Corridor- and stopover-use of the Hawaiian goose (*Branta sandvicensis*), an intratropical altitudinal migrant

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Abstract: We outfitted six male Hawaiian geese, or nene (*Branta sandvicensis*), with 45-g solar-powered satellite transmitters and collected four location coordinates d^{-1} from 2010 to 2012. We used 6193 coordinates to characterize migration corridors, habitat preferences and temporal patterns of displacement for 16 migration events with Brownian bridge utilization distributions (BBUD). We used 1552 coordinates to characterize stopovers from 37 shorter-distance movement events with 25% BBUDs. Two subpopulations used a well-defined common migration corridor spanning a broad gradient of elevation. Use of native-dominated subalpine shrubland was 2.81 times more likely than the availability of this land-cover type. The nene differed from other tropical and temperate-zone migrant birds in that: (1) migration distance and the number of stopovers were unrelated (Mann–Whitney test W = 241, P < 0.006), and; (2) individual movements were not unidirectional suggesting that social interactions may be more important than refuelling en route; but like other species, nene made more direct migrations with fewer stopovers in return to breeding areas (0.58 ± 0.50) than in migration away from breeding areas (1.64 ± 0.48). Our findings, combined with the direction and timing of migration, which is opposite that of most other intratropical migrants, suggest fundamentally different drivers of altitudinal migration.

Key Words: Brownian bridge movement models, habitat use, migration corridors, nene, net squared displacement, stopover ecology, utilization distributions

INTRODUCTION

The role of corridors and stopovers for birds that migrate entirely within the tropics may differ fundamentally from that of migrants originating in temperate zones (Boyle 2010). Migration is a widespread adaptive response throughout bird taxa to exploit the availability of ephemeral resources (Alerstam *et al.* 2006, Boyle & Conway 2007, Pulido 2007). While latitudinal migrations characterize many temperate-zone birds, short-distance altitudinal migration is common among tropical species (Ornelas & Arizmendi 1995, Stiles 1988). Underlying drivers of intratropical altitudinal migration differ from latitudinal migration and may include predation, parasites or storms in addition to resource availability (Boyle 2008, 2010; Boyle *et al.* 2010, Loiselle & Blake 1991). Although the diversity of habitats tropical bird species encounter across relatively short-

distance altitudinal migrations can be as dramatic as those of latitudinal migrants (Chesser 1994), the role of stopovers may differ according to drivers of migration and landscape connectivity.

The functional connectivity of migration routes is dependent on the landscape matrix and vagility of different species; birds are able to fly over unsuitable habitat patches, whereas non-volant animals may need contiguous suitable habitat to complete migration (Bennett 2003, Berger *et al.* 2006, Uezu *et al.* 2005). Refuelling at stopovers within corridors is often essential during the course of migration, requiring more stopovers to complete longer-distance migrations (Sawyer & Kauffman 2011). Latitudinal migrants may select stopovers for a variety of reasons, including forage quality and density, water resources, weather conditions and predator densities (Batbayar *et al.* 2011, Dingle & Drake 2007, Weber *et al.* 1998). Although stopover ecology is a prominent area of avian research (Bonter *et al.* 2008, Erni *et al.* 2002, Newton 2008), the role of stopovers has been studied in few other intratropical

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migrants and is little known in island species (Davenport *et al.* 2012, Powell & Bjork 2004).

Our objective was to quantify how population-level patterns of altitudinal migration in an insular tropical bird, the endangered Hawaiian goose or nene (*Branta sandvicensis* Vigors), differ from temperate zone ancestors and other intratropical altitudinal migrant birds. Although probable migration routes have been identified, the spatial extent of corridors, use of stopovers and habitat preferences during migration have not been investigated (Hess *et al.* 2012). We hypothesized that: (1) nene subpopulations use common, well-defined corridors and stopovers during altitudinal migration that lie within its historical geographic range prior to severe population decline; (2) the nene makes longer-duration migrations with more stopovers en route to non-breeding areas than in return to breeding areas as do other goose species; (3) habitat use during migration is similar to the non-breeding period; (4) migration distance and the number of stopovers are related as in other migratory animals; and (5) stopovers occur along unidirectional movements. Hypotheses 4 and 5 would both indicate that refuelling en route is necessary to complete migration. We used Brownian bridge utilization distribution (BBUD) models to characterize migration corridors, stopovers and habitat preferences during migration and shorter-distance movements (Bullard 1999, Prosser *et al.* 2011, Sawyer & Kauffman 2011, Sawyer *et al.* 2009). We also used measures of displacement to independently define stopovers and analyse temporal patterns in movement (Bunnefeld *et al.* 2011, Kareiva & Shigesada 1983, van Wijk *et al.* 2011).

METHODS

Study species and area

The movements of nene are opposite in direction and timing of most other intratropical altitudinal migrants which typically move from higher-elevation breeding ranges to lower-elevation non-breeding ranges (Boyle 2010, Hobson *et al.* 2003, Johnson & Maclean 1994, Ornelas & Arizmendi 1995). Although the seasonal timing of nene migration roughly corresponds to that of the Canada goose (*Branta canadensis* Linnaeus) from which nene evolved ~1 Mya (Paxinos *et al.* 2002), altitudinal migration is not known in the Canada goose (Mowbray *et al.* 2002). The nene breeds and moults at lower-elevation areas during September to April, and then migrates to higher-elevation areas during the non-breeding season, but with substantial individual variation (Banko *et al.* 1999, Hess *et al.* 2012).

