wild palila or other honeycreepers within PCH.

Breeding Demography

Although palila live and breed to at least 17 years of age (Banko *et al.* 2013), we found during 1999–2002 that the mean breeding age varied annually between 4.2 and 6.1 years; almost 20% of nesting adults were older than 6 years, and a few adults older than 10 years were breeding each year. Breeding palila were significantly older than birds not associated with nests, due mainly to a greater proportion of 9–10-year-old birds in the breeding population. Although we did not determine whether older parents had higher fledgling success rates, it is likely that experienced adults formed a larger proportion of the breeding population in years when food availability was marginal than when it was abundant. Increasing the carrying capacity of the habitat should provide younger palila with more opportunities for breeding and breeding activity should increase annually among all pairs.

In agreement with Pratt *et al.* (1997), we found that palila nested in the same general area each year. Assuming that nest location was influenced mainly by the distribution of food or prior nest success, increasing the density of māmane trees around nesting sites might boost the breeding frequency and nesting success of individual pairs. Similarly, enhancing habitat quality where palila nesting density is low should attract new breeding pairs. Although Fancy *et al.* (1993) reported limited dispersal by palila, we found that the nests of some palila were separated by more than 1.7 km from year to year. This suggests that palila should readily colonize restored habitat adjacent to or near their core range.

Genetic studies indicated that males may gain nesting experience by helping at the nests of parents or close relatives (Patch-Highfill 2008), which likely increases nesting success and reduces the overall costs of nesting (Miller 1998). Nest helping by males may increase if the sex ratio becomes increasingly male-biased.

Breeding Phenology, Productivity, and Nesting Success

Palila nesting activity varied considerably in timing and in terms of the number of pairs breeding from year to year, presumably mostly in response to food availability (Pratt *et al.* 1997, Banko

et al. 2002a, Banko *et al.* 2009). We found a positive correlation between the number of active nests during the breeding season and the number of māmane pods available. For example, the number of pods per tree was higher in the spring of 2002 than in the previous three years, which may partly explain the peak of palila numbers in early 2003 (Banko *et al.* 2013). The ability of palila to nest vigorously in some years may help offset drought years with poor productivity (Lindsey *et al.* 1997, Banko *et al.* 2013).

We found that nest density was usually higher in māmane-dominated forest than it was in naio-dominated forest, although the naio habitat encompassed a large area of the western slope and supported many nesting pairs, at least in some years. Māmane-dominant forest was distributed at a higher elevation, making māmane seeds available earlier in the season (Banko *et al.* 2002a). More palila should nest in the lower elevation forest, which is now dominated by naio, as māmane regeneration continues to outpace naio regeneration there (Hess *et al.* 1999), and the trend toward more māmane will accelerate once browsing ungulates have been eliminated. Other measures of improving habitat to encourage nesting in naio-dominated areas would be planting māmane and reducing the cover of invasive grasses and other weeds.

The availability of food during the breeding season may also affect nest success, although further research is needed to understand the underlying mechanisms and interactions among variables. We found that 33–67% of palila nests were successful annually during 1996–2004 (excluding 2001), which was similar to the range (39–55%) reported by Pratt *et al.* (1997) during 1989–1993. Nevertheless, palila nestlings are potentially vulnerable to predators and storms for 21–30 days (van Riper 1980a, Pletschet and Kelly 1990, Banko *et al.* 2002b). Reducing predation increased nesting success. Feral cats (*Felis catus*) were responsible for many nest failures annually (Laut *et al.* 2003, Hess *et al.* 2004), but intensive trapping alleviated the problem. Reducing feral cat populations will be critical to the persistence and growth of small subpopulations of palila, and it could facilitate the spread of larger populations into marginal but recovering habitats. Nevertheless, some nests were depredated by native raptors, specifically pueo (*Asio flammeus sandwichensis*). An investigation of raptor ecology within the range of the palila could help determine their level of impact.

Nest Site Selection

Our model identifying the important vegetation characteristics associated with palila nest success identified the native mint, *Stenogyne microphylla*, as an important factor. The additional foliage of *S. microphylla* may have added important protection to nests, especially when māmane foliage may have been sparse due to drought. Palila also eat the buds, flowers, and young leaves of *S. microphylla*, which may have been important alternate foods in years of low māmane pod production.

Trees selected by palila for nesting during 1999–2004 were larger and taller than those in Pletschet and Kelly's (1990) study, suggesting that palila select larger trees when they are available. Large māmane will become more common on Mauna Kea as the young cohort of trees (Banko *et al.* 2009) continues to grow. To the extent that the growth of young trees is slowed by browsing, there should be faster growth and a greater number of preferred nest sites after ungulates are eliminated from PCH.

Palila nested primarily in māmane trees, but about 10% of nests were placed in other trees or shrubs, and one was placed in a grass clump. This variety of nesting sites suggests that palila may have used a much wider range of nesting sites before the composition of the forest was altered by ungulate browsing. Rats (*Rattus rattus*) might also affect the range of nest sites. For

example, we never found a nest in `iliahi (*Santalum paniculatum*), which may be a species preferred by rats for foraging. Additionally, the amount of canopy overlap with neighboring trees was negatively associated with nest success, possibly because branches of neighboring trees increase the number of routes available to nest predators, such as rats and cats. Even so, we found that nest success also decreased as distance to nearest neighbor trees increased, suggesting that adjacent trees can provide additional cover from adverse weather and may help hide nests from aerial predators, such as owls. These results contrast with Pletschet and Kelly (1990), who found that nest trees isolated from neighboring trees proved to be more successful. The optimal amount of foliage overlap may change between years, depending on the different trade-off between cover and predation risk in any particular year. Our results suggest that reducing the risk of predation would result in palila nesting more frequently in denser tree cover, and tree cover will increase after browsers are eliminated (Scowcroft and Conrad 1988, 1992; Hess *et al.* 1999; Reddy *et al.* 2012).

Behavior at Nests

Only females incubated eggs and brooded nestlings. During the pre-fledgling stages, female palila were most attentive during the egg stage, presumably due to the embryo's greater sensitivity to changes in temperature than nestlings and the male's ability to provision the female more frequently before eggs hatch (Laut *et al.* 2003). Nest attendance decreased during the nestling period with break length increasing greatly over time as chicks became more covered with feathers and capable of thermoregulation (van Riper 1980a). We observed no evidence of heat stress in the behavior of females or nestlings. The need to simultaneously brood chicks and supply food explains why females recessed more frequently but for shorter periods during the early nestling period.

In our study, the average number of adult feeding visits did not change as nestlings aged, but Pletschet and Kelly (1990) reported that rates of feeding decreased later in the nestling stage. Our data were collected continuously and were less likely than theirs to misinterpret nest visits as feeding events. The growth rate of palila nestlings is slower than that for passerines of similar mass, which is probably due to their low rate of provisioning, specialized diet, and evolutionarily low risk of predation (van Riper 1980a, Laut *et al.* 2003, Banko and Banko 2009).

The long nesting period of palila makes them especially vulnerable to introduced mammalian predators. Predator control is important for palila recovery. Nest monitoring can be an effective method of evaluating predator removal programs. Video surveillance can identify predators at nests as well as document other factors contributing to nest failure.

Habitat Use and Food Ecology

Habitat Use, Home Range, and Movements

Understanding how palila interact with their habitat is critical to palila recovery. Although we found no significant differences between the home range sizes of translocated and non-translocated birds, translocated birds' daily movements were smaller than non-translocated birds. This suggests that there are differences between the quantity or quality of habitats on the northern and western slopes of Mauna Kea that influence palila habitat use. Mature māmane stands and mixed māmane-naio woodlands were less abundant on the northern slope, possibly influencing the persistence time of translocated palila.

We determined that the habitat selected for nighttime roost sites differed from that of daytime use areas. Mixed māmane-naio woodlands were important to palila for night roosting, probably

because the dense canopy provided abundant cover. Maintaining sufficient night roosting cover could improve the success of translocations and releases of captive-reared birds.

Previously, palila were not known to move far around Mauna Kea (Banko *et al.* 2002b), but we found that palila were more mobile than previously suspected. We observed that translocated palila travelled between the northern and western slopes over a distance of up to 16 km. Nevertheless, radio-tagged, commuting palila were not detected between the two slopes, suggesting that palila moved rapidly and without using the habitat between the slopes. Restoring habitat between the two slopes might encourage the movement of palila and connectivity of reintroduced populations around the mountain. We also found that palila translocated to the northern slope used two distinct patches of māmane habitat that were separated by about 3 km of shrub habitat. Focusing resources on restoring and enlarging patches of current habitat might allow palila to persist among multiple sites until habitat can be restored across the wider landscape.

