Multi-Scale Habitat Selection of the Endangered Hawaiian Goose

Authors: Leopold, Christina R., and Hess, Steven C.

MULTI-SCALE HABITAT SELECTION OF THE ENDANGERED HAWAIIAN GOOSE

Christina R. Leopold[1,2] and Steven C. Hess[3,4]

[1]*Hawaiʻi Cooperative Studies Unit, University of Hawaiʻi at Hilo, P. O. Box 44, Hawaiʻi National Park, HI 96718*
[2]*Tropical Conservation Biology and Environmental Science Graduate Program, 200 West Kawili Street, University of Hawaiʻi at Hilo, Hilo, HI 96720*
[3]*Pacific Island Ecosystems Research Center, U.S. Geological Survey, Kīlauea Field Station, P. O. Box 44, Hawaiʻi National Park, HI 96718*

Abstract. After a severe population reduction during the mid-20th century, the endangered Hawaiian Goose (*Branta sandvicensis*), or Nēnē, has only recently re-established its seasonal movement patterns on Hawaiʻi Island. Little is currently understood about its movements and habitat use during the nonbreeding season. The objectives of this research were to identify habitats preferred by two subpopulations of the Nēnē and how preferences shift seasonally at both meso- and fine scales. From 2009 to 2011, ten Nēnē ganders were outfitted with 40- to 45-g satellite transmitters with GPS capability. We used binary logistic regression to compare habitat use versus availability and an information-theoretic approach for model selection. Meso-scale habitat modeling revealed that Nēnē preferred exotic grass and human-modified landscapes during the breeding and molting seasons and native subalpine shrubland during the nonbreeding season. Fine-scale habitat modeling further indicated preference for exotic grass, bunch grass, and absence of trees. Proximity to water was important during molt, suggesting that the presence of water may provide escape from introduced mammalian predators while Nēnē are flightless. Fine-scale species-composition data added relatively little to understanding of Nēnē habitat preferences modeled at the meso scale, suggesting that the meso-scale is appropriate for management planning. Habitat selection during our study was consistent with historical records, although dissimilar from more recent studies of other subpopulations. Nēnē make pronounced seasonal movements between existing reserves and use distinct habitat types; understanding annual patterns has implications for the protection and restoration of important seasonal habitats.

Key words: Branta sandvicensis, *Hawaiian Goose, multi-scale habitat selection, Nēnē, satellite telemetry.*

Selección de Hábitat a Múltiples Escalas de la Especie en Peligro *Branta sandvicensis*

Resumen. Luego de una reducción poblacional severa durante mediados del siglo 20, la especie en peligro *Branta sandvicensis* ha re-establecido recientemente su patrón de movimiento estacional en la isla de Hawái. Poco se conoce actualmente sobre sus movimientos y uso de hábitat durante la estación no reproductiva. Los objetivos de este estudio fueron identificar los hábitats preferidos por *B. sandvicensis* y cómo estas preferencias cambian estacionalmente tanto a la escala intermedia como fina. De 2009 a 2011, equipamos diez individuos con transmisores satelitales de 40-45 g con capacidad de posicionamiento geográfico. Usamos regresiones logísticas binarias para comparar el uso del hábitat con su disponibilidad y un enfoque teórico de la información para la selección del modelo. El modelado del hábitat a escala intermedia reveló que los gansos prefirieron los pastos exóticos y los paisajes modificados por los humanos durante las estaciones reproductiva y de muda, y los arbustales subalpinos naturales durante la estación no reproductiva. El modelado del hábitat a escala fina también indicó una preferencia por los pastos exóticos, rosetas de pastos y ausencia de árboles. La proximidad al agua fue importante durante la muda, sugiriendo que la presencia de agua puede brindar una vía de escape de los mamíferos depredadores introducidos durante el periodo en que los individuos aún no pueden volar. Los datos de composición de especies a escala fina agregaron relativamente poco para entender las preferencias de hábitat de *B. sandvicensis* modeladas a la escala intermedia, sugiriendo que esta escala es apropiada para la planificación de manejo. La selección de hábitat durante nuestro estudio fue consistente con los registros históricos, aunque distinta de estudios más recientes de otras subpoblaciones. Los individuos de *B. sandvicensis* realizaron notables movimientos estacionales entre las reservas existentes y usaron distintos tipos de hábitat; el entendimiento de los patrones anuales tiene implicancias para la protección y restauración de hábitats estacionales importantes.

INTRODUCTION

Habitat selection occurs simultaneously on a number of scales and is a central component for understanding important life-history dynamics of populations (Rettie and Messier 2000, Manly et al. 2002). To measure habitat selection at multiple levels, we can follow the "orders" or scales of habitat selection described by Wiens (1973) and Johnson (1980): the first order being a population's geographic range, the second order (meso scale) pertaining to local site selection, the third order (fine

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scale) addressing use patterns, and the fourth order specifically regarding food items. Meso-scale modeling can inform understanding at a regional level, while fine-scale modeling may identify preferred topographic features or important habitat characteristics (Apps et al. 2001). Habitat selection at more coarse scales reflects broader limiting factors (Rettie and Messier 2000, McLoughlin et al. 2002), while fine-scale habitat-selection analyses may reveal the limiting resource within a habitat type (Hutto 1985). Identifying how habitat preferences shift across scales is important for characterizing the complexities of habitat selection and provides a greater understanding of the species of interest and its habitat.

It is commonly assumed that species occupy habitats that most suit their dietary and reproductive preferences as long as benefits received outweigh the risk from competitors and predators (Manly et al. 2002). However, when preferred resources become difficult to find or the risk of occupying preferred habitat becomes too great, a population must occupy alternative habitats or face local extirpation. Endangered species present a special case in that they often do not use their full historic range and may be restricted to specific locations or habitat types that are not most preferred sites (Zarnetske et al. 2007). Individuals may persist because of the remoteness of the periphery rather than habitat quality, which may confound the interpretation of habitat preferences (Lomolino and Channell 1995). Nonetheless, these locations may provide insights into the potential range of habitats used, even if not most preferred or ideal habitats from a management standpoint.