We studied the nene from two breeding sites on Hawai'i Island: Big Island Country Club golf course

(BICC; 625–665 m asl) and Hakalau Forest National Wildlife Refuge (Hakalau; 995–2030 m asl). These two subpopulations were re-established after 1991 and 1996, respectively, but were isolated from each other until traditional seasonal movement patterns became re-established coincident with steady recovery from near-extinction (Henshaw 1902, Hess 2011, Perkins 1903, Smith 1952, USDI 2004). Both subpopulations move seasonally to the Kahuku Unit of Hawai'i Volcanoes National Park (Kahuku; 585–3885 m asl) (Hess *et al.* 2012). Predominant ground cover at BICC was non-native grass (*Cenchrus clandestinus* (Hochst. ex Chiov.) Morrone). Higher-elevation shrubland at Kahuku was dominated by native species including *Leptecophylla tameiameia* (Cham. & Schltdl.) C. M. Weiller and *Vaccinium reticulatum* Sm. with sparse ground cover of the native grass *Deschampsia nubigena* Hillebr. and large areas of recent lava flows with sparse vegetation (Hess *et al.* 2012, Leopold & Hess 2013). Modified areas included water features and turf mowed for recreational sports primarily at BICC. Hakalau was formerly a densely forested environment unsuitable for nene, but large areas were converted to several species of non-native pasture grasses.

Satellite telemetry

We outfitted six male nene in 2010 and 2011 with 45-g solar-powered platform transmitter terminals (PTTs) equipped with global positioning system (GPS) capability (Microwave Telemetry, Columbia, MD). PTTs measured $57 \times 30 \times 20$ mm and were attached dorsally with a double-threaded backpack harness made of Teflon® ribbon (Bally Ribbon Mills, Bally, PA). Capture, handling and transmitter attachment procedures were approved by University of Hawai'i IACUC Protocol 08–636. Transmitter packages weighed $\leq 3\%$ of each bird's mass. PTT units were fitted only on males to reduce potential interference with breeding and because mates are generally monogamous and migrate together. Candidates for PTTs must have nested at Hakalau or BICC, been observed at Kahuku, but were not related or members of the same social group. All PTTs were programmed to record GPS coordinates at 00h00, 10h00, 14h00 and 19h00 HST to capture movements from midday to evening and nightly roosts. Data were retrieved every 3 d (CLS America Inc., Largo, MD). We conducted stationary trials for PTTs prior to deployment and found 95% of GPS coordinates were horizontally accurate ±15 m.

We defined a migration event as the departure and return of an individual to a breeding site, and included 5 d of location data before and after each migration event. If 5 d of data comprised >50% of locations, data from breeding grounds were reduced to 50% of locations per migration event to limit weighting of BBUDs at

terminal destinations. We included all available data in cases where transmitters ceased functioning before an individual returned to its breeding grounds. We also examined shorter-duration movement events defined as the departure from a site and arrival at the same site or another within a season. For analysis, we included data from a 24-h period prior to departure, all data collected while in transit, and 24 h after reaching a destination. We used migration events to address hypothesis 1 and movement events to address hypotheses 4 and 5.

Movement modelling

We created BBUDs for each migration event using the ADEhabitatHR package (version 0.3.4) in program R (R Development Core Team, v. 2.12.2) to determine migration corridors. We used a 15-m location error to correspond with the error radius of GPS coordinate data, and a grid cell size of 100×100 m to generate BBUDs. We generated discrete BBUDs at 2.5% intervals ranging from 5–99% to create high-precision BBUD polygons for each migration event. All areas outside of each 99% BBUD were assigned a dummy category value. We used linear regression to determine if the number of locations was related to the area or natural logarithm of area for 95%, 75%, 50% and 25% BBUDs. BBUD polygon data were imported into ArcMap v. 10 (ESRI, Redlands, CA) and converted to raster datasets with 30×30-m resolution. We averaged each subject's BBUDs and averaged BBUDs among subjects from each breeding area (BICC, $n = 4$; Hakalau, $n = 2$) to make inferences at the subpopulation level. We also averaged among all subjects to make inferences at the population level ($n = 6$). To simplify interpretation of averaged BBUDs, we rescaled categories by quartiles in the same manner as Sawyer *et al.* (2009): highest use ($\leq 25\%$), moderate–high use (>25–50%), low-moderate use (>50–75%), and lowest use (>75–99%).

We created BBUDs for each movement event and converted polygon data to raster datasets as described above. We used linear regression to determine if the number of locations was related to the area or natural logarithm of area for 95%, 50% and 25% BBUDs. In six cases, 95% BBUDs were clipped to the shoreline of Hawai'i Island because they exceeded the geographic range of nene. We defined stopovers as 25% BBUDs occurring outside breeding and non-breeding areas for each subject (Sawyer *et al.* 2009). We overlaid 25% BBUDs and summed values among all movement events to identify frequently used stopovers. We compared the locations of current migration corridors, stopovers and non-breeding areas to the historic geographic range of nene from observations made prior to 1944 (Baldwin 1945).

We used displacement thresholds to independently identify stopover sites (van Wijk *et al.* 2011). We defined a displacement threshold as a cluster of consecutive locations within 10 km from the previous location and occurring >10 km from breeding or non-breeding sites. Stopover coordinates were defined as the mean latitude and longitude of each cluster. We used Mann–Whitney tests to determine if number of stopovers differed between BBUDs and our displacement criteria. We also used a Mann–Whitney test to evaluate whether the number of stopovers differed between migrations to and from breeding and non-breeding sites. We used linear regression to determine if there was a relationship between the total distance travelled during movement events and the number of stopovers used en route to non-breeding areas, during return to breeding areas, in movements between other areas, and in all combined movement events. We also used net squared displacement (NSD) values from BBUD migration event output to examine directionality through time during migration (Bunnefeld *et al.* 2011, Kareiva & Shigesada 1983). We presented the expected squared distance, rather than linear distance, which increases linearly with time (Börger *et al.* 2008).

We used Hawai'i Gap Analysis data (http://gis1.usgs.gov/csas/gap/viewer/ land_cover/ Map.aspx) classified at 30×30-m resolution with land-cover categories modified as per Leopold & Hess (2013) to determine habitat characteristics at stopovers. We also assessed the proportion of land-cover types within BBUDs of stopover and non-breeding sites and compared values relative to land-cover availability within study sites and Hawai'i Island overall. Only habitats within the documented altitudinal range of ≤ 2760 m were included in analyses (Hess *et al.* 2012).