Habitat Use and Foraging Patterns

Palila habitat use is strongly influenced by the distribution and phenology of māmane, the seeds of which constitute the main portion of the diet (Banko *et al.* 2002a,b). Palila consumed reproductive parts and foliage of māmane, but took a higher proportion of māmane pods than other māmane food items relative to their availability. Palila spend proportionally more time in māmane trees and use māmane foods in much greater proportion to their availability compared to other foods. In mixed naio-māmane woodland, where naio density was greater than māmane density, palila spent more than twice as much time in māmane trees. Palila densities were related to pod availability and were higher in māmane woodland than in mixed woodland where māmane density was lower (Hess *et al.* 2001). Palila demonstrated limited ability to exploit alternate food resources, using naio fruits only occasionally and when māmane resources were scarce (Hess *et al.* 2001). Although palila consumed more flowers than pods in mixed woodland, they spent more time foraging on pods than other food items in both woodland types. Caterpillars were also consumed by palila and were taken mainly from inside māmane pods (Banko *et al.* 2002b).

The importance of māmane seeds in relation to movement, breeding, and survival of palila has been well documented (van Riper 1978, 1980a; Scott *et al.* 1984; Fancy *et al.* 1993; Lindsey *et al.* 1995; Hess *et al.* 2001; Banko *et al.* 2009, 2013). The nutritional value of seeds is high (Banko *et al.* 2002c) and contributes the largest proportion of food mass in the diet of palila (Banko *et al.* 2002a). Palila consume flowers and flower buds in the course of searching for pods, but palila densities were not related to flower availability (Hess *et al.* 2001).

This degree of single species dependency on plant foods, primarily seeds, is rare among birds and illustrates unique adaptations that also occurred in other Hawaiian species that are now extinct (Banko and Banko 2009). Palila are morphologically and behaviorally adapted to open unripe māmane pods and consume the seeds, possessing a stout bill for tearing open pods while they grasp them with their feet. Captive-reared palila learned to open māmane pods and consume seeds without the guidance of adult birds, but methods for opening pods and extracting seeds varied somewhat from methods used by wild birds (Frayne 2007), demonstrating an innate ability to recognize and process pods, but also suggesting the benefits of parental teaching (Miller 1998).

There is little information on palila foraging ecology and habitat use from outside of their current range, but historically they likely occurred exclusively in dry forests dominated by

māmane. The contemporary diversity of native trees and shrubs in subalpine Mauna Kea is very low (Hess *et al.* 1999), and there are limited opportunities to observe palila foraging on rare plant resources. Although palila were seldom observed using rare alternative foods, they may have eaten fruits of pilo (*Coprosma montana*), 'iliahi (*Santalum paniculatum*), 'ākala (*Rubus hawaiensis*), and other dry forest trees and shrubs when they were more common and widely distributed. We observed translocated palila eating portions of 'iliahi leaves and feeding on the fruits and young green stems of pilo and the fruits of pohā (*Physalis peruviana*) and 'ākala on the northern slope of Mauna Kea. This behavior was not documented on the western slope probably due to extremely low availability (Hess *et al.* 1999). Increasing the availability of a wide range of native plant species appropriate to subalpine Mauna Kea could help palila survive when māmane resources become scarce.

In areas of mixed woodland where browsing ungulates have been culled, māmane regeneration is much greater than naio, and the woodland community is shifting towards māmane dominance (Hess *et al.* 1999). If māmane density continues to increase in the mixed naio-māmane woodland, palila densities may also increase, although they may ultimately be limited by drought (Banko *et al.* 2013). Restoration of māmane in mixed woodland and other areas, such as the northern and southern slopes of Mauna Kea and areas on the western slope adjacent to the core habitat of the palila population, would increase the overall phenological diversity and the likelihood of birds finding more food patches in years of low food availability (van Riper 1980b, Scott *et al.* 1984, Banko *et al.* 2002a). Habitat restoration would benefit the recovery of the palila and allow this highly specialized Hawaiian honeycreeper to recolonize areas within its former range (Scott *et al.* 1984, 1986; Fancy *et al.* 1993, 1997; Banko *et al.* 2009).

Diet

The palila diet consists overwhelmingly of māmane seeds. We found no difference in the diets of adults between the breeding and non-breeding seasons, when nutritional requirements might be expected to shift to high-protein foods, such as insects. We found that caterpillars were an important supplementary food throughout the year in the diets of adult palila, and they were especially important in the diets of nestlings (Banko *et al.* 2002b). *Cydia* caterpillars, which feed within the seeds of māmane pods where they spend their larval life (Oboyski 2011), were the main insect prey in our samples. To be consumed by foraging birds, caterpillars must be extracted from māmane pods, but they may be found incidentally by birds ripping open pods to access seeds. Hatch-year palila require several months of foraging with adults before their strength, coordination, or possibly other factors are sufficiently developed for obtaining māmane seeds on their own (Miller 1998, Banko *et al.* 2002b).

Understanding the diet composition of different age groups may eventually help explain differential survival rates of palila. Nestling palila consumed *Cydia* caterpillars at the highest rate; *Cydia* fragments were found in the feces of virtually all palila nestlings but in less than two-thirds of adult birds. Nestlings are dependent on adults for all of their food, indicating that adult palila feed caterpillars to their chicks more frequently than they consume this food themselves. Of all age classes, second-year palila consumed *Cydia* least frequently, suggesting that experience is needed to forage effectively for caterpillars within māmane pods. Second-year palila consumed other arthropods about as frequently as did other age groups, suggesting that insects found on foliage and branches were exploited equally by self-sufficient birds of all ages but that differences in *Cydia* consumption were due to search efficiency or experience. Auxiliary foods, such as flower stamens, grass seeds, and arthropods other than *Cydia*

(*Scotorythra* spp.), were found more often in feces of nestlings, suggesting that other age groups relied more on māmane seeds.

Although highly specialized on māmane seeds, our results indicated that palila consume other types of food. This raises the possibility that other native plants and arthropods might help sustain palila when māmane seeds are scarce, if they can be identified and made more available to palila. Identifying alternate foods may be challenging, given the relatively low biodiversity of subalpine Mauna Kea following many decades of habitat destruction by feral ungulates (Scowcroft and Giffin 1983) and invasion of many species that disrupt the food web that sustains palila (Banko *et al.* 2002a). Foods that might have been important historically may now be unavailable to palila in their present range. For example, Perkins (1903) found the stomachs of several palila to be full of *Uresiphita polygonalis virescens* (Crambidae) caterpillars, but *U. polygonalis* is relatively uncommon in PCH today, and we found no indication of them in the diets of birds we sampled. New insights about alternate foods could emerge as the habitat recovers from browsing damage, but increasing the abundance and diversity of some native plant species through strategic planting might also reveal important information.

Food Chemistry

We showed that māmane embryos are extremely well-balanced nutritionally and contain relatively low levels of fiber and high levels of carbohydrate, lipid, and protein (a ratio of about 1:2:2), as well as relatively balanced profiles of essential amino acids and minerals (Banko *et al.* 2002c). Based on our estimate of daily seed consumption, the amount of nitrogen and protein consumed by palila is likely to meet their requirements for daily activities. Although we did not assay minor organic constituents, such as vitamins, māmane embryos seem particularly well-balanced nutritionally, which largely explains the heavy reliance of palila on this food for their daily diet and for rearing offspring. We showed that embryos contained high levels of several different alkaloids, including the highly toxic quinolizidine cytisine, which exceeded 1.5% of seed dry mass. Although the physiological mechanism is unknown, the tolerance of palila to such high levels of alkaloid may be the product of intestinal uptake followed by detoxification in the liver (with consequent effects on relative liver size), non-absorption from the gut (unlikely because quinolizidines are lipophilic under alkaline conditions of the gut and should diffuse into the body), or active export via P-glycoprotein-type ATP-binding cassette (ABC) transporters.

Relative to embryos, seed coats contained higher levels of phenolics and fiber, but lower levels of most major nutrients. Palila reject seed coats when they eat embryos, probably because of their lower overall nutritional value and possible negative influence of phenolic-based secondary metabolites. Alkaloid levels in the two hardened seeds that were collected from brown pods were similar to levels in seeds of green pods that were sampled at the same time in early August. This suggests that palila may reject brown pods more on the basis of their toughness than because of seed toxicity, although we did not analyze the nutritional content of the hardened seeds. Additionally, palila may occasionally open brown pods to extract *Cydia* caterpillars that are sometimes found within. Oboyski (2011) found live mature larvae in hollowed-out, dry mature seeds, while in the laboratory some larvae survived for more than 18 months in drying seeds and emerged as adults shortly after the application of a moist tissue, suggesting the capacity for facultative diapause.