The Nēnē, or Hawaiian Goose (*Branta sandvicensis*), was reduced nearly to extinction in the late 1940s with an estimated 30 wild and 11 captive birds on Hawaiʻi Island (Smith 1952, Kear and Berger 1980). Although breeding success remains low and predation high, decades of captive propagation and releases into the wild have resulted in a population of approximately 2000 Nēnē statewide, which is not yet self-sustaining (USDI 2004). Nēnē have reestablished some patterns of seasonal movement across Hawaiʻi Island similar to those documented by early naturalists (Hess 2011), but more sedentary segments of the population face increased mortality from dehydration and starvation (Black et al. 1997). Much is known of the species' habitat selection during the breeding season, but all published information is from subpopulations that move little seasonally (Banko et al. 1999). Platform transmitter terminal (PTT) units with Global Positioning System (GPS) capability offer the opportunity for locations of Nēnē to be recorded throughout the species' current range and for previously undocumented locations in the nonbreeding season and at night to be identified. Recognizing that habitat-selection analyses at multiple scales may yield different results, we chose to model preferred habitat types within reserves across Hawaiʻi Island (meso scale) and the species composition and height of vegetation within habitats (fine scale).

To better conserve and manage Nēnē, our primary objective was to model habitat use versus availability, including vegetation composition and height during breeding, molting, and nonbreeding seasons on Hawaiʻi Island. We predicted differences in preference for both habitat type and elevation between the breeding and nonbreeding seasons at the meso scale. We expected habitat preferences to shift seasonally, as found by Black et al. (1997) and Woog (1999), who demonstrated that Nēnē prefer short, exotic grasses for nonbreeding-season foraging and native desert shrubland for nesting and molting. We investigated whether during molt Nēnē prefer locations near water, as observed among other species of geese (Madsen and Mortensen 1987, Kahlert 2003, Radtke and Dieter 2010). We explored shifts in diel habitat use, particularly fine-scale preferences for more densely vegetated areas during the day and sparsely vegetated areas at night as previously found by Woog (1999). To identify the appropriate scale for future management planning in context of previous studies, we also examined how habitat-selection results shifted between scales of analysis.

METHODS

STUDY AREA AND STUDY SITES

To determine habitat selection at the meso scale across Hawaiʻi Island, we selected five accessible study sites used by and managed for Nēnē (Fig. 1). Study sites included the Kahuku unit of Hawaiʻi Volcanoes National Park (Kahuku; 585–3885 m elevation), Hakalau Forest National Wildlife Refuge (Hakalau; 995–2030 m), Kīpuka ʻAinahou Nēnē Sanctuary (Kīpuka ʻAinahou; 1750–2720 m), Kūlani Correctional Facility (Kūlani; 1410–1845 m), and the Big Island Country Club golf course (BICC; 625–665 m). For fine-scale habitat modeling, we sampled vegetation from 2009 to 2011 at four locations: Kahuku, Hakalau, Kīpuka ʻAinahou, and BICC.

We defined three primary seasons: (1) breeding, from September to February; (2) molting, from March to May; and (3) nonbreeding, from June to August (Banko et al. 1999), although there is substantial variation among individuals in the timing of breeding and molt. The birds bred and molted at BICC and Hakalau. Other locations were used during the nonbreeding season. Our study took place during an extended drought; rainfall in 2009, 2010, and 2011 was 67.8%, 46.2%, and 65.7% of the long-term annual mean rainfall at 21, 34, and 31 stations, respectively, on Hawaiʻi Island (National Weather Service, Honolulu, Hawaiʻi).

SATELLITE TELEMETRY

We outfitted two cohorts of Nēnē with PTT units equipped with GPS capability (Microwave Telemetry, Columbia, MD). PTTs measured 57 × 30 × 20 mm and were attached dorsally with a double-threaded backpack harness made of Teflon ribbon (Bally Ribbon Mills, Bally, PA). Transmitter packages weighed ≤3% of each bird's mass. Capture, handling, and transmitter attachment procedures were approved by protocol
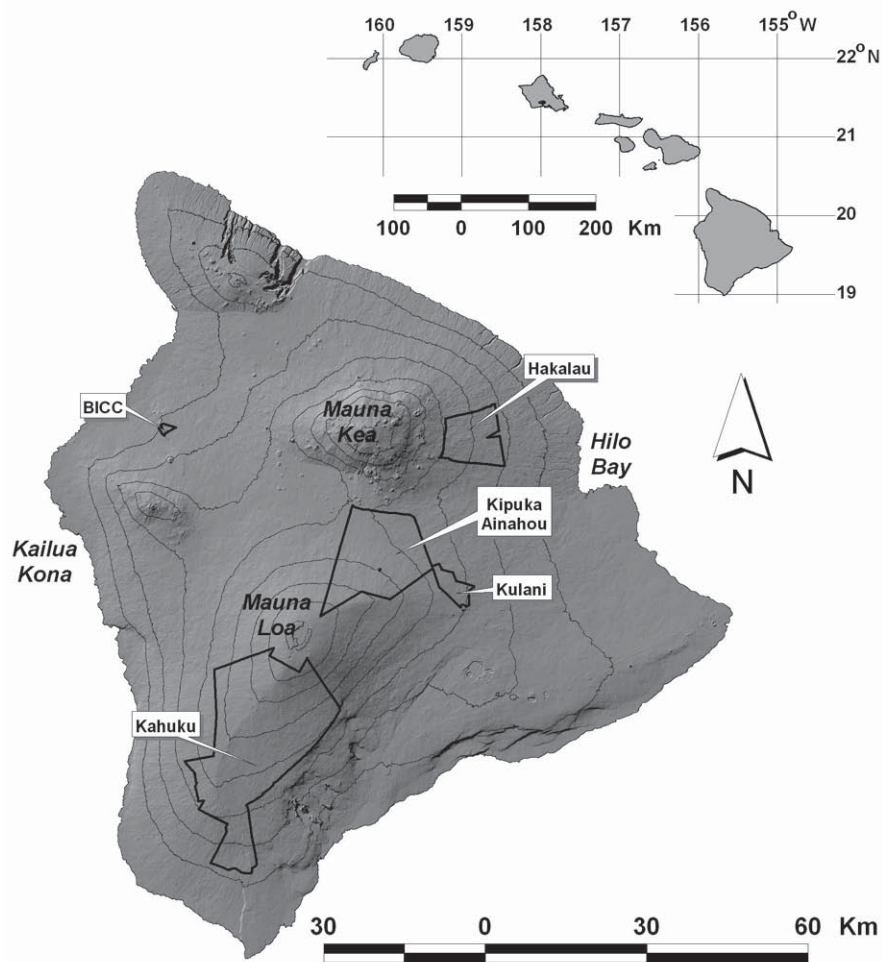
FIGURE 1.   Study areas for satellite telemetry and habitat selection of the Nēnē on Hawai'i Island, 2009–2011. Five study sites were used to evaluate meso-scale habitat selection: the Kahuku unit of Hawai'i Volcanoes National Park (Kahuku), Hakalau Forest National Wildlife Refuge (Hakalau), Kīpuka 'Ainahou Nēnē Sanctuary (Kīpuka 'Ainahou), Kūlani Correctional Facility (Kūlani), and the Big Island Country Club (BICC). Four study sites were used in fine-scale analyses: Kahuku, Hakalau, Kīpuka 'Ainahou, and BICC. Elevation contours are at 500-m intervals.