RESULTS

Data from six nene with PTT units during 2010–2012 provided a GPS coordinate fix rate of 95%. A total of 6193 GPS coordinates were used to estimate BBUDs for 16 migration events, although only 14 were suitable for analysis (Figure 1; Appendix 1). Estimated 95% BBUDs ranged in area between 7095–106 349 ha. The area of 75%, 50% and 25% BBUD estimates were not related to numbers of locations, indicating sufficient sample size. However, 95% BBUDs were negatively related to numbers of locations, indicating that sample sizes were not sufficient for determining precise BBUD size (Table 1). The 5 d of origin and destination data that we used to define each migration event likely affected this relationship, particularly for BBUDs with fewer locations en route. Highest-use areas were identified at breeding sites of Hakalau (Figure 2a, b) and BICC (Figure 2c, d),
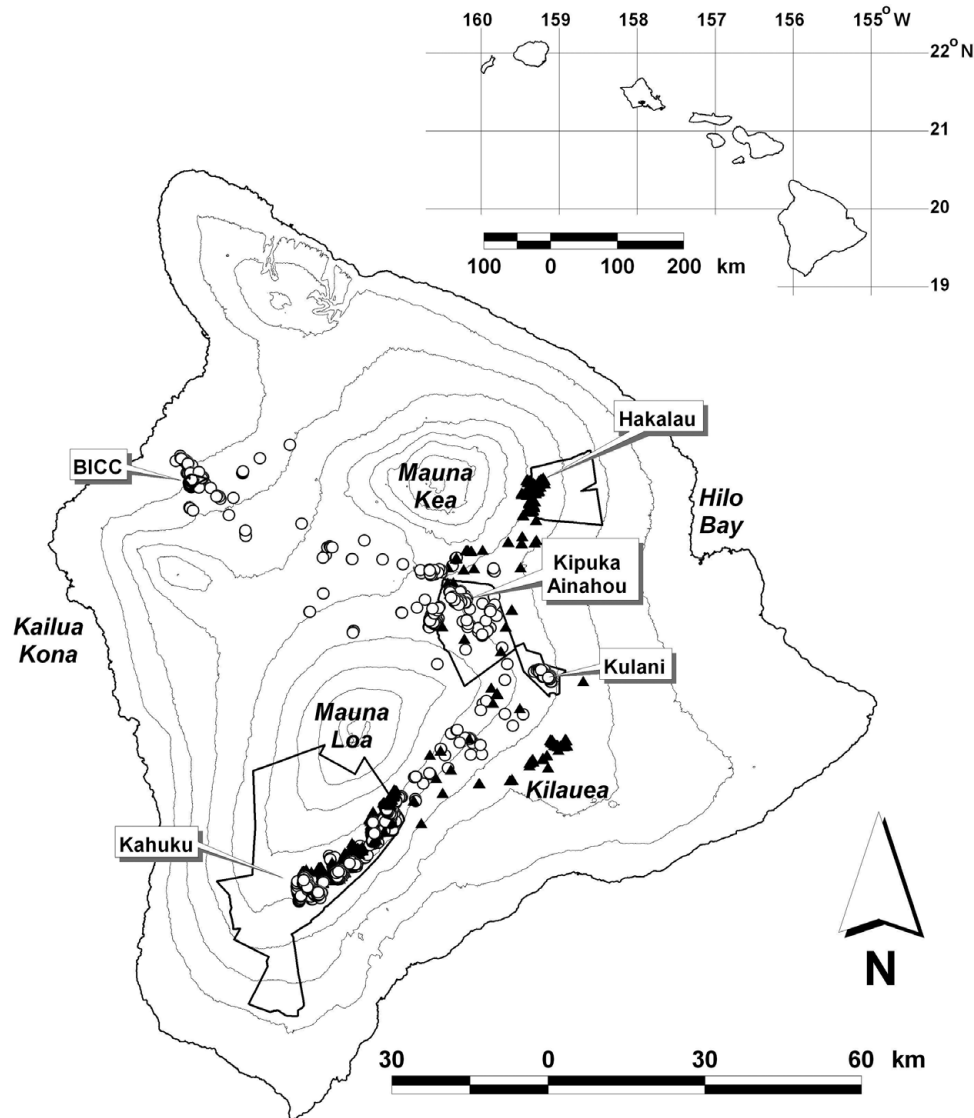
Figure 1. Five areas on Hawai'i Island used by nene (*Branta sandvicensis*) during migrations in 2010–2012. Breeding areas were at Hakalau Forest NWR (Hakalau; black triangles) and Big Island Country Club (BICC) golf course (white circles); non-breeding areas included Kīpuka 'Ainahou Nene Sanctuary (Kīpuka 'Ainahou), Kūlani Correctional Facility (Kūlani), and the Kahuku unit of Hawai'i Volcanoes National Park (Kahuku). Total $n =$ 6193 locations from satellite telemetry. Elevation contours are at 500-m intervals.

Table 1. Relationship between area of Brownian bridge utilization distributions (BBUDs) and number of locations during migration ($n =$ 6193) and movement ($n = 1552$) events of six nene (*Branta sandvicensis*) individuals on Hawai'i Island, 2010–2012.