In addition to being found conveniently inside māmane pods, our data suggest that *Cydia* caterpillars are relatively non-toxic sources of lipid, protein, and other nutrients, and thus represent occasional, relatively high-quality resources (Banko *et al.* 2002c). In an evolutionary

context, relatively non-toxic, nutritious foods would be important to the survival and development of birds that were susceptible to alkaloid toxicity. Although *Cydia* larvae have a much higher level of phenolics than do seed embryos, total phenolics in the insects were similar to the level found in seed coats. Assuming that the phenolics within *Cydia* bodies are of māmane origin and have similar internal, anti-nutritional effects when consumed by palila regardless of the source, seed coats are far less nutritious than are *Cydia* larvae. Our data suggest that *Cydia* caterpillars break down the alkaloids in the course of digestion, and we found no evidence that *Cydia* caterpillars sequester significant quantities of these alkaloids in their bodies.

Both palila and *Cydia* feed heavily within certain trees and lightly upon others, and additional research might identify factors that influence the selection of individual māmane by consumers. A hypothesis to explain this is that seeds of heavily exploited individuals are especially rich in certain required nutrients (lipids, carbohydrates, protein, essential amino acids, etc.); alternatively, favored trees may be particularly low in certain toxic secondary metabolites. An additional unanswered question is what environmental factors contribute to variability in seed chemistry? We were unable to relate the pattern of increasing then decreasing levels of cytosine during summer to environmental conditions, although we did not examine rainfall patterns. Similarly, we did not consider whether rainfall or other factors might account for the relatively minor annual variation in the seed chemistry of individual trees. Our analyses of variation in seed alkaloid levels, though limited, suggest that many trees must be sampled to address the question of whether toxic secondary metabolites can account for preferences by palila or *Cydia*.

To the extent that variability in māmane seed chemistry is genetically influenced, there may be value in including seeds of trees that are favored by palila and *Cydia* in reforestation efforts. Limited observations suggest that trees favored by palila in one year are also favored in subsequent years, but this needs to be tested at a larger spatial and temporal scale. If this holds true, seeds could be collected from favored trees and distributed to ensure that they are widely available to their consumers. Additional analysis may also reveal what fraction of available trees is heavily exploited by palila. This information could help managers better understand the habitat requirements of palila. However caution should be exercised, and the costs to māmane and the dry forest of this level of genetic selection should also be considered.

Food Availability: Māmane Phenology and *Cydia* Caterpillars

In the seven-year (1998–2005) study we describe here, māmane pod abundance peaked relatively briefly and at the same time at all elevations. This contrasts with the results of a 10-year study (1992–2001) in which pod abundance varied seasonally with elevation and was high for many months at any given elevation (Banko *et al.* 2002a). These earlier results indicate that trees distributed along a large elevation gradient can provide māmane pods, flowers, and *Cydia* caterpillars throughout the year (Scott *et al.* 1984, Fancy *et al.* 1993, Lindsey *et al.* 1995, Banko *et al.* 2009), although palila densities are positively correlated with the number of māmane pods at different elevations (Hess *et al.* 2001), and the population is concentrated in areas containing large, mature trees (van Riper *et al.* 1978).

A factor contributing to the greater synchronization of pod production during 1998–2005 was likely the drought conditions that prevailed during most of that time (Banko *et al.* 2013). If true, then a trend toward drier conditions in subalpine Mauna Kea might lead to shorter breeding seasons for the palila, because pods would be abundant across the landscape for less time. Additionally, drought reduces the size of pod crops (Banko *et al.* 2013), and we found that the

number of pods per tree in 1998–2005 was half the number recorded in 1992–2001 at high elevation on the western slope.

In our 1998–2005 study, māmane pods were available around Mauna Kea throughout the year, although the actual abundance varied seasonally. Māmane seeds were most available during the palila nesting season, which is generally March through September (van Riper 1980a, Pletschet and Kelly 1990, Banko *et al.* 2002b). The abundance of *Cydia* caterpillars was episodic in all areas of Mauna Kea. The number of *Cydia* per pod peaked in November when pods were relatively uncommon. Presumably as pods become less abundant, *Cydia* become more concentrated in the remaining pods. Nevertheless, the overall availability of caterpillars per tree was highest in June when pods were abundant and many palila were breeding.

The productivity of māmane trees on the western and northern slopes tended to be greater at higher elevations (see also Banko *et al.* 2002a). Investigating factors that reduce flower and pod production at lower elevations could provide useful insights for managing palila habitat at the landscape scale.

Food Availability: Foliar Caterpillars

Caterpillars found on māmane foliage were generally uncommon in the subalpine forests of Mauna Kea. *Scotorythra artemidora* was the most abundant caterpillar collected in both years of the study, but it was collected most frequently in 1999. Possible explanations for these trends are small sample sizes, differences in microhabitats, variation in rainfall, and uneven timing of sampling during the year.

Virtually all caterpillars collected in this study were early instars. This suggests that our daytime sampling was likely biased against older, larger caterpillars, which typically would be expected to spend daylight hours in seclusion while feeding at night (Perkins 1913; M. Heddle, University of California at Berkeley, personal communication). Even so, our sampling took place during the hours when birds would be most actively foraging, which realistically reflects food availability for palila and other birds.

Additional research into the life history of *Scotorythra* and other species of foliar caterpillars would help understand their interactions with host plants and other arthropods. It would be particularly important to determine how forest restoration and the possible increase of other host plant species in PCH would affect the abundance and diversity of moths and caterpillars.

Food Availability: Insect Surveys in the Pu`u Mali Mitigation Parcel

Although many invasive arthropod threats, including ants, predacious wasps, and parasitoid wasps, were identified in surveys of the Pu`u Mali mitigation parcel, we did find two moth species formerly thought to be extinct and one undescribed moth species. Additionally, almost all caterpillars we collected were *Uresiphita polygonalis*, which has been observed feeding heavily on māmane and being eaten by palila in the past (Perkins 1903, 1913). Although originally thought to be endemic, Zimmerman and Hardy (1958) concluded that *U. polygonalis* was a naturalized species. Nevertheless, further work is needed to understand its potential as prey for palila at the lower margins of PCH.

Threats to Food Resources: *Cydia* Caterpillar Parasitism

Cydia caterpillars that feed in māmane seeds were parasitized by four widespread generalist wasp species on Mauna Kea: *Pristomerus hawaiiensis*, *Calliephialtes grapholithae*, *Diadegma blackburni*, and *Euderus metallicus* (Brenner *et al.* 2002, Oboyski *et al.* 2004). Historically,

P. hawaiiensis, *Trathala flavo-orbitalis* [Cameron] (Ichneumonidae), and *Eupelmus pelodes* Perkins (Eupelmidae) were known to parasitize *Cydia* caterpillars in Hawai'i (Perkins 1913, Swezey 1954, Zimmerman 1978), but we did not recover *T. flavo-orbitalis* or *E. pelodes* from *Cydia* caterpillars that we reared. The origins of these species are somewhat obscure, but *P. hawaiiensis* may be endemic.

In both the 1997 and 1998–2001 studies, parasitism rates by different wasp species varied with elevation. Overall parasitism decreased with elevation in 1997, due mostly to the high incidence of two wasp species (*C. grapholithae* and *P. hawaiiensis*) at lower elevations and the inclusion of two low elevation sites in Pōhakuloa Training Area (PTA). In the 1998–2001 study, which excluded the two PTA sites, overall parasitism did not vary significantly with elevation, although parasitism by particular wasp species was related to elevation. A major difference between the two studies was the higher rate of parasitism by *E. metallicus* in 1998–2001, particularly at higher elevations (Oboyski *et al.* 2004). In 1997, *E. metallicus* was distributed more evenly across all elevations. Our results suggested that this suite of parasitic wasps, many of which have been present on Mauna Kea for over 100 years, were partitioning the landscape and its resources to some degree. Nevertheless, parasitism of *Cydia* caterpillars overall was about 40%, representing a major impact on an important food of the palila.

Threats to Food Resources: Foliar Caterpillar Parasitism

Five parasitoid species were reared from caterpillars collected from the foliage of three common host trees and shrubs within PCH. The overall rate of parasitism on the most common caterpillar, *Scotorythra artemidora*, was 26%. *Scotorythra artemidora* was collected from māmane and was attacked by four parasitoid species. *Peridroma albiorbis* that we collected from māmane was also parasitized at a frequency of 26% by three species. The most frequent parasitoid reared from *S. artemidora* and *P. albiorbis* was *Hyposoter exiguae*, an alien wasp that preys on many species of exposed caterpillars. The next most frequent parasitoid we reared was *D. blackburni*, an introduced wasp that also attacked *Cydia* caterpillars within māmane pods (Brenner *et al.* 2002, Oboyski *et al.* 2004). *Chaetogaedia monticola* is a large fly that was purposefully introduced and it parasitized both *S. artemidora* and *P. albiorbis*. Only a few individuals of the intentionally introduced wasp, *Metorus laphygmae*, were reared from *S. artemidora*, but it was the most common wasp reared from *Scotorythra* (new species 15) in PTA training areas 1 and 2 (Oboyski *et al.* 2002).