08-636 of the University of Hawai'i's Institutional Animal Care and Use Committee. We selected candidates for PTTs on the basis of several criteria: males were selected to reduce risk of the transmitter interfering with breeding, candidates must have nested at Hakalau or BICC and been observed at Kahuku, and no candidates were immediate relatives of one another or of the same social group.

In 2009 the first cohort of five ganders was fitted with 40-g battery-powered PTT units programmed to take GPS coordinates at 00:00 and 10:00 HST. In 2010 and 2011 the second cohort of six ganders was fitted with 45-g solar-powered PTTs programmed to take GPS coordinates at 00:00, 10:00, 14:00, and 19:00. One of the ganders used in 2009 was refitted with a solar-powered PTT in 2010; therefore, there were a total of ten study subjects. All PTTs uploaded data to satellites every 3 days (CLS America, Inc., Largo, MD). We tested stationary PTTs before deploying them, and 95% of GPS coordinates were horizontally accurate ±15 m.

MESO-SCALE DATA COLLECTION

We used satellite telemetry locations from eight Nēnē in meso-scale analyses, with a stratified random subsample of 30 daytime and 30 nighttime locations from each subject at each study site. All available GPS coordinates were used from sites where 30 random GPS coordinates were not available. These data comprised 676 records. We compiled predictor variables from land-cover imagery in ArcGIS 9.3 (ESRI, Redlands, CA). Land-cover class was categorized by the Hawai'i Gap Analysis Program's (HIGAP) raster data, a classification system derived from 30-m-resolution LAND-SAT images with 37 discrete cover classes (Hawai'i Gap Analysis Program 2006). We collapsed cover classes into six categories for analysis: exotic grass, native shrubland, no vegetation, open forest (25–60% canopy cover), closed forest (>60% canopy cover), and modified habitat. Modified habitat consisted of areas converted for human use, e.g., the

golf course at BICC and a ball field at Kūlani. Additional variables included elevation from a 10-m digital elevation model and distance from nearest water based on a compilation of imagery layers. We randomly generated a number of points equal to the number of use locations with Hawth's Tools (Beyer 2004) in ArcGIS to represent locations available to Nēnē at each study site, for a combined total of 1352 records. We assigned season and time of day randomly to available locations.

FINE-SCALE DATA COLLECTION

We defined the fine-scale level to include the habitat characteristics of species composition and height. These high-resolution data were not available from existing geospatial databases and remote imagery. At four study sites, BICC, Hakalau, Kahuku, and Kīpuka ʻAinahou, we sampled all HIGAP cover classes that offered food resources suitable for Nēnē (mainly grass or berries) and were accessible by flight, e.g., we excluded closed-canopy forest. The proportion of available cover classes varied according to site (Table 1). We randomly selected ten daytime and ten nighttime locations used by each subject per study site, and, using Hawth's Tools, randomly generated ten plot locations in each cover class per study site below 3000 m, the species' maximum documented elevation (Black et al. 1997, Hess 2011). We used all available GPS coordinates from sites where 10 random GPS coordinates were not available. A total of 246 plots used by Nēnē and 150 random vegetation plots were measured, yielding 396 records included in the fine-scale analyses. We collapsed cover classes into six categories for fine-scale analyses: exotic grass, native shrubland, no vegetation, open forest, exotic shrubland, and modified habitat. We included exotic shrubland to determine if Nēnē prefer native shrubland over shrubland in general.

We established vegetation plots to measure species composition and structure at locations used by Nēnē and at randomly generated locations representing available habitat. At each location coordinate, we employed the point-intercept method to estimate vegetation cover and structure within circular plots of 15 m radius to match the error radius of GPS coordinates recorded by PTT units. One measurement at the center of the plot plus three in each of the four cardinal directions at 5-m intervals were recorded for a total of 13 vegetation measurements per plot. We identified vegetation to species and recorded its maximum height to the nearest mm. All cover classes at sample locations in this study were categorized correctly by HIGAP imagery.