| BBUD (%)	n	Area					(*ln*) Area			
		Mean (ha)	Coefficient	F	P	r^2	Coefficient	F	P	r^2
Migration events	14									
95		33,200	−49.4	5.18	0.042	24.3	−0.002	7.17	0.020	32.2
75		8590	−11.7	3.37	0.091	15.4	−0.001	3.52	0.085	16.2
50		3560	−4.57	3.56	0.083	16.5	−0.001	4.02	0.068	18.8
25		846	−1.67	3.49	0.087	16.0	−0.002	2.88	0.115	12.7
Movement events	33									
95		105,000	−751	5.89	0.021	13.3	−0.013	46.8	<0.001	58.5
50		18,000	−148	5.24	0.029	11.7	−0.018	58.0	<0.001	64.0
25		6200	−53.2	4.73	0.037	10.4	−0.024	84.7	<0.001	72.3
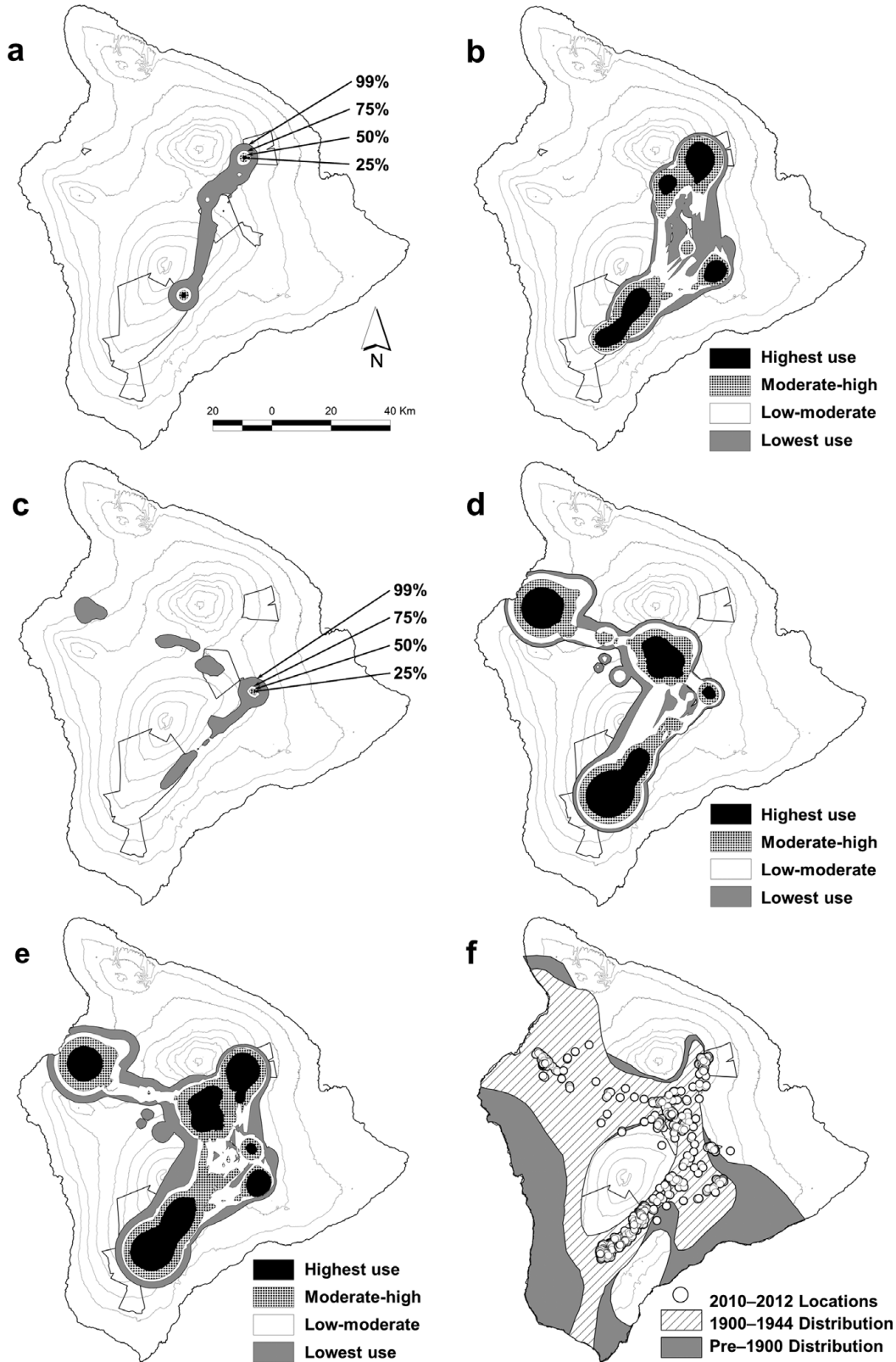
Figure 2. Migration corridors of nene (*Branta sandvicensis*) on Hawai'i Island 2010–2012 based on Brownian bridge utilization distributions (BBUD). A BBUD was generated for each migration event from nene breeding at Hakalau (a) and averaged (*n* = 7) across two study subjects (b). A BBUD was generated for each migration event from nene breeding at BICC (c) and averaged (*n* = 7) across four study subjects (d). BBUDs of all migration events were averaged across six study subjects (e). All telemetry locations from 2010–2012 were overlaid on the historical distribution of nene prior to 1944 (f).

at Kīpuka ʻAinahou Nene Sanctuary (Kīpuka ʻAinahou; 2000 m asl), a nearby reservoir on Mauna Kea (2188 m asl), and at non-breeding areas of Kahuku and Kūlani Correctional Facility (Kūlani; 1580 m asl; Figure 2e). A corridor of moderate to high use occurred between both breeding sites and Kīpuka ʻAinahou, then merged and extended to Kahuku (Figure 2e). Three nene subjects flew directly from non-breeding to breeding sites on four occasions and one subject completed four migration events during 2010. Approximately 11.8% of satellite telemetry locations occurred outside of the reported pre-1900 distribution of nene (Figure 2f). We found no evidence for migration corridors in the former range of leeward Mauna Loa and Hualālai volcanoes (Baldwin 1945; Figures 2e, f).

A total of 1552 GPS coordinates were used to estimate 25% BBUDs from 37 movement events, although only 33 were suitable for analysis. Estimated 95% BBUDs ranged in area 23.4–37 010 ha (Appendix 2). The number of locations included in movement events ranged from 8–274, although the event with 274 locations was due to the use of an alternative breeding site that was not within any study area. The area of 95%, 50% and 25% BBUDs were negatively related to numbers of locations, indicating that sample sizes were not sufficient for determining the precise area of BBUDs (Table 1). Highest-use areas were identified at breeding sites of Hakalau (Figure 3a) and BICC (Figure 3b). The sum of all 25% BBUDs from movement events contained 30 stopovers between Mauna Kea and Mauna Loa, including a reservoir on Mauna Kea and a large area at Kīpuka ʻAinahou (Table 2; Figure 3c).