Parasitism rates reached 47% in *P. albiorbis* at 2,650 m elevation, indicating the potential of parasitoids for limiting the availability of this common caterpillar to foraging birds. Palila may have fed more frequently on foliar caterpillars in the past (Perkins 1913), but we did not find them frequently in palila fecal samples (see Chapter 14: Diet). This suggests that parasitoids may reduce the availability of caterpillars to palila and other native birds.

Threats to Food Resources: Yellowjackets

Although *Vespula* species are especially effective predators of caterpillars, they harvest the most easily obtained arthropods on vegetation or the ground (Gambino and Loope 1992). Consequently, they have the potential to reduce the availability of arthropod prey to palila and other native birds and could start a trophic cascade that might otherwise alter food webs on Mauna Kea.

The abundance of yellowjackets on Mauna Kea varied depending on the slope, year, and elevation. The only consistent pattern was the seasonal cycle of occurrence. The distribution of shrub and herbaceous ground cover, which may affect the availability of preferred prey, might

also explain the differences in the abundance of yellowjackets on the four slopes. In particular, abundant pūkiawe (*Leptecophylla tameiameia*) shrubs may have helped support large yellowjacket populations on the northern and eastern slopes. Yellowjacket nests were significantly more common under pūkiawe shrubs than elsewhere on Haleakalā (Gambino *et al.* 1990). Additionally, over 90% of yellowjacket foraging bouts targeted pūkiawe on Haleakalā, where yellowjackets were attracted to honeydew secreted by an endemic sap-feeding mealybug.

Our results indicate several areas of yellowjacket ecology that warrant additional study on Mauna Kea. The first is to determine the actual impact of yellowjacket predation on native arthropod communities and the ramifications for the entire subalpine ecosystem on Mauna Kea. The second is to confirm that yellowjacket colonies overwinter above 2,200 m elevation on Mauna Kea. The detection of workers during winter months indicates the possibility of overwintering nests nearby, but the implications of overwintering for yellowjacket population dynamics and impacts are unknown. Another research need is to identify yellowjacket nesting habitat and colony distribution on Mauna Kea to improve survey methods and develop control strategies. The palila population is concentrated on the western slope of Mauna Kea (Banko *et al.* 2013), where yellowjacket abundance and occurrence tend to be lowest. Nevertheless, additional studies could determine whether arthropod prey are becoming less available to palila and other native birds due to yellowjacket predation and whether there may be other ecosystem impacts.

Threats to Food Resources: Ants

We collected seven ant species in five surveys over six years, including three species not previously reported in this region. Our results indicated a significant increase in the range of three species, especially *Cardiocondyla kagutsuchi*. Distributional patterns of the three most common species in our survey area differed, suggesting that each species' invasion had a different series of interactions with local habitat conditions or arthropod communities. *Linepithema humile* was distributed in two concentrated populations whose boundaries shifted through time, *Pheidole megacephala* ranged within one relatively fixed area, whereas *C. kagutsuchi* was found scattered over the survey area.

The rapid expansion and patchy distribution of *C. kagutsuchi* suggest that nuptial flights were relatively common on Mauna Kea. Although spreading less rapidly, both *L. humile* and *P. megacephala* were detected at stations far from their main concentrations, suggesting long-distance, jump-dispersal, which might have been aided by human activity. Of particular concern is that *L. humile* suddenly might appear within the nesting range of the endangered palila, potentially putting the birds' eggs, young, and arthropod prey at risk. Further invasion of palila habitat seems likely because this area is traversed by roads and frequented by people. The persistence of *P. megacephala* for six years at 1,900 m elevation, well above its typical range, may indicate adaptation to the local environmental conditions. Relatively little is known about the effects of *C. kagutsuchi* on arthropod communities, although its rapid spread on Mauna Kea, both laterally and in elevation, warrant additional monitoring and research.

Continued invasion of the native woodland and shrubland communities by ants could disturb native arthropod and bird communities through predation, competition, and disruption of food and pollinator webs (Holway *et al.* 2002, Lach 2008). Human activity on Mauna Kea may increase the likelihood of ant invasion through long-distance jump-dispersal. There are no effective tools for controlling ants at the landscape level; therefore, stopping or slowing the

spread of ants into PCH may offer the most practical protection for reducing their threats to caterpillars and other arthropod prey of palila. Additional monitoring by baiting and substrate searching to detect ant encroachment into high-elevation palila habitat would help managers to eradicate local invasions before they became widespread and more difficult to control.

Threats to Food Resources: Predacious Ground Beetle

The impact of the introduced, generalist arthropod predator, *Laemostenus complanatus*, on palila food resources is unknown, but like most other carabid beetles, *L. complanatus* preys on other insects. During daylight these beetles were found under rocks, plants, and the loose bark of trees, but at night we observed them moving on the ground or in māmane and naio trees within PCH. Although capture rates of *L. complanatus* dropped markedly between 1992 and 2002, suggesting an overall decrease in abundance of the beetle, its range expanded. Range expansion and the occasional abundance at which we observed it suggest that it could add to the overall impacts of other invasive arthropod predators on food webs and trophic interactions of importance to the palila. Investigating the impacts of *L. complanatus* on palila food availability and the arthropod community of subalpine Mauna Kea could provide useful guidance about the management of this potential food web disruptor.

Vegetation Ecology

Vegetation Structure and Composition

By combining data obtained from satellite imagery with aerial photographs and intensive field surveys, we obtained a detailed thematic vegetation classification for exploring ecological relationships between the palila and its environment. Although we were able to confirm the general boundaries between the major vegetation associations in the Jacobi (1979) aerial photo interpretation, we typically found little correspondence between the remote imagery and tree cover and other attributes measured on our survey plots. Contributing to these differences would have been changes in tree cover since the time of the aerial photographs (due to the limited regeneration of māmane resulting from the annual culling of ungulates) and dissimilarities in the methods used in the two approaches.

Our thematic classification revealed the effects of feral ungulates in PCH and provided a means for predicting changes in forest structure and composition after browsers are completely and permanently removed. We expect that the most dramatic change will occur in the mixed shrub community (type 5). Māmane regeneration was relatively high in this association and the density of māmane is likely to continue to increase if feral sheep (*Ovis aries*), European mouflon sheep (*O. gmelini musimon*), and their hybrids are completely eliminated. Recovery of this habitat would provide a habitat corridor between woodland on the western and northern slopes of Mauna Kea. Currently, palila are restricted to the western slope where they are at risk from a catastrophic event such as a large wildland fire.

Māmane regeneration also was relatively high in bare regions (type 1), where long-term browsing has been especially severe at the tree line (Scowcroft and Giffin 1983). Regeneration near tree line was mostly confined to rocky ridges and was lacking in large expanses of cinder and ash, possibly because rocky cracks create microclimates where young trees can become established. In addition to the recovery of māmane-dominated woodlands, māmane will likely increase in the mixed woodlands at lower elevations due to a higher rate of regeneration following the culling of sheep (Hess *et al.* 1999).

Despite the culling of sheep populations, some areas of heavily browsed habitat are recovering poorly. Tree mortality was high and māmane regeneration was poor in grassy māmane-dominated woodland. In the pasture grasslands (type 9) in PCH that have been leased for cattle grazing, standing dead trees were more common than live ones and regeneration was extremely low.

Our spatially explicit thematic classification of vegetation provides a baseline for longitudinal comparisons to evaluate the effect of management actions such as the eradication of browsers. As sheep are eliminated from PCH, we expect vegetation to be highly dynamic with recovery occurring at different speeds in some regions and vegetation associations. Species dominance will likely change, alien plants may continue to invade, and ecosystem properties may change over time.

Vegetation Survey in Palila Critical Habitat

We identified 180 plant species on the survey of vegetation in PCH. Over two-thirds of the species were alien, including several species that had not been recorded previously on Hawai'i Island. Although most herbaceous and grass species were alien, most of the trees, shrubs, and ferns were native.

Although trees were widely distributed in PCH, tree cover was generally patchy and sparse except on the southwestern slope, where naio and māmane were relatively abundant and where palila were concentrated (Banko *et al.* 2013). Māmane was the most broadly distributed tree species, but māmane cover was likely too low to support palila in most areas around Mauna Kea. Nevertheless, a small but relatively dense patch of māmane forest on the northern slope was extensively used by palila translocated there (Banko *et al.* 2009).

Although we recorded māmane trees as tall as 11 m on vegetation plots, most trees in PCH were small, averaging 3.7 m in height. Nearly two-thirds of māmane trees were under 4 m tall, indicating widespread regeneration within the preceding 25 years, based on the growth models of Scowcroft and Conrad (1988). Although māmane saplings (<2 m in height) were found in 91% of survey plots, only 38% of plots contained densities equivalent to at least one sapling per 100 m². Thus, the condition of the forest is improving, but not with sufficient speed to prevent steep declines in palila numbers during drought (Banko *et al.* 2013). Forest recovery will proceed more quickly after browsers have been completely removed.