MESO-SCALE STATISTICAL ANALYSES

We selected model predictors on the basis of hypotheses corresponding to findings from previous studies of habitat selection by the Nēnē and other closely related species (Table 2). We used diagnostic statistics to examine the assumption of independence of model predictors and identify possible confounding factors (Alldredge and Griswold 2006). We assessed whether land-cover composition differed by site with chi-squared tests. We used one-way ANOVAs to examine relationships between levels of cover class and elevation, cover class and distance to water, and distance to water and season. We examined the severity of correlation between distance to water and season with Pearson's correlation statistic.

We selected reference categories for two categorical predictors with three or more levels to compare how levels differed from one another in meso-scale habitat-selection modeling. To minimize a high variable-inflation factor, we chose reference categories that were as neutral as possible (Wissmann et al. 2007). Exotic grass was the reference category for cover class, and we selected the breeding season as the reference category for season because we were particularly interested in identifying patterns of relative habitat use during the molting and nonbreeding seasons. On the basis of diagnostic statistics we included five main effects: cover class, elevation, distance to water, season, and time of day, and three interactions: cover class × elevation, distance to water × season, and cover class × distance to water. We restricted interaction terms to those that were

TABLE 1.   Extent of study sites and proportion of land-cover classes for analyses of habitat selection of the Nēnē on Hawaiʻi Island, 2009–2011. The five study sites were the Kahuku unit of Hawaiʻi Volcanoes National Park (Kahuku), Hakalau Forest National Wildlife Refuge (Hakalau), Kīpuka ʻAinahou Nēnē Sanctuary (Kīpuka ʻAinahou), Kūlani Correctional Facility (Kūlani), and the Big Island Country Club (BICC). Land-cover classes were obtained from HIGAP raster data (Hawaiʻi Gap Analysis Program 2006).

		Proportion land-cover class					
Site	Area (ha)	Closed forest	Exotic grass	Modified	Native shrubland	No vegetation	Open forest
BICC	60	0.05	0.73	0.19	0.00	0.03	0.00
Hakalau	9798	0.69	0.08	<0.01	<0.01	<0.01	0.22
Kahuku	46 858	0.03	0.02	<0.01	0.23	0.65	0.07
Kīpuka ʻAinahou	14 234	0.01	0.06	0.00	0.30	0.56	0.06
Kūlani	2915	0.43	0.10	0.01	0.01	0.01	0.44

TABLE 2.   A priori hypotheses for habitat preferences of the Nēnē corresponding to factors and levels used in meso- and fine-scale logistic-regression models.

Model scale and hypothesis	Time of year
Meso and fine scales	
Habitat preferences shift seasonally[a]	Year round
Cover class: native shrubland preferred[b]	Breeding, molting
Cover class: native shrubland preferred[c,d]	Nonbreeding
Cover class: exotic grass preferred[b]	Nonbreeding
Goose species prefer close proximity to water[e]	Molting
Nēnē have no preference for proximity to water[f]	Year-round
Elevation: low[c,d]	Breeding
Elevation: high[c,d]	Nonbreeding
Time of day: daytime in grassland; roost in native shrubland[g]	Breeding
Cover class × elevation: exotic grass at lower elevation preferred	Breeding, molting
Cover class × elevation[c,d]	Nonbreeding: native
Fine scale: all models	
Grass preferred[a,d]	Year-round
Fine scale: full and grass composition	
Exotic grass preferred[b,g]	Nonbreeding
Short grass preferred[g]	Breeding, molting
Fine-scale: full and vegetation	
Shrubs preferred[c,d]	Nonbreeding
Trees preferred for shade	Breeding, molting
Herbs within short exotic grass preferred[g]	Nonbreeding
Bunch grass within native shrubland preferred[d]	Nonbreeding
Season × short grass preferred	Breeding, molting
Fine-scale: vegetation and grass composition	
Season × grass: preference during breeding and molting[g]; no preference during nonbreeding[b]	Seasonal shifts in use
Fine-scale: full	
Cover class × bunch grass preferred[c,d]	Nonbreeding
Tree × short grass preferred	Breeding, molting
Fine-scale: grass composition	
Season × exotic grass preferred	Breeding, molting
Fine scale: vegetation	
Season × tree: preference during breeding and molting; avoidance during nonbreeding	Seasonal shifts in use

[a]Banko et al. (1999).
[b]Black et al. (1997).
[c]Henshaw (1902).
[d]Perkins (1903), and Baldwin (1945).
[e]Madsen and Mortensen (1987), Kahlert (2003), and Radtke and Dieter (2010).
[f]Banko (1988).
[g]Woog (1999).

biologically meaningful for conservation and management (Guthery 2008).

To determine habitat preferences, we used a forward stepwise approach for logistic-regression analyses of the dependent variable of use (1) and availability (0) with covariate attributes. We ranked models by Akaike's information criterion (AIC) corrected for small sample sizes and potentially overdispersed data (QAIC$_c$), and used Akaike weights (w_i) to evaluate the relative importance of top models (Burnham and Anderson 2002, Anderson 2008). Because several subjects were not represented throughout all seasons, models were unbalanced, did not converge, and we were unable to use a repeated-measures approach. Therefore, we standardized the number of subsamples and pooled locations used by multiple individuals, treating each location as an independent observation. For logistic regression and chi-squared analyses we used R (version 2.12.2; R Development Core Team 2011), for ANOVAs, Minitab, version 15 (Minitab, Inc., State College, PA).

FINE-SCALE STATISTICAL ANALYSES

We used diagnostic statistics to identify relationships between levels of cover class and season at locations used by Nēnē (Alldredge and Griswold 2006). In chi-squared tests but not in further analyses, we combined the categories of exotic grass and modified cover because of their similar vegetation structure and expected values <5 (Crawley 2007). We examined the severity of correlation between distance to water and season with Pearson's correlation statistic.