We identified 50 stopovers using displacement thresholds (Table 2; Figure 3d). Stopover locations included frequent use of Kīpuka ʻAinahou in addition to locations scattered across the northern and eastern slopes of Mauna Loa at 1225–2710 m asl. Plots of NSD on ordinal date demonstrated multiple migration patterns and four of six subjects demonstrated non-unidirectional movements during the non-breeding season. Some individuals such as 90848 flew to Kahuku and returned to breeding sites with few pauses (Figure 4a); 90849 repeatedly flew between multiple stopover areas and multiple non-breeding areas (Figure 4b); 90847 flew repeatedly between multiple non-breeding areas (Figure 4c); and 90853 completed full migration twice prior to breeding (Figure 4d).

Confidence intervals of the mean number of stopovers determined with 25% BBUDs and displacement threshold criteria were exclusive for breeding to non-breeding movements and for other movement events (Table 2). We found a greater number of stopovers used in movements from breeding to non-breeding sites than from non-breeding to breeding sites with both displacement threshold and 25% BBUD criteria, respectively (Mann–Whitney test $W = 241$, $P < 0.006$; $W = 227$, $P =$

0.032). We found no relationship between number of stopovers determined by displacement thresholds and direct distance between breeding and non-breeding sites ($F_{1,31} = 0.11$, $P = 0.738$, $r^2 < 0.01$), although the relationship between number of stopovers and total distance travelled by nene was significant ($F_{1,31} = 25.8$, $P < 0.001$, $r^2 = 43.7$). Nene travelled a mean distance of 1.95 times further than the direct distance between destinations (Appendix 2).

Nene demonstrated strong preferences for particular land-cover classes relative to overall availability based upon 50% migration corridor BBUDs and 25% movement event BBUDs, disproportionately using native shrubland and sparse vegetation at stopovers during migration (Table 3). Nene underutilized exotic grass and open forests, and avoided closed forests and modified areas of mowed turf. Habitat preferences during migration and stopovers reflected historical records of non-breeding locations, although the use of stopovers near water features was not previously reported (Baldwin 1945).

DISCUSSION

We found well-defined common migration corridors and stopovers used by nene during annual migrations from two widely separated breeding populations that were previously isolated from each other. Subjects from respective breeding populations used separate corridors during altitudinal migration to access a common stopover site at Kīpuka ʻAinahou near the centre of the island, where they joined to use a common corridor on windward Mauna Loa to access the southern non-breeding destination at Kahuku. Nene typically stopped at several locations en route during movement events, nearly doubling their total movement distance, but were clearly capable of moving between terminal destinations regardless of habitat, occasionally flying directly between non-breeding and breeding destinations. All of the migration corridors, stopovers and non-breeding areas we identified were within the historical geographic range of nene. Although we found no evidence for any current use of the leeward western flanks of Mauna Loa or Hualālai volcanoes documented by Baldwin (1945), it is possible that other individuals may use these areas.

Stopovers at Kīpuka ʻAinahou were used by several subjects for weeks, suggesting the area may also serve as an alternative non-breeding destination. Many other nene from Hakalau and BICC also spent extended periods at Kīpuka ʻAinahou during the non-breeding season (Hess *et al.* 2012). Baldwin (1945) reported numerous non-breeding season observations in this area and surrounding vicinity from 1890–1942 as nene approached their historic minimum abundance, indicating traditional use of this area by the relictual
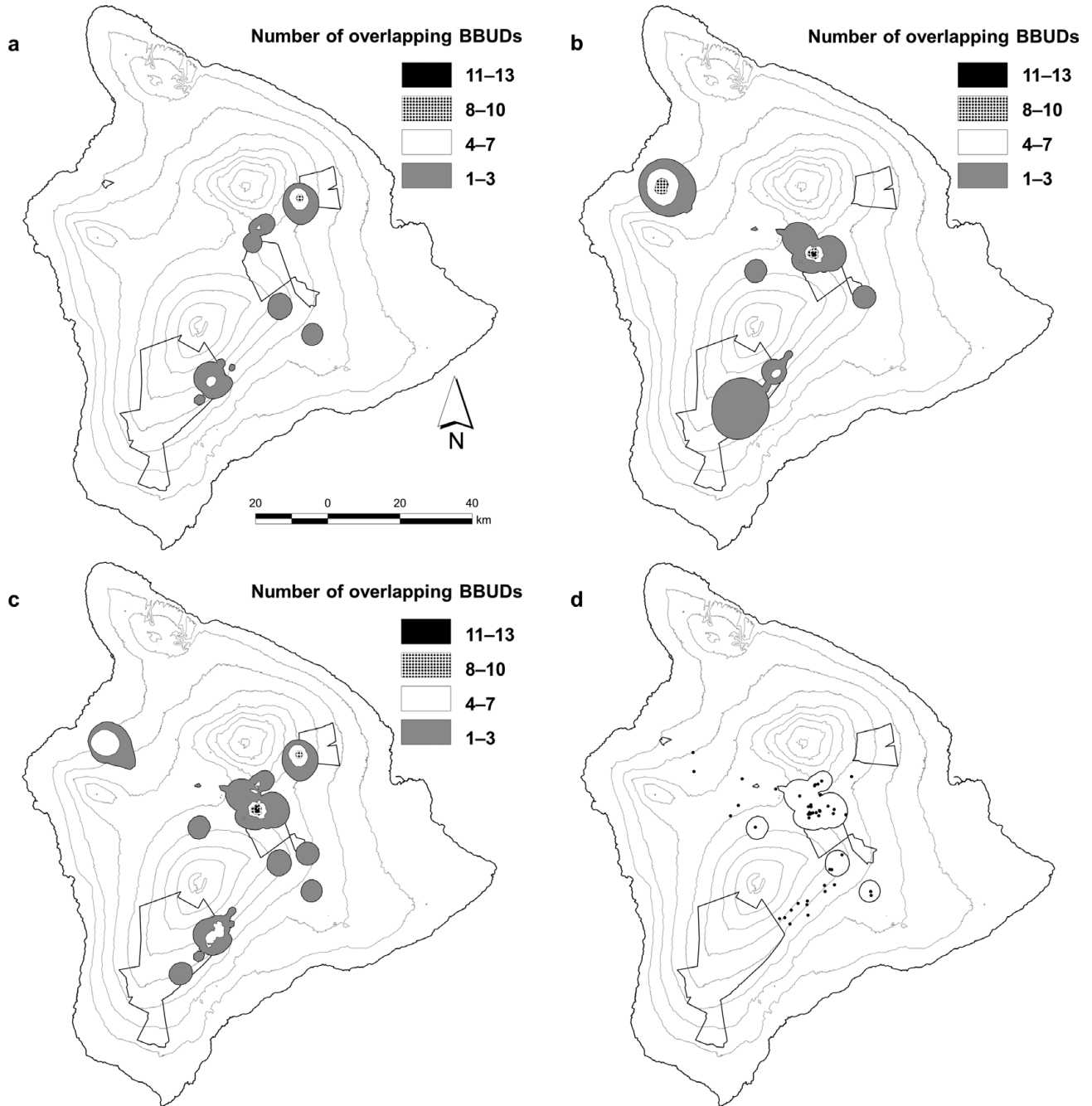
Figure 3. Stopover sites of nene (*Branta sandvicensis*) on Hawai'i Island from 2010–2012 defined by 25% Brownian bridge utilization distributions (BBUDs) and displacement thresholds of movement events. All BBUDs (*n* = 13) of two nene breeding at Hakalau were summed (a) and BBUDs (*n* = 20) of four nene breeding at BICC were summed (b). All 25% BBUDs of six study subjects from both breeding location were summed (c). The locations of stopovers determined by displacement thresholds (black circles) were overlaid on the outlines of stopovers determined by 25% BBUDs (d).