Palila primarily utilize larger māmane trees (Scott *et al.* 1984, Pletschet and Kelly 1990) due to their more abundant food resources, better concealment from predators, and protection from unfavorable environmental conditions. That only 39% of māmane trees were more than 4 m in height indicates that palila spend most of their time in a limited set of trees across the landscape.

We found evidence of sheep and other ungulates on a majority of plots on the southwestern slope, indicating their attraction to māmane as a food source. This evidence also suggests that māmane will increase once browsing is eliminated.

We encountered many dead and dying māmane trees on vegetation plots throughout PCH. We did not identify causes of mortality, but contributing factors may include fungal root rot, browsing, alien weeds, and drought (Banko *et al.* 2013).

The woody vegetation of PCH is dominated by a few native species that are critically important to the endangered palila. This dry, subalpine woodland is dynamic with widespread regeneration of māmane but also with relatively high levels of mortality. Palila recovery can be expedited by increasing māmane cover, which can be accomplished by eliminating browsing ungulates, planting seedlings, sowing seed, and suppressing alien grasses and other invasive weeds that may compete with māmane.

Vegetation Surveys on Mitigation Parcels

Surveys at Pu'u Mali and Ka'ohe established the baseline conditions of the vegetation on the mitigation parcels soon after the termination of cattle grazing. Five individuals of *Bidens campylotheca campylotheca*, a species of concern, were discovered on the Pu'u Mali parcel. The five tree species that were recorded at Pu'u Mali represent the majority of the native tree species expected in this region. This suggests that existing seeds and scattered trees could promote forest regeneration at the local, if not landscape, scale.

Individual trees were concentrated in localized patches within the 'a'ā flow at Pu'u Mali, whereas Ka'ohe supported fewer tree species, and they were generally more scattered and less abundant. Tree density was lowest on transect 101 at Ka'ohe, suggesting that planting and other management will be needed to accelerate habitat restoration. The disparity in tree distribution between the two mitigation parcels affords an opportunity to attempt different restoration techniques designed for the conditions at each site.

Invasive plants may impede native species recovery in both mitigation parcels. Although both areas have been invaded or are imminently threatened by relatively few habitat-modifying weeds, Kikuyu grass (*Cenchrus clandestinus*) is of particular concern because it forms large, nearly impenetrable mats of vegetation that hinder germination of native shrubs and trees. Other alien species, such as cape ivy (*Delairea odorata*), gorse (*Ulex europaeus*), and banana poka (*Passiflora tarminiana*), which are common on Mauna Kea in places outside of PCH, could also hinder restoration efforts if they are allowed to become established or spread.

Weed Survey in Palila Critical Habitat

In 1999, we surveyed PCH for 15 species of invasive weeds representing the greatest potential for increasing fire hazard, competing with native plants, and facilitating pest arthropods. Nevertheless, the effects of many of these weeds on regional hydrological processes, nutrient cycling, and other ecosystem processes are not well known. The species we selected were somewhat biased towards weeds that were already abundant on the western slope of Mauna Kea, the core of the palila's range (Banko *et al.* 2013). In addition to target species, we noted localized populations of other weeds that posed potential threats and warranted monitoring.

Despite a large source population of fountain grass (*Cenchrus setaceus*) on the lower southern and southwestern slopes of Mauna Kea, the abundance of this serious fire hazard increased only slightly in the 20 years following surveys by Jacobi and Warshauer (1992). Several populations located in 1981 were absent in 1999, but we also discovered a small number of new populations that were not detected 20 years earlier. Nevertheless, the main fountain grass infestation occurred below the area sampled by the 1981, 1999, and 2006–2007 surveys, so we are uncertain about its rate of spread upslope towards PCH. Fountain grass was found mostly in small, disturbed sites, suggesting that native vegetation may replace it once disturbance from ungulates has been eliminated.

Cape ivy also increased modestly since 1980. Although it remained concentrated on the lower western slope of Mauna Kea, it increased in the mixed naio-māmane forest. Satellite populations in the māmane forest at higher elevations were rare in 1999, but indicated its potential for continued spread.

Invading PCH much more rapidly was fireweed (*Senecio madagascariensis*). Fireweed was found at only 10% of our transect stations in 1999, but by 2007 it occupied 86% of stations ($n = 381$) and had spread to tree line around Mauna Kea (U.S. Geological Survey unpublished data).

The threat of fire in PCH is a major concern for palila recovery due to the dramatic spread of fireweed and the longstanding, dense beds of fine fuels formed by invasive grasses, including the six species targeted in our survey (Thaxton and Jacobi 2009). Although widespread on Mauna Kea, orchard grass (*Dactylis glomerata*), velvet grass (*Holcus lanatus*), sweet vernal grass (*Anthoxanthum odoratum*), and Kentucky blue grass (*Poa pratensis*) were rare or absent on the southwestern slope, which is largely dominated by dense naio stands at higher elevations and naio-`a`ali`i shrubland at lower elevations. Nevertheless, fountain grass occurs extensively on the southwestern slope and has the potential to begin a grass/fire cycle that would be difficult to break. The native bunchgrass, *Eragrostis atropioides*, also is common on the arid southwestern slope and flourished after wildfires in 1991 and 1995 that started along the road skirting the lower edge of the forest (U.S. Geological Survey unpublished data). Further research is needed to determine whether grass/fire cycles based on native grass species may develop on Mauna Kea.

Most of the grasses found on Mauna Kea likely increase the threat of fire, but fire hazard and impact escalate where grass densities are high and the fuel bed is continuous. Grass density was high over several extensive areas of the mountain: 1) mid elevations on the western and eastern slopes where orchard grass, velvet grass, sweet vernal grass, and Kentucky blue grass dominate, 2) lower elevations of the western slope where Natal redtop (*Melinis repens*), perennial ryegrass (*Lolium perenne*), and smutgrass (*Sporobolus africanus*) were common, and 3) low elevations on the southern slope close to Mauna Kea State Park where needlegrass (*Stipa cernua*), purple veldtgrass (*Ehrharta calycinae*), and fountain grass were abundant. Local conditions in each area also may affect fire behavior and impacts. Several alien shrubs, most notably gorse and Russian thistle (*Salsola kali*), also have the potential to change the fire regime, especially if they become more abundant and widespread. Although gorse was concentrated in alien-dominated pasture below PCH on the eastern slope, it has the potential to spread higher and into PCH, increasing the risk of fire.

A wide variety of herbaceous weed species cover PCH. Taken together, herbaceous weeds have considerable potential for displacing native species, although the competitive ability of individual species has not been evaluated. Two vines, cape ivy and banana poka, climb on trees and shrubs, thereby reducing the availability of light, competing for water and nutrients, breaking branches, and suppressing seedlings and saplings (Cuddihy and Stone 1990). Both species of vine spread when ungulates disturb the understory.

Prior to our survey, banana poka had not been reported within PCH. The two plants we found and destroyed on the western slope represented the highest elevation reported for the species in Hawai`i and both were heavily laden with fruit that had been partly eaten by birds and rodents. The occurrence of these two individual plants so far away from other known

populations and in a highly disturbed site suggests dispersal by humans. Nevertheless, once established and producing fruit, birds or feral pigs could serve as dispersal agents.

Cape ivy was a conspicuous component of mid-elevation mixed māmane-naio forest on western Mauna Kea with smaller satellite populations indicating its potential to spread. Although long distance dispersal is probably common, establishment seems to be rare based upon the few satellite populations we found. Nevertheless, these outlying populations have the potential to expand. We observed that the vines may cover individual trees for over 10 years without killing them; nevertheless, tree vigor and reproduction seemed conspicuously reduced compared to non-infested trees. Cape ivy may also suppress seedlings of native species. Although the vines wilt and die during prolonged drought, the extensive root system allows plants to quickly sprout when rainfall increases.

Weeds also provide food and shelter for many alien invertebrates and some vertebrates, such as the house mouse (*Mus musculus*). Some weeds provide nectar that may help sustain introduced wasps and flies that parasitize the caterpillars of native moths (Brenner *et al.* 2002, Oboyski *et al.* 2004) that are eaten by palila and other native birds. Invasive weeds also may facilitate the spread and sustain populations of other alien insects, such as predatory ants and wasps (Jervis *et al.* 1993, Idris and Grafius 1995), but studies are needed to evaluate interactions between weeds and pests on Mauna Kea. Mullein (*Verbascum thapsus*) was the only targeted herbaceous species we found on the eastern slope of Mauna Kea. Nevertheless, gosmore (*Hypochoeris radicata*) and several clover species (*Trifolium* spp.) were widespread and common and both might provide nectar for invertebrate pests.

Eliminating or controlling weeds in PCH may speed habitat recovery, but more information is needed to demonstrate both the severity of impacts of particular species on the native vegetation and the feasibility of control measures. Many weeds are likely to persist a long time on Mauna Kea, and reducing the consequences of weed invasions may be a more realistic goal than control. For example, since subalpine Mauna Kea is dry with a year-round fire season, fire prevention and suppression and fuel management through the establishment of fuel breaks is needed until tree cover has increased sufficiently to reduce the density of fine fuels (Thaxton and Jacobi 2009).