Vegetation categories from plots were collapsed into six primary groups for fine-scale logistic-regression modeling: grass, tree, shrub, sedge, herb, and fern. For analyses, we further divided the grass category into three subcategories: exotic grass, bunch grass, and short grass (≤12 cm). We categorized grass measurements into four cover classes to broadly assess grass abundance in each vegetation plot: ≤10%, 11–50%, 51–76%, and ≥77%. Plants over 1.5 m tall were considered trees.

Logistic-regression procedures were the same as for meso-scale analyses. To determine whether fine-scale vegetation analyses could predict habitat preferences more accurately than at the meso-scale, we used the best model from meso-scale analyses as the "base" model for fine-scale analyses. Three suites of predictors served as parallel analyses corresponding to hypotheses of fine-scale habitat selection (Table 2). In the full analysis, we included four predictors and two interactions from the base model, ten fine-scale predictors, and four additional interactions potentially relevant to the Nēnē's habitat selection: time of day, grass, tree, shrub, herb, fern, sedge, exotic grass, bunch grass, short grass, season × exotic grass, season × short grass, tree × short grass, and cover class × bunch grass. Fine-scale vegetation analysis included all predictors in the base model plus time of day, grass, tree, shrub, fern, herb, sedge, season × tree, and season × grass. In the third analysis, we examined the role of grass composition in habitat selection, including the predictors in the base model predictors plus time of day, grass, short grass, bunch grass, exotic grass, season × grass, and season × short grass.

RESULTS

MESO-SCALE HABITAT-SELECTION MODELING

The chi-squared test of data on available habitat indicated that land cover at the Hakalau and Kūlani sites was similar and that land cover at the Kahuku and Kīpuka ʻAinahou sites was similar (Table 1). However, contingency tables subdivided post hoc identified sites that differed from one another: BICC differed from the combinations of Hakalau–Kūlani and Kahuku–Kīpuka ʻAinahou (χ^2_{10} = 1006.2, $P < 0.001$), Hakalau and Kūlani differed from one another (χ^2_2 = 26.0, $P < 0.001$), and Kahuku and Kīpuka ʻAinahou differed from one another (χ^2_4 = 18.5, $P < 0.001$). Overall, sites differed sufficiently from one another in cover-class composition to allow cover class to serve as a proxy for site and not confound further analyses (χ^2_{20} = 1063.4, $P < 0.001$).

Data from eight Nēnē with PTT units in 2009 and 2010 provided a rate of GPS coordinate fixes of 95% for meso-scale habitat-selection modeling. One-way ANOVAs confirmed strong relationships between six levels of cover class and elevation ($F_{5,1346}$ = 295.2, $P < 0.001$) and between cover class and distance to water ($F_{5,1346}$ = 263.9, $P < 0.001$). We found a relationship between distance to water and season ($F_{2,1349}$ = 24.8, $P < 0.001$) with no significant difference between breeding and molting seasons ($F_{2,824}$ = 0.5, $P = 0.48$) but a strong difference between the nonbreeding and breeding seasons ($F_{1,956}$ = 29.2, $P < 0.001$) and between the nonbreeding and molting seasons ($F_{1,918}$ = 40.1, $P < 0.001$). We also found a moderate positive correlation between elevation and distance to water (Pearson's r = 0.7, $P < 0.001$).

The logistic-regression model most strongly supported by $QAIC_c$ model weight (w_i = 0.91) contained four main effects and two interaction terms: cover class, elevation, distance to water, season, cover class × elevation, and distance to water × season (Table 3). The model ranked second highest carried most of the remaining weight (w_i = 0.06) and included all predictors from the top model along with the additional

TABLE 3.   Meso-scale logistic-regression models, ranked by $QAIC_c$, of the Nēnē's habitat selection on Hawaiʻi Island, 2009–2010. Four top-ranked models and the null model are presented.

Model[a]	K	$\Delta QAIC_c$[b]	w_i
[b]LC × ELEV + DW × S	17	0.00	0.91
[b]LC × ELEV + DW × S + LC × DW	22	5.40	0.06
[b]Time of day + LC × ELEV + DW × S + LC × DW[c]	23	7.50	0.02
[b]LC × ELEV	15	21.00	<0.001
Null	1	772.20	<0.001

[a]LC, land-cover class; ELEV, elevation; DW, distance from water; S, season.
[b]Akaike's information criterion adjusted for small sample sizes and potentially overdispersed data; lowest $QAIC_c$ = 2456.60.
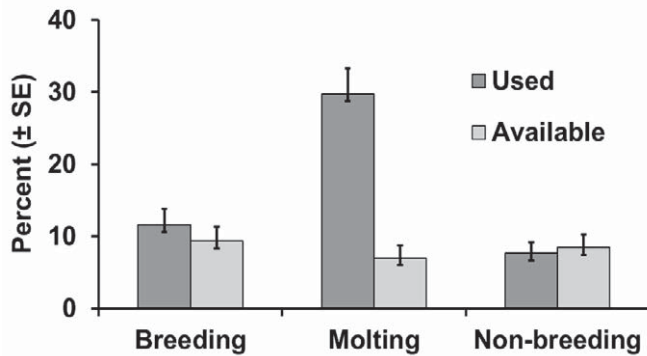[c]Full model.

FIGURE 2.   Percent of locations used by eight Nēnē and available locations ≤50 m from water by season on Hawai'i Island, 2009–2010 (n = 1352). Meso-scale analyses of habitat selection implied that locations ≤50 m from water were used disproportionately during the molting season but not during the breeding and nonbreeding seasons.

interaction term cover class × distance to water. We used a chi-squared test to explore the interaction term distance to water × season by examining locations ≤50 m from water, which we interpreted as the greatest distance that allows escape from threats. Used and available locations in the breeding and non-breeding seasons differed from those in the molting season (χ^2_2 = 7.7, P = 0.02), when Nēnē were found at the greatest proportion of locations ≤50 m from water (Fig. 2). Nēnē also used native shrublands disproportionately during the nonbreeding season (χ^2_2 = 90.0, P < 0.001; Fig. 3). Time of day was not a factor in any of the top-ranked models. Meso-scale model coefficients are presented in Appendix 1, available at http://dx.doi.org/10.1525/cond.2012.120022.