population. The origin of individuals and significance of migration routes, corridors and stopovers, however, were unknown at that time.

Migration routes and long-distance movements are culturally transmitted from adults to goslings in many goose species, including nene (Banko *et al.* 1999, Sutherland 1998), suggesting that current use of these

stopover locations within corridors may be strongly influenced by traditional knowledge from previous generations, presumably from those that survived the severe population reduction of the mid-20th century. If nene form pair-bonds during the non-breeding season as do many other goose species (Robertson & Cooke 1999), overlapping migration corridors may serve to enhance

Table 2. Relationship between number of stopovers and total distance travelled during movement events of six nene (*Branta sandvicensis*) individuals on Hawai'i Island, 2010–2012 determined by Brownian bridge utilization distributions (BBUDs) and displacement threshold criteria. The number of stopovers during movements from breeding to non-breeding areas did not differ between BBUD and displacement criteria (Mann–Whitney test W = 242, P ≤0.057); movements from non-breeding to breeding areas also did not differ (W = 153, P >0.090); however, stopovers during all other movements differed (W = 145, P < 0.011).

|	*n* Movement events	Stopovers				Distance travelled				
		n	Median	Mean	95% CI	Mean (km)	Coefficient	*F*	P	*r*²
Breeding to non-breeding						153				
BBUD	14	15	1	1.07	0.718–1.42		0.002	2.70	0.127	11.5
Displacement	14	23	2	1.64	1.16–2.13		0.003	2.43	0.145	9.90
Non-breeding to breeding						101				
BBUD	12	6	0	0.500	0.076–0.924		0.004	2.05	0.182	8.70
Displacement	12	7	0	0.583	0.085–1.08		0.004	1.45	0.256	4.00
Other						146				
BBUD	11	9	1	0.818	0.418–1.22		0.002	0.600	0.458	0.000
Displacement	10	20	2	2.00	1.26–2.74		0.004	1.33	0.283	3.50
Combined						134				
BBUD	37	30	1	0.81	0.151–1.47		0.003	6.58	0.015	13.4
Displacement	36	50	1	1.39	0.339–2.44		0.004	7.55	0.010	15.8
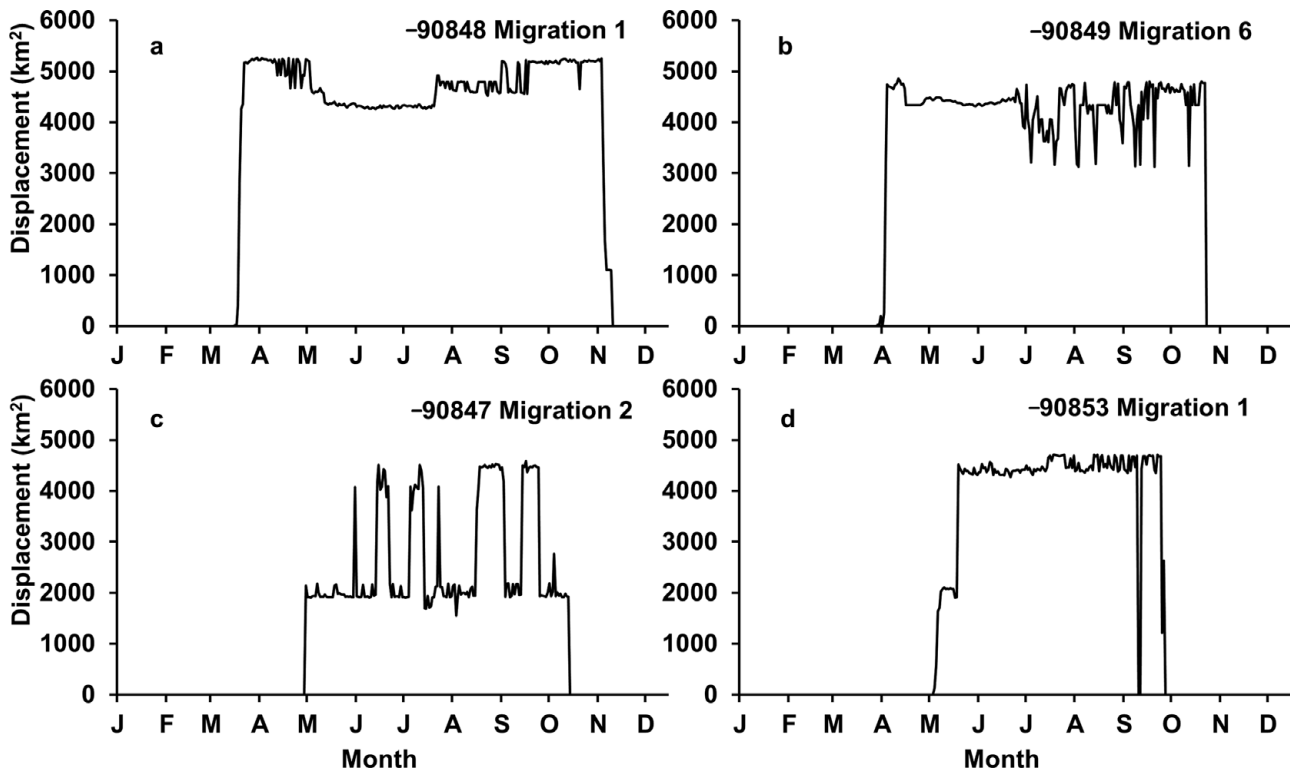
Figure 4. Temporal patterns in nene (*Branta sandvicensis*) migration determined by net squared displacement for four migration events on Hawai'i Island during 2010–2012. Patterns included direct flights with few pauses between breeding and non-breeding areas (a), flights between multiple stopovers and multiple non-breeding areas (b), flights between multiple non-breeding areas (c), and multiple complete migrations between breeding and non-breeding areas (d).