Eliminating habitat disturbance by feral ungulates is the critical step towards forest recovery in PCH and elsewhere in Hawai'i (Loope and Scowcroft 1985, Banko *et al.* 2009). Efforts to eradicate feral sheep, mouflon sheep, and feral goats (*Capra hircus*) were begun by the Hawai'i Division of Forestry and Wildlife in 1980, and māmane and other native plants are beginning to recover (Hess *et al.* 1999, Banko *et al.* 2009). Feral pigs (*Sus scrofa*) will continue to be managed for sport hunting, although their digging is widespread in PCH (see Chapter 25: Vegetation Survey in Palila Critical Habitat) and it creates favorable conditions for weeds while reducing native plant density (Spatz and Mueller-Dombois 1975).

Although many alien plant species are beyond control, others with small, localized populations might be eliminated through herbicide treatment or hand-pulling. Small populations of banana poka, Russian thistle, California poppy (*Eschscholzia californica*), prickly-pear cactus (*Opuntia ficus-indica*), and coffeeberry (*Rhamnus californica*), all of which have potential for rapid spread and significant impacts on native vegetation, could be eliminated from PCH with prompt attention and regular surveillance for new populations.

It may be possible to stop the spread of some species by eliminating satellite populations. We removed patches of cape ivy by hand at a number of locations above the main infestation on the western slope of Mauna Kea, and these sites were not recolonized even after several years.

Biological agents may also prove useful in controlling some weed species in PCH. Species targeted for biological control are gorse (Markin *et al.* 1996), fireweed (Ramadan *et al.* 2011), and banana poka (Ramadan *et al.* 2008). Lepidoptera are the principal agents being released, and the moth released for fireweed control may also feed on cape ivy in the wild, as it does under quarantine conditions (M. Ramadan, Hawai'i Department of Agriculture, personal communication). Other insects are also being tested against these and other weed species.

To limit the impacts of new weeds in PCH it is important to prevent their establishment. Weeds invade above tree line on Mauna Kea and even the summit area (4,000 m) is vulnerable. In these extreme environments, native plants may be especially sensitive to even low densities of weeds. Precautions and monitoring during the construction of firebreaks, fences, and game bird watering units, would help to reduce the inadvertent introduction of weeds. Although poorly documented, some alien plants, such as coffeeberry and several grass species, were introduced as supplemental food resources for game birds (L. Pratt, U.S. Geological Survey, personal communication). Introducing alien plants in or near PCH could have serious consequences for restoring palila habitat.

A monitoring program would provide information about the rate at which alien species are spreading in PCH and would better identify weeds that might seriously threaten native species and communities. Our survey was designed to provide a quick assessment of the distribution of select weeds and can be easily repeated, as we did in 2007 to document the rapid spread of fireweed. As the subalpine forest recovers from long-term ungulate damage, it will be helpful to anticipate changes in community structure and composition and interactions between native and alien species. Monitoring and research may reveal that some alien plants benefit native communities by preventing soil erosion and providing hospitable microhabitats for native seedlings and invertebrates. On the other hand, control strategies and management capacity are needed for species that clearly threaten PCH. Tree planting and other efforts to restore the forest may be most effective in reducing weed populations and may be necessary to reestablish native species in sites dominated by alien grasses. Grasses and other weeds may be inhibited where tree canopies substantially reduce light availability at ground level and produce sufficient litter accumulation (Thaxton and Jacobi 2009). Forest restoration can be promoted by reducing disturbance by ungulates, fire, and human activity.

Weed Survey on Southwestern Mauna Kea

To evaluate weed threats to PCH from areas immediately below, we surveyed the lower slopes of southwestern Mauna Kea in 1999. We searched for three particularly noxious weed species: fountain grass, cape ivy, and prickly pear cactus.

Fountain grass was recorded at about one-third of all stations, but it was distributed patchily in low densities (often as individuals or small clumps). Most plants were associated with disturbance or gullies that could act as dispersal corridors. Eliminating disturbance from introduced ungulates may reduce the potential for spread to higher elevations, but eliminating small patches in and near PCH would also protect the forest.

Our survey revealed isolated patches of cape ivy outside the main concentration on the western slope. Cape ivy generally spreads by fleshy roots and rhizomes, but viable seeds are produced

in Hawai'i, and plants flower profusely on Mauna Kea in wetter years, offering an additional mechanism for long-distance dispersal. One patch of cape ivy was growing in a very dry 'a'ali'i shrubland with scattered short trees, suggesting that the potential for invasion in many parts of Mauna Kea is high. Several isolated patches were also identified in pure māmane forest on the western slope in the June 1999 weed survey (see Chapter 27: Weed Survey in Palila Critical Habitat). Furthermore, the problem was not confined to the western slope; a small, but significant clump was noticed on the northern slope in a gully in March 2000 (U.S. Geological Survey unpublished data). Such isolated colonies can be eliminated to prevent further spread. Cape ivy dies back considerably during drought, but individual plants sprout rapidly from rootstock when rains return, suggesting that this weed poses a long-term threat to PCH.

Although we encountered only one prickly pear cactus during our survey, a number of other individuals are known to occur on the southern and western slopes. Three small patches have been identified on Pu'u Ahumoa on the western slope, and two individuals were found upslope of Bradshaw Airfield within PTA on the southern slope. Destroying individuals when discovered will prevent the spread of this species.

Fire Ecology

We investigated the effects of the 1999 Pu'u Loa fire on the subalpine vegetation in wooded pastureland and adjacent ungrazed forest on the eastern slope of Mauna Kea. Ten months after the fire, we inspected all trees within the burn to evaluate mortality and regeneration of ground and epicormic (growing from underneath the bark of a trunk, stem, or branch) sprouts. These data were compared to trees within an adjacent unburned control area 20–100 m outside the edge of the burn. We also assessed vegetation structure and composition within 0.04 ha circular plots (11.3-m radius).

Among the burned areas, alien grass species were less common in forest control plots (U.S. Geological Survey unpublished data), suggesting that fine fuel loading increases following fire. The forested area also harbored species that did not recover from the fire, supporting the idea that fire is rare in this and other native communities in Hawai'i (Smith and Tunison 1992). The fire burned with its highest intensity within the forested area, where the density of māmane and fine grass fuels were higher. Grazing by cattle reduced the grass biomass in the pasture, which resulted in a short sward and lower fire intensity. Although two-thirds of the trees in the forest were defoliated, many of these were producing suckers close to their bases. This trend was even more dramatic in the pasture, where a tenfold increase in suckers was observed in the burned area compared to control plots. In addition, the proportion of ground suckers near live trees was twice as high for scorched trees as it was for unburned trees in the pasture, suggesting that low intensity fire can stimulate root suckers. Nevertheless, at high intensities, as was observed in the forest, fire reduced the amount of māmane regeneration. Results from a prescribed burn in Hawai'i Volcanoes National Park (HAVO) also suggest a higher rate of root suckering following a less intense burn (R. Loh, HAVO Resources Management, personal communication).

Māmane saplings were more abundant in the burned pasture plots compared to the unburned plots. This may have resulted from decreased competition from the temporary reduction of grass and increased input of nutrients from burned plants rather than the direct effects of heat on seed germination. Māmane regeneration from seeds was not observed following a controlled burn in HAVO (R. Loh personal communication), and māmane seed viability was reportedly decreased by fire (C. W. Smith, Cooperative National Park Resources Studies Unit, University of

Hawai'i at Mānoa, personal communication). Moreover, māmane trees showed little phenological response to fire, suggesting that they did not evolve in a community shaped by frequent fires.

Our results indicate that a low-intensity fire may increase māmane regeneration, but unwanted consequences could be expected. Although carefully implemented controlled burning might promote māmane regeneration within the derelict forest of the pasture, burning could encourage the spread of fire-promoting grasses, which would increase the frequency and intensity of fire. Moreover, other native species (e.g., pūkiawe and *Deschampsia nubigena*) respond poorly to fire (Tunison *et al.* 1993). Therefore, our limited data should not be used to justify controlled burning within PCH to speed māmane regeneration. Instead, planting native species and controlling aggressive alien weeds are more likely to be effective in restoring degraded forest. As tree density increases, grass density may decrease (Thaxton and Jacobi 2009), and a succession of species may follow due to changes in microclimate around the trees. In time, species composition and the increase in moisture due to fog drip may reduce fire potential.

Predator Ecology and Management

Techniques for Determining Predator Activity Patterns

We found feral cats to be very active during daylight hours, but their activity peaked at night between 2000 and 2200 hours, which may have been the most favorable time to forage for rats and roosting birds. The period of lowest cat activity (0400–0600 hours) coincides with the lowest diurnal temperatures at the study site (Juvik *et al.* 1993). Radio signals often became weak or non-receivable during this period, suggesting that cats may have been entering dens or sheltered areas to avoid colder temperatures.