A one-way ANOVA of the results from the meso-scale models revealed that levels of cover class differed in mean elevation (F_4 = 249.0, P < 0.001, r^2 = 0.60). The interaction term cover class × elevation in the model was explained by cover classes of modified habitat and exotic grass being available largely at lower-elevation breeding and molting sites, while the cover classes of native shrubland, open forest, and no vegetation were used mostly during the nonbreeding season at high-elevation sites, specifically Kahuku and Kīpuka 'Ainahou.

FINE-SCALE HABITAT-SELECTION MODELING

From 2009 to 2011, data from ten Nēnē with PTT units provided rates of GPS coordinate fixes of 95% for use in fine-scale habitat-selection modeling. Diagnostic statistics for used and available habitat revealed that exotic grass and modified cover classes were not independent of season (χ^2_2 = 27.7, P < 0.0001). The cover classes of open forest (χ^2_2 = 4.2, P = 0.12) and no vegetation (χ^2_2 = 3.6, P = 0.16) were independent of season. Use of native shrubland was not independent of season (χ^2_2 = 12.8, P = 0.001). Elevation and distance to water yielded a moderate positive correlation (Pearson's r = 0.6, P < 0.001). Nēnē did not use exotic shrubland.

The strongest predictor in each group of model tests was cover class; elevation was second. Two additional main effects and two interaction terms from the top meso-scale model, distance to water, season, cover class × elevation, and distance to water × season, always followed the main effect of grass or exotic grass in reducing models' deviance (Table 4). The top-ranked full model included exotic grass, bunch grass, tree, and all predictors from the base model with strong model
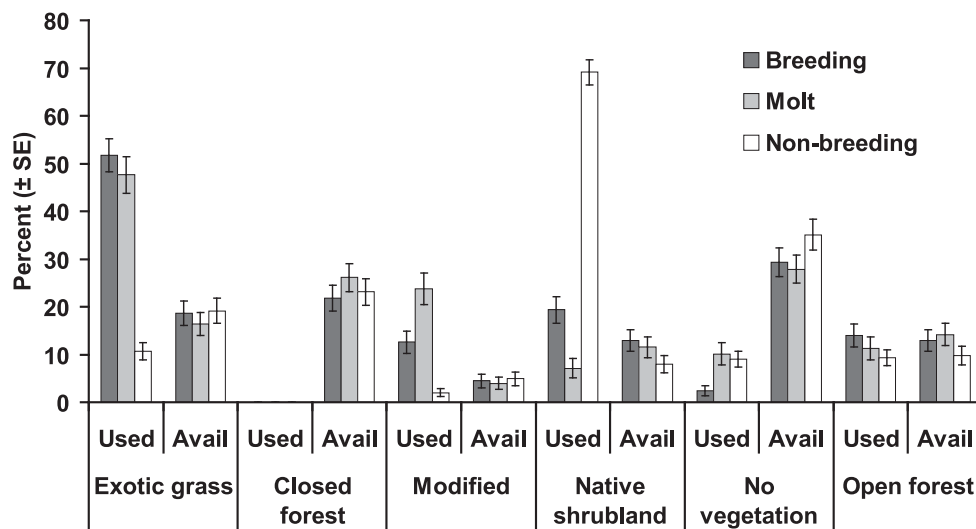

FIGURE 3.   Percent of locations used by eight Nēnē and locations in available land-cover classes by season on Hawai'i Island, 2009–2010 (n = 1352). Meso-scale analyses of habitat selection implied that the classes of exotic grass and modified land cover were used disproportionately during breeding and molting but were used less than expected during nonbreeding. Native shrubland was used disproportionately less during molt and disproportionately more during nonbreeding. The land-cover classes of closed forest and no vegetation were used less than expected from their availability during all seasons. "Avail" indicates locations available to Nēnē.

TABLE 4.   Fine-scale logistic regression-models, ranked by $QAIC_c$, of the Nēnē's habitat selection on Hawaiʻi Island, 2009–2011. Four top-ranked models and the full model from each analysis are presented.

Model[a]	K	$\Delta QAIC_c$ [b]	w_i
Full models			
Exotic grass + bunch grass + tree	20	0.00	0.71
Exotic grass + bunch grass	19	2.94	0.16
Meso-scale base model	17	4.72	0.07
Exotic grass	18	4.95	0.06
Time of day + grass + tree + shrub + herb + fern + sedge + exotic grass + short grass + S × exotic grass + S × short grass + bunch grass + tree × short grass + LC × bunch grass[c]	37	65.51	<0.01
Vegetation models			
Grass + S × grass	20	0.00	0.35
Meso-scale base model	17	0.04	0.34
Grass	18	0.27	0.31
Grass + tree + shrub + fern + herb + sedge + S × tree + S × grass[c]	24	9.63	<0.01
Grass models			
Exotic grass + bunch grass	19	0.00	0.55
Meso-scale base model	17	1.78	0.23
Exotic grass	18	2.01	0.20
Grass + short grass + bunch grass + exotic grass + S × Grass + S × short grass[c]	24	7.39	0.01

[a]All fine-scale models included four main effects and two interaction terms from meso-scale base model: land-cover class (LC) + elevation (ELEV) + distance from water (DW) + season (S) + LC × ELEV + DW × S. The base model was run independently of forward stepwise regression.
[b]Akaike's information criterion adjusted for small sample sizes and potentially overdispersed data; lowest $QAIC_c$ = 755.04, 759.72, and 757.98, for the full, vegetation, and grass models respectively.
[c]Full model.

weight ($w_i = 0.71$). Two vegetation models were separated by <2 $QAIC_c$ units from one another and the base model but were not more informative than the most parsimonious base model (Burnham and Anderson 2002). Top models in both the vegetation-composition and grass-composition analyses included all predictors in the base model. Fine-scale model coefficients are presented in Appendix 1.