genetic exchange between subpopulations. Further investigation of social dynamics and traditional use of stopovers and non-breeding destinations may reveal additional factors related to the seasonal importance of these locations during migration.

The role of stopovers for species that migrate only moderate distances may differ from that of long-distance migrants which require refuelling en route. Altitudinal migrants may need few stopovers if overall migration distance is relatively short, or may use many stopovers for

Table 3. Habitat use relative to habitat availability for migration corridors based on 50% Brownian bridge utilization distributions (BBUDs) of migration events, and 25% BBUD estimates of stopover and non-breeding locations, respectively, of six nene (*Branta sandvicensis*) individuals on Hawai'i Island, 2010–2012. Odds ratios are based on habitat used relative to total available habitat.

Site	Area (ha)		Closed forest >60% cover	Open forest 25%–60% cover	Exotic grass	Modified	Native shrubland	Sparse vegetation
Migration								
	164 000	Used	0.177	0.110	0.162	0.005	0.259	0.288
	971 000	Available	0.214	0.152	0.223	0.049	0.140	0.221
Odds ratio			0.790	0.690	0.674	0.098	2.15	1.43
Stopover								
Kīpuka 'Ainahou		Used	0.058	0.035	0.107	0.000	0.351	0.449
	14 200	Available	0.100	0.057	0.092	0.003	0.272	0.475
Other		Used	0.151	0.061	0.203	0.008	0.230	0.346
	957 000	Available	0.224	0.136	0.227	0.050	0.143	0.223
Non-breeding								
Kahuku		Used	0.058	0.060	0.005	0.000	0.560	0.318
	46 800	Available	0.072	0.055	0.030	< 0.001	0.296	0.548
Kūlani		Used	0.040	0.832	0.106	0.008	0.003	0.011
	2910	Available	0.099	0.687	0.164	0.009	0.017	0.024
Stopover and		Used	0.109	0.089	0.139	0.005	0.314	0.343
Non-breeding Total	971 000	Available	0.214	0.152	0.223	0.049	0.140	0.221
Odds ratio used/available	–		0.449	0.545	0.563	0.010	2.81	1.84

relatively long time periods to exploit ephemeral resources as they move through altitudinal zones. Drivers of migration may also differ between upslope and downslope movements for intratropical altitudinal migrants (Boyle 2010, Boyle *et al.* 2010). Nene used numerous stopovers during migration away from breeding areas, but used fewer stopovers and returned more quickly during migrations back to breeding areas. Other bird species also exhibit protracted post-breeding migration patterns (O'Reilly & Wingfield 1995). If stopovers were necessary for refuelling, the number of stopovers used and migration distance should be positively related (Sawyer & Kauffman 2011). The fact that nene travelled substantially further than direct distances after breeding indicates factors others than refuelling influenced both the duration and routes of migration. Social avian species are known to congregate at stopovers, suggesting that the role of social interactions may be important during migration (Kruckenberg & Borbach-Jaene 2004).

We found that habitat preferences along migration routes and stopovers corresponded with preferences at non-breeding areas (Cornett 2011, Leopold & Hess 2013). Nene encountered a wide diversity of habitats over a broad altitudinal gradient, ranging from non-native low-elevation grasslands to nearly barren lava flows at >2700 m asl. Stopovers primarily occurred at the confluence of movement between the two breeding subpopulations, most frequently in native-dominated subalpine shrubland, but also at an unnatural water feature surrounded by mixed exotic and native grassland. Stopovers were not dominated by exotic grass habitats such as those strongly preferred during breeding and moulting (Leopold & Hess 2013). Further research using spatial patterns of NDVI may help determine if intratropical migrants such as nene follow the phenology of vegetation during migration to take advantage of the seasonal availability of food resources in space and time as do some migrant geese that breed in temperate zones (van der Graaf *et al.* 2006, van Wijk *et al.* 2011). Alternatively, the timing of migration initiation may be unrelated to food resource availability and subject to endogenous control as in other tropical bird species which are influenced by small shifts in photoperiod (Styrsky *et al.* 2004). Our findings, and the direction and timing of migration, which is opposite that of other intratropical altitudinal migrants, suggest that the drivers of nene migration may differ fundamentally from most other tropical birds.