The pronounced diurnal activity pattern that we found in mongooses (*Herpestes auropunctatus*) in subalpine Mauna Kea confirms the findings of other studies (Tomich 1969, Keith *et al.* 1990). A mongoose that we tracked occupied a large home range (at least 1 km²), which was consistent with home range sizes reported by Tomich (1969) and Keith *et al.* (1990).

We discovered that rats were active from sunset to about 0300 hours. They spent most of their time foraging on naio fruit in the upper canopy of trees. We tried to document rat behavior in the presence of a roosting bird, but no birds were encountered. We located three rat dens in naio trees, two in māmane, and another was underneath a pile of lava rocks. During the life of her transmitter, a female rat occupied a home range of 1,179 m². When she was re-tagged seven weeks later, she had moved to a new territory 2,500 m away and occupied a home range of about 650 m². A male rat occupied a home range of 2,772 m².

Information about the home range size and behavior of feral cats, mongooses, and rats were used in conjunction with the results of other ecological studies to develop strategies for reducing predator impacts in PCH.

Feral Cat Home Range and Movements

Mean home ranges of feral cats on Mauna Kea were the largest reported among seven other studies from the Pacific region for females (772 ha) and the second largest for males (1,418 ha; Goltz *et al.* 2008). We found that home ranges of male feral cats on Mauna Kea were 60% larger, and females were 71% larger than those reported from Hakalau, which is approximately 25 km in distance from our study site (Smucker *et al.* 2000).

We found some evidence that the spatial arrangement and low density of feral cats on Mauna Kea was tied to social organization. There were strong differences between sexes in home range size, which we attributed primarily to mate-seeking behavior in males, and denning behavior in females. Although females on Mauna Kea occupied large areas relative to other study locations, their overall mean home ranges were only 54% as large as males. Nevertheless, their core activity areas were larger than those of males indicating they use smaller areas more intensively while males use larger areas more extensively.

Although we did not find other reports of daily movements in the literature, we documented average daily movements of about 82 m/day and some much greater maximum movements. Because mean daily movements on Mauna Kea did not differ between sexes, males apparently did not always return to the same location on a daily basis, given their larger home ranges, whereas females may have been tied to a central location, such as a den. It is unlikely that all dens were permanent, but some lava tubes were used more than once, sometimes by different cats. Lava tube dens were probably used repeatedly since they provide good shelter.

Male cat home ranges overlapped extensively. There was no overall seasonal pattern to home range overlap, although the range of one male extended to lower elevation primarily during March–August 2001 and then was subsequently centered in higher elevations. Evidence for territorial encounters between males on Mauna Kea comes from the prevalence of feline immunodeficiency virus (FIV), which is primarily transmitted by biting and scratching (Yamamoto *et al.* 1988). While 17% of 39 males from Mauna Kea tested positive for FIV, all 29 females were negative (Danner *et al.* 2007). Overall female home ranges on Mauna Kea overlapped only slightly, and core activity areas did not overlap.

Hansen *et al.* (2007) estimated that 17.6% of cats per generation on Mauna Loa, primarily males, had emigrated more than 53 km from Mauna Kea. Male cats tend to be more wide-ranging than females; therefore, males may encounter more palila and other native birds while foraging. For example, the mean home range of male cats on Mauna Kea represents more than 10% of the entire range (140 km²) occupied by the palila (Scott *et al.* 1986). Because male home ranges were also nonexclusive, palila may be simultaneously exposed to predation by several different individual cats.

If trapping feral cats is used to protect palila, trap spacing should account for minimum daily movements and differences between sexes in home range. The radius of a circular area equivalent to the home range of female feral cats on Mauna Kea is 1568 m, and for males it is 2125 m. Cats may be expected to encounter traps when traps are spaced at shorter distances, but daily movements may be used to guide minimum spacing between transects during short-term (two-to-three day) trapping sessions. Most subjects moved more than 100 m per day. The implications of large home ranges in male cats are that large trapping areas are needed to confine immigration to buffer zones on the perimeter of endangered species habitat in this environment in Hawai'i.

Other considerations are also important for effective trapping programs. Short *et al.* (2002) found that feral cats that did not use rubbish dumps were more likely to be caught in concealed foot-hold traps than cage traps. Rubbish dumps do not exist within the range of cats on the western slope of Mauna Kea, and other forms of human subsidies are infrequent and small.

Feral Cat and Mongoose Diet

We identified bird remains in 79% of cat and 47% of mongoose samples, indicating a higher incidence of bird predation compared to other studies on Mauna Kea and elsewhere on Hawai'i Island. For example, Hess *et al.* (2007a) found bird remains in less than 30% of cat digestive tracts collected from Mauna Loa and Kīlauea volcanoes in HAVO. Although Snetsinger *et al.* (1994) identified bird fragments in many feral cat scats in subalpine Mauna Kea, rodents were more frequently found. Moreover, our finding of bird fragments in 47% of the mongoose samples was approximately 10 times greater than the frequency reported by Mostello (1996) and Kami (1964). Similar to our results, Kami (1964) reported insects in 41–80% of mongoose scats, but he found a higher incidence of rodent remains (24–72%) compared to our results. Amarasekare (1994) observed rat, mouse, and insect, but no bird fragments in mongoose scats collected on the western slope of Mauna Kea.

Much of the discrepancy in reported occurrences of prey types probably arises from differences in methodology. We expect that examining stomach contents produces more identifiable remains than examining scat, in which contents pass through the entire digestive system. We could often distinguish between gallinaceous and passerine bird fragments in predator stomachs, but we could not distinguish between native and alien passerine fragments. Nevertheless, our findings indicate that the exceptionally high rate of predation on passerine birds by feral cats in PCH poses a significant threat to palila.

Rodent Survey

We conducted 10 rodent surveys for one month biannually during winter (January and February) and summer (June and July) 2000–2005 on the western slope of Mauna Kea to better understand the threats posed to palila and other native birds. We also examined rodent habitat use patterns, morphology, age, sex ratios, and pregnancy rates during selected surveys. We determined rodent arboreal activity in a single, separate, and independent trapping session.

Mice inhabited the māmane, mixed, and naio forests in similar abundances, but rarely utilized pasture, where the grass cover was continuous. The scarcity of mice in the pasture may have been due to increased exposure to predators or to the scarcity of grass seed resulting from Kikuyu grass, a species that spreads vegetatively, dominating the pasture. Cattle grazing may also have kept grass seed availability low. Mouse abundance did not vary significantly in relation to elevation on the western slope. There was a positive, but non-significant, relationship between mouse abundance and six-month median precipitation.

The changes in mouse abundance over all 10 surveys did not seem directly dependent on season (winter or summer), but there might have been a subtle non-seasonal population cycle (Tomich 1986). Mouse and rat capture rates were high throughout the winter 2005 survey, indicating an intense population irruption during that time. The magnitude and length of the irruption were greater than any other recorded since reliable observations were recorded (1970s, P. Tomich, Hawai'i Department of Health [retired], personal communication).

We observed that adult female mice weighed more than adult males, which was inconsistent with other studies in Hawai'i (Tomich 1981). The pregnancy rate was higher in summer (49.1%) than in winter (2.2%).

We found snap trapping to be a more sensitive method of detecting mouse presence than were census blocks, based on the mean probability of mouse detection. Even so, there were fewer than 50 instances (7.3% of station-nights) in which census blocks were more sensitive than

snap traps in detecting mice. Our comparison of mouse detection methods did not independently compare census blocks with snap traps, but to do so we suggest: 1) monitoring a transect with one census block per station for four consecutive nights, then 2) monitoring the same transect with one snap trap per station over the following four consecutive nights. This method would yield temporally independent data and provide a more robust comparison of survey methods. Conducting rodent surveys before and after control efforts could help determine the efficacy of diphacinone baits in areas where palila are reintroduced.

The scarcity of rats on the western slope was consistent with results of previous studies and may be attributable to factors associated with high elevation, such as low temperatures or lack of water (Amarasekare 1994) or possibly depredation by carnivores. Although we were unable to determine the relationship of rats to habitat type due to low capture rates, the frequency with which they were trapped near *Santalum* trees suggests some level of attraction. Our finding that both mice and rats exhibit arboreal activity agrees with results from Amarasekare (1993). Mice are not thought to be nest predators or competitors of palila (Amarasekare 1993), but we do not entirely discount their potential to cause disturbance to nesting birds. Video images of a mouse at the nest of a palila were recorded by a surveillance camera (see Chapter 9: Breeding Phenology, Productivity, and Nesting Success), although there was no indication of negative consequences.