On the basis of results with these models, we examined differences between cover classes of exotic grass with post hoc chi-squared tests. Nēnē used locations with ≥77% exotic grass cover disproportionately during the breeding and molting seasons ($\chi^2_1 = 19.1$, $P < 0.001$) but during the nonbreeding season used locations with ≥51% exotic grass cover less than expected from their availability ($\chi^2_2 = 22.9$, $P < 0.001$). To explore the role of bunch grass in fine-scale models, we compared the use and availability of native and exotic bunch grasses and that of bunch grasses in general. Differences between use and availability of bunch grasses in general were equivocal and confounded because the growth forms of some exotic bunch grasses were similar to that of the exotic sward grasses with which they occurred (≤10% cover $\chi^2_2 = 4.8$, $P = 0.09$; 11–76% cover $\chi^2_2 = 9.15$, $P = 0.01$). During the nonbreeding season, there was no significant difference between the use and availability of exotic bunch grasses ($\chi^2_2 = 2.5$, $P = 0.29$), but native bunch grasses

were used disproportionately ($\chi^2_1 = 5.9$, $P < 0.02$; Fig. 4). We found only exotic grasses in vegetation samples at Hakalau and BICC, so we did not test for differences in use of native and exotic grasses during breeding and molting. Locations with trees, the third predictor in the top model, were used less than expected from their availability, reflecting greater overall use of grass and shrubland in all seasons ($\chi^2_2 = 13.1$, $P < 0.002$).

DISCUSSION

IMPLICATIONS OF HABITAT SELECTION

All Nēnē we studied used multiple sites, shifted habitat use with the seasons, and closely tracked traditional movements reported by early naturalists (Henshaw 1902, Perkins 1903, Smith 1952). At both scales measured, they strongly preferred exotic grass and human-modified habitats during the breeding and molting seasons, native shrublands during the nonbreeding season, and sites in close proximity to water during the molting season. A preference for areas of cultivated grass during seasons of high caloric need (breeding and molting) contrasts with that reported in previous studies of the Nēnē's habitat selection (Banko et al. 1999). Although Black et al. (1994) and Woog (1999) found that exotic sward grasses are highly nutritious, they also found that Nēnē preferred native
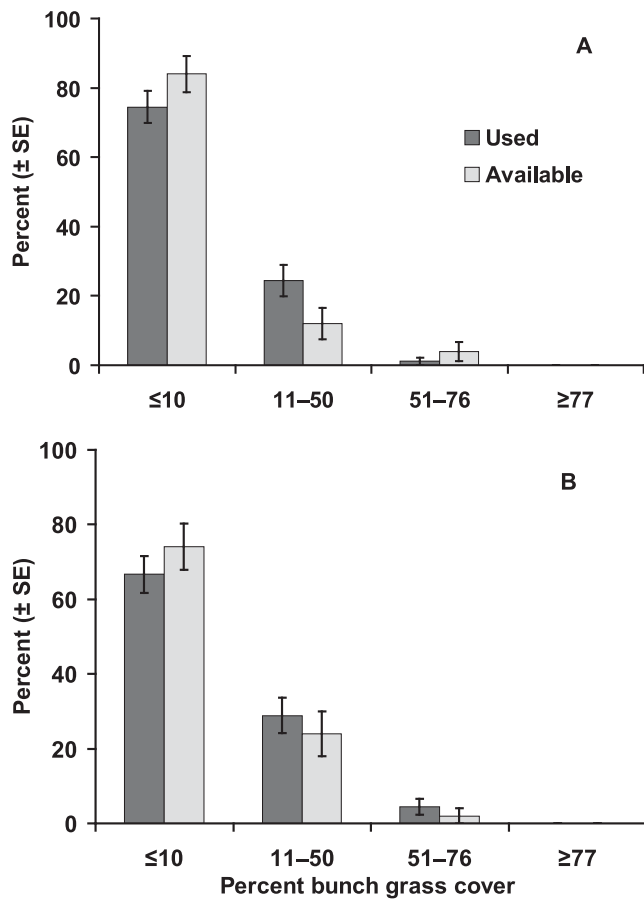
FIGURE 4. Percent of native bunch grass (A) and exotic bunch grass (B) cover at locations used by 10 Nēnē and at locations available to them during the nonbreeding season on Hawaiʻi Island, 2009–2011 ($n = 396$). Locations were divided into four cover classes: ≤10%, 11–50%, 51–76%, and ≥77%. Locations with 11–50% native bunch grass cover were used disproportionately. Use of other cover categories of native and exotic bunch grasses did not differ from that expected from their availability.

desert shrubland for nesting and molting. The Nēnē we studied demonstrated a strong preference for native shrublands during the nonbreeding season but little preference for shrublands during the breeding season or avoidance of them during the molting season. Historical records indicate that Nēnē used upper-elevation native shrublands during the nonbreeding season (Henshaw 1902, Perkins 1903, Baldwin 1945). Baldwin (1945) reported that at upper elevations Nēnē fed on berries of ʻōhelo (*Vaccinium reticulatum*), a species found in scrub at mid- to high elevations and fruiting primarily from June to September (Wagner et al. 1999), during the Nēnē's nonbreeding season. The patterns of movement we documented suggest that Nēnē may shift habitat use seasonally according to their nutritional needs, as do a number of other goose species (Bairlein and Gwinner 1994, Hupp and Robertson 1998, Hassall et al. 2001).