ACKNOWLEDGEMENTS

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Appendix 1. Identities, origin, destination, number of locations, sample period, and area of Brownian bridge utilization distributions (BBUDs) for migration events of six nene (*Branta sandvicensis*) individuals on Hawai'i Island, 2010–2012. Migration events were defined as a departure from and return to a breeding location including 5 d of location data at the breeding site before and after each migration. Dashes indicate migration event was excluded from analyses.

Bird ID	Origin	Destination	Migration event	Number of locations	Begin date	End date	95% UD area (ha)
90847	BICC	Kūlani, Kahuku	1	484	8 May 2010	11 September 2010	7090
90847	BICC	Kūlani, Kahuku	2	689	24 April 2011	18 October 11	17 900
90848	Hakalau	Kahuku	1	937	12 March 2011	16 November 2011	9600
90848	Hakalau	Kahuku	2	473	20 May 2012	16 September 2012	13 000
90849	Hakalau	Kahuku	1	84	24 July 2010	14 August 2010	17 900
90849	Hakalau	Kahuku	2	83	13 August 2010	3 September 2010	39 800
90849	Hakalau	Kahuku	3	68	9 September 2010	26 September 2010	37 400
90849	Hakalau	Kahuku	4	53	28 October 2010	13 November 2010	65 300
90849	Hakalau	Kahuku	5	314	19 November 2010	17 February 2011	–
90849	Hakalau	Kahuku	6	840	25 March 2011	27 October 2011	9650
90849	Hakalau	Kahuku	7	20	29 October 2011	3 November 2011	–
90850	BICC	Kahuku	1	630	13 May 2010	23 October 2010	35 700
90850	BICC	Kahuku	2	511	22 April 2011	29 August 2011	15 700
90852	BICC	Kahuku	1	295	21 April 2011	15 July 2011	16 700
90853	BICC	Kahuku	1	592	28 April 2011	1 October 2011	44 700
90853	BICC	Kahuku	2	110	6 October 2011	4 November 2011	106 000
Total/Range	–	–	16	6193	8 May 2010	16 September 2012	7090–106 000

Appendix 2. Identities, origin, destination, number of locations, sample period, and area of Brownian bridge utilization distributions (BBUDs) for movement events of six nene (*Branta sandvicensis*) individuals on Hawai'i Island, 2010–2012. Dashes indicate movement event was excluded from analyses. Movement index was calculated as the ratio of total distance travelled by Nēnē to direct distance between breeding and non-breeding areas.

Bird ID	Origin	Destination	Movement event	Number of locations	Begin date	End date	25% UD area (ha)	Movement index
90847	BICC	Kūlani	1	15	11 May 2010	15 May 2010	4470	1.44
	Kūlani	Kūlani	2	13	4 July 2010	8 July 2010	3960	2.28
	Kūlani	BICC	3	19	2 September 2010	7 September 2010	7050	1.28
	BICC	Kahuku	4	183	28 April 2011	14 June 2011	311	4.77
	Kahuku	Kahuku	5	72	19 June 2011	7 July 2011	621	3.62
	Kahuku	Kahuku	6	141	12 July 2011	17 August 2011	30.7	5.70
	Kahuku	Kahuku	7	51	31 August 2011	14 September 2011	1100	2.50
	Kahuku	BICC	8	82	23 September 2011	14 October 2011	1050	2.94
90848	Hakalau	Kahuku	1	17	16 March 2011	20 March 2011	3990	1.01
	Kahuku	Hakalau	2	21	3 November 2011	10 November 2011	3750	1.11
	Hakalau	Kahuku	3	139	23 May 2012	27 June 2012	258	1.88
90849	Hakalau	Hakalau	1	59	25 July 2010	10 August 2010	477	1.97
	Hakalau	Kahuku	2	9	17 August 2010	19 August 2010	11 800	1.04
	Kahuku	Hakalau	3	16	26 August 2010	30 August 2010	2640	1.14
	Hakalau	Kahuku	4	14	13 September 2010	16 September 2010	4340	1.20
	Kahuku	Hakalau	5	8	20 September 2010	22 September 2010	–	–
	Hakalau	Kahuku	6	10	1 November 2010	4 November 2010	9080	1.05
	Kahuku	Hakalau	7	9	6 November 2010	9 November v10	9120	1.02
	Hakalau	Kahuku	8	274	23 November 2010	10 February 2011	23.4	5.63
	Kahuku	Hakalau	9	9	11 February 2011	13 February 2011	3910	1.02
	Hakalau	Kahuku	10	20	29 March 2011	3 April 2011	3140	1.31
	Kahuku	Hakalau	11	8	21 October 2011	23 October 2011	–	–
	Hakalau	Hakalau	12	17	28 October 2011	2 November 2011	3190	2.40
90850	BICC	Kahuku	1	64	16 May 2010	1 June 2010	2120	2.20
	Kahuku	Kahuku	2	31	13 June 2010	21 June 2010	1040	2.54
	Kahuku	Kahuku	3	19	1 July 2010	6 July 2010	3290	1.87
	Kahuku	Kahuku	4	20	1 August 2010	7 August 2010	2690	2.03
	Kahuku	Kahuku	5	24	22 August 2010	28 August 2010	2740	2.69
	Kahuku	BICC	6	8	17 October 2010	19 October 2010	–	–
	BICC	Kahuku	7	14	24 April 2011	28 April 2011	6540	1.14
90852	BICC	Kahuku	1	19	24 April 2011	29 April 2011	12 400	1.07
90853	BICC	Kahuku	1	72	30 April 2011	19 May 2011	1190	1.79
	Kahuku	Kahuku	2	17	8 September 2011	12 September 2012	37 000	2.84
	Kahuku	BICC	3	8	9 September 2011	10 September 2011	–	–
	Kahuku	BICC	4	16	23 September 2011	27 September 2011	19 100	1.11
	BICC	Kahuku	5	25	10 October 2011	17 October 2011	8220	1.29
	Kahuku	BICC	6	9	29 October 2011	31 October 2011	33 900	1.25
Total/Range/Mean	–	–	37	1552	11 May 2010	12 September 2012	23.4–37 000	1.95 (1.01–5.70)