Forensic Techniques for Predator Identification

To help identify mammalian predators of palila whose carcasses were found in the wild, we initiated a study to help recognize diagnostic clues left by different species. Our method was to observe predators feeding on the carcass of a small bird in a controlled setting to determine whether the predator could be identified solely on clues observed on the carcass. We observed predator feeding habits, videotaped their behavior, and described and cataloged the remains. We used this information to develop methods and skills for identifying species responsible for nest destruction and bird mortality.

Using our methods, the remains of dead palila sometimes provided clues to the identity of the predator that killed them. Nevertheless, scavengers usually could not be distinguished from predators. Scat, hair, and tracks provided important evidence in determining predator and scavenger identity.

Impact of Predators at Bird Nests

We monitored wild bird nests on two 500 x 500 m grids in māmane forest and mixed māmane-naio forest on the western slope of Mauna Kea in 1999 to determine the impact of introduced mammalian predators. Predation at nests on both study grids occurred at similarly high levels (56.2% in māmane and 57.1% in mixed forest). However, fledgling production was higher on the māmane grid, where 43.8% of nests fledged at least one chick, than on the mixed forest grid, where 21.4% of nests fledged a chick. Three nests in the mixed forest grid were abandoned possibly due to prolonged rain and cold weather in late February 1999.

Our failure to capture rats in 2,360 trap-nights on the two study grids supports other findings of low rat density on the western slope. The lack of trapping success could reflect seasonal or annual variation in rat population levels or a decline in rat densities due to drought conditions that prevailed during the study.

Mouse abundance was also lower in our study than has been reported previously (Amarasekare 1994, see Chapter 33: Rodent Survey). Low abundance supports the idea that drought may

have depressed rodent populations during the 1999 breeding season. Mice are not known to be predators or competitors of palila (Amarasekare 1994), but mice climb trees and may disturb palila at their nests, especially during the egg stage. In addition, owls prey on native birds on Mauna Kea (Snetsinger *et al.* 1994, Klavitter 2009). Detecting the impact of these predators, however, is much more problematic than for mammals because they may leave no trace at nests. In such cases, it may be difficult or impossible to confirm depredation of specific nests by owls without the use of surveillance cameras. The two types of tracking boards we placed at nests were not effective in detecting predators of any kind.

Predator Management

We tested techniques for removing predators on the northern and western slopes of Mauna Kea during 1998–2005. Methods for reducing feral cat and mongoose numbers focused on the effectiveness of different spatial and temporal distributions of live traps during nine sessions. Research into reducing rat threats consisted of varying the placement and duration of poison baits. The ultimate response variable of interest for both rats and carnivores was the effect of different treatments on the depredation of palila. Nevertheless, due to personnel limitations, we used predator abundance as a proxy for depredation rate.

Overall capture rates for feral cats during our study were similar to capture rates recorded during other studies on Mauna Kea, although our capture rates ranged between 0.64–7.42 per session. The wide range in capture rates may partly reflect environmental variability in subalpine Mauna Kea over six to eight years of trapping effort. Additionally, changes in the cat population through removal (by trapping), reproduction, and environmental factors such as prey availability, may have affected capture rates among sessions.

Controlling the feral cat population on Mauna Kea may not require continual, high-intensity trapping as we found that many cats were removed during the initial 1,000 trap-nights. Feral cat capture rates declined significantly during sessions 3 and 8 and non-significantly during sessions 6 and 7. After decreasing, the capture rates during the longer trapping sessions stabilized at a lower level, suggesting continued low-level immigration from surrounding areas after the removal of all resident cats. Nevertheless, cat capture rates increased significantly in session 9. The beginning of session 9 trapping coincided with a rodent irruption on Mauna Kea (see Chapter 33: Rodent Survey), and the overabundance of prey may have made our baits less attractive. Moreover, the abundance of food may have increased cat survival, reproduction, and immigration, potentially increasing the number of cats available to be trapped later in the session. Because cat trapping may be an ineffective control method during rodent irruptions, the availability of natural prey should be considered before beginning a trapping program.

Interruptions between and during our trapping sessions suggest that breaks of up to two months did not affect the subsequent cat capture rate. On the other hand, long breaks in trapping were followed by higher capture rates, as we observed on the western slope during the initial 150 trap-nights of session 7, which began 10 months after the conclusion of session 6. The high cat capture rate and high percentage of juveniles captured during session 7 (July and August) may have been due to juvenile dispersal from the surrounding areas. Alternatively, low prey availability may have accounted for the increased capture rate as animals may have expanded their home ranges in search of food. Session 7 occurred during a dry year when rodent populations were relatively low (Chapter 33: Rodent Survey), possibly increasing the attractiveness of our baits.

Our estimated initial abundance of cats was always lower than the actual number of cats removed during that session. This may have been an artifact of our circulating trapping effort. Approximately 600 trap-nights were required to cover the entire trapping area. Therefore, we would not expect to capture all resident cats until we had trapped throughout the entire area. Immigration could also have affected capture rates, as may have occurred in session 6.

Although our overall mongoose capture rate was lower than that of van Riper (1978), his result was bracketed by the range of our capture rates per session (0.38–3.94). We found that mongooses bred primarily in the summer months but also bred during the winter. Therefore, we expected the majority of juvenile dispersal to occur in the late summer or fall. Nevertheless, trapping data from session 6 suggested that juveniles were more abundant during May–July. Mongoose capture rates decreased significantly during the only long session without diphacinone application (session 6). Even so, we still captured animals regularly up to about 2,000 trap-nights during session 6. Current carnivore trap arrays are spaced according to cat movement data, and our results suggest that closer trap spacing may be more effective for mongoose control. In addition, very young mongooses were able to escape from our live traps. The lack of mongoose captures where diphacinone bait was applied to control rodents suggested that poison bait was effective for mongoose management. Intensive poison baiting on a larger grid before reintroducing palila to an area, during the nesting season, and during mongoose dispersal may be the most effective methods for protecting palila from mongooses (Hays 1999).

Rats and mice entered diphacinone bait boxes and consumed bait. Mice depleted diphacinone baits quickly, making it necessary to continually stock bait stations with diphacinone to remove rats. Although we did not evaluate changes in rodent populations before and after distributing diphacinone, we observed dead mice at the bait stations. Although poison-killed rodents might pose a potential hazard for `io (*Buteo solitarius*) and other raptors, results of other studies suggest that rats tend to die underground or in other inaccessible locations, thus minimizing threats (Lindsey and Mosher 1994, Spurr *et al.* 2003). Secondary poisoning is even less likely to occur due to the low number of poisoned rodents we found outside bait stations and the small number of `io we saw or that were reported (Scott *et al.* 1986, Klavitter 2000) in subalpine Mauna Kea.

Palila experience less predation when measures are taken to reduce populations of small introduced mammals. During the 1999–2001 palila nesting seasons, when there was no predator control on the western slope, feral cats depredated 8–11% of active nests annually (see Chapter 9: Breeding Phenology, Productivity, and Nesting Success). In contrast, we observed no nest predation by cats during the 2002 breeding season, when we trapped intensively. Additionally, we did not control small mammal numbers during the second translocation trial, and we implicated rats in the deaths of two palila and the deaths or scavenging of three others (see Chapter 2: Translocating Wild Palila). Predation decreased markedly during the third, fourth, and fifth translocation trials.

This study demonstrated that removing small introduced mammals can be effective in reducing predatory threats to the palila and other native birds on Mauna Kea. Our trapping program also led to practical information about the population genetics, demography, diseases, and habitat relationships of feral cat populations in Hawai'i (Hess *et al.* 2007b,c). The genetic structure of feral cats in Hawai'i indicates great dispersal ability between the slopes of Mauna Kea and even between the volcanoes of Hawai'i Island (Hansen *et al.* 2007). This suggests that control will be

difficult due to high rates of immigration as cats are removed from areas. Moreover, high rates of reproduction and survival can be supported by abundant bird prey, and male cats may be limited more by the availability of mates than of food (Hess *et al.* 2007b). Relatively high survival (to 11 years of age) and reproduction also allows individual cats to affect palila for many years and enables cat populations to recover quickly after control efforts (Danner *et al.* 2010). Feline immunodeficiency virus, feline leukemia virus, and *Toxoplasma gondii* may depress the feral cat population on Mauna Kea to some degree, but their occurrence suggests they would not be effective agents in a biological control strategy (Danner *et al.* 2010). Cats were captured more often on the western slope and in māmane woodland (Hess *et al.* 2007c), and increasing control efforts near sites of multiple captures may prove more effective than trapping uniformly across the landscape. The number of mongooses captured at a trap was positively correlated to the number of cat captures even though mongooses pre-empted traps; therefore, using alternate control measures, such as diphacinone, might increase the rate of cat captures (Hess *et al.* 2007c). Our extensive research on feral cats and other introduced small mammals on Mauna Kea provides additional information that can be used in an adaptive management framework to improve the effectiveness of predator control to protect palila (Hess *et al.* 2007c, 2009).

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