Although the Nēnē is often described as one of the most terrestrial of geese (Banko 1988, Batt 1992), during the molting season the birds we studied preferred locations near water. This seasonal preference for water suggests that a predator-avoidance strategy may persist in a species that evolved over 0.89 million years without mammalian predators (Paxinos et al. 2002). The Black Brant (*Branta bernicla nigricans*), Pink-footed Goose (*Anser brachyrhynchus*), Greylag Goose (*A. anser*), Barnacle Goose (*B. leucopsis*), and the closest relative of the Nēnē, the Canada Goose (*B. canadensis*), also rely on sources of water to escape from predators while flightless (Madsen and Mortensen 1987, Fox and Kahlert 2000, Radtke and Dieter 2010, Lewis et al. 2011). It is possible that Nēnē never lost their behavioral affinity for water but were simply restricted to high-elevation environments with few water resources.

We documented both daytime and nighttime locations of Nēnē, and our models found no diel pattern in habitat preference at either scale. During the nonbreeding season, however, we observed a strong pattern of movement between daytime and nighttime locations at Kahuku, Kīpuka ʻAinahou, and Kūlani that was also consistent with predator avoidance. At this season, at Kahuku and Kīpuka ʻAinahou, Nēnē spent the night almost exclusively in patches of sparsely vegetated, smooth-textured lava surrounded by rough-textured lava, which may deter resident feral dogs (*Canis familiaris*). It is possible that we were unable to measure biologically meaningful distinctions between daytime and nighttime locations. Complex landscape characteristics that may limit predators' movement, such as the texture and size of patches of lava, were not available. No spatial data were available on the sites' differences in predator communities. We did not observe patterns of diel movement during breeding and molting when ganders were defending nests or unable to fly.

Because the last remaining wild Nēnē were found in native shrublands at high elevations, these locations had been selected for reintroduction. Restriction to remote locations was caused by hunting, habitat loss, and predation by non-native mammals (Baldwin 1945, Banko et al. 1999). Black et al. (1997) found that Nēnē that remained at upper elevations year round experienced reduced productivity and higher mortality than those that dispersed from release sites. Black et al. (1994) argued that pastures were essential for population recovery, and during breeding and molt we documented preference for such grasslands when available. Hess et al. (2012) reported altitudinal migration of Nēnē on Hawaiʻi Island, from lower elevations during breeding and molting to subalpine locations during the nonbreeding season. This behavior was historically documented and thought to have been lost after the species' population decline in the 20th century.

Our findings highlight important considerations for the continued recovery of the Nēnē, addressing key knowledge gaps outlined in the recovery plan for this species, particularly during the nonbreeding season (USDI 2004). The protection and restoration of seasonally preferred habitats may

allow Nēnē to reoccupy additional portions of their historic range. Although the native shrublands at Kahuku and Kīpuka 'Ainahou occupied during the nonbreeding season by the Nēnē we studied are currently under state and federal protection, alteration of habitat by invasive species is a persistent threat. Introduced mammalian predators pose a persistent risk to population recovery without long-term trapping, particularly during breeding. However, the availability of water during molt may provide opportunity for Nēnē to escape predators. These findings may not apply to other subpopulations, whose patterns of diel and seasonal movement notably different (see Black et al. 1997, Woog 1999).

Because Nēnē strongly preferred exotic grasslands during breeding and molt, the restoration of these areas with native grass species may not be warranted. Moreover, similar low-elevation locations with restored native grassland may not attract Nēnē. Conversely, a strong preference for native shrubland at nonbreeding locations suggests the enhancement of exotic grasses in these areas may not benefit Nēnē. The importance of native bunch grasses within native shrublands during the nonbreeding season is still unclear because our study took place during an extended drought; native bunch grasses were desiccated during much of the study. Historically, during the nonbreeding season, Nēnē used native bunch grasses within shrubland (Baldwin 1947), although more contemporary studies report preference for exotic grasses (Black et al. 1994, Woog 1999). It is possible that Nēnē opportunistically shifted away from native grasses as more nutritious exotic grasses were cultivated for improved pastures and other purposes.

MEASURING HABITAT SELECTION ACROSS SPATIAL SCALES

Habitat measurements at multiple scales can clarify aspects of selection, including tradeoffs at different scales of use (Battin and Lawler 2006, Crampton and Sedinger 2011) and habitat selection at multiple resolutions (Rettie and Messier 2000, Apps et al. 2001). The rate of successful fixes provided by the PTTs we deployed was high, allowing us to record previously unavailable fine-scale data from remote, inaccessible locations spanning both the diel and annual cycles. We measured habitat selection at two scales to identify the optimal resolution for capturing appropriate habitat characteristics and variation in use patterns (Porter and Church 1987).

We expected the underlying mechanisms of the Nēnē's habitat selection to be driven by fine-scale factors, as suggested by Apps et al. (2001). Our results supported habitat selection strongly at the meso scale but less conclusively at the fine scale. The predictive ability of two of three fine-scale models, one containing broad vegetation categories, the other a grass-composition model, was not substantially better than that of the top-ranked meso-scale model. The term for exotic grass in the full fine-scale model did not provide additional insight beyond that for cover of exotic grass in the meso-scale

model. Grass height may not have been an important predictor of Nēnē presence at the fine scale because only short exotic grasses were available at breeding and molting sites. Woog and Black (2001) found a preference for grasses ≤11 cm tall, and at our study sites the species of short grass were overwhelmingly exotic, particularly at locations with dense grass cover.

For purposes of conservation and management, the additional complexity of the top-ranked full fine-scale model, including costs of data collection, added relatively little information to the meso-scale model. Nevertheless, the similarity of results of analyses at two resolutions emphasized that the predictors in the models were biologically appropriate and that meso-scale geospatial data appear to be sufficient for modeling, understanding, and managing Nēnē habitats.

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