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SEX AND AGE DIFFERENCES IN SITE FIDELITY, FOOD RESOURCE TRACKING, AND BODY CONDITION OF WINTERING KIRTLAND'S WARBLERS (*SETOPHAGA KIRTLANDII*) IN THE BAHAMAS

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Abstract.—Distribution of nonbreeding migrant birds in relation to variation in food availability has been hypothesized to result from the interaction of dominance hierarchies and variable movement responses, which together may have sex- and age-specific consequences. We predicted that site fidelity, movements, and abundance of Kirtland's Warblers (*Setophaga kirtlandii*) wintering on the island of Eleuthera in the Commonwealth of the Bahamas (hereafter "The Bahamas") would be correlated with food abundance but vary by sex and age. We found that the species' food resources (fruits and arthropods) typically declined during a winter but varied between winters (years) and study sites. Rainfall is a driver of variation in fruit abundance, as indicated by an information-theoretic evaluation of abiotic factors that influence fruit abundance. Despite variation in food availability, the proportions of fruits and arthropods in the diet of Kirtland's Warblers (88% of 90 fecal samples with both) varied little within or between winters or with sex or age class. Overwinter site persistence was low and variable among study sites (average = 43%, range: 11–67%); as predicted, site fidelity within and between winters differed by sex (males > females) and age class (adults > juveniles). However, knowledge of only sex and age was insufficient to predict site persistence in a model-selection framework in the absence of other contributing variables from the confidence set of models (i.e., food resources and/or habitat structure) for two model sets. These analyses further indicated that measures of food resources, either foliage arthropods or fruits, were reliable positive predictors of site fidelity, given the respective confidence set of models. Birds that shifted between study sites within a winter moved to sites with higher biomass of ripe fruit and ground arthropods, such that late-winter densities of Kirtland's Warblers were positively related to the biomass of fruits and ground arthropods. Sex and age differences in corrected body mass and fat were significant from midwinter through late winter, consistent with expected outcomes of dominance and experience. Differences in corrected body mass were evident by 16 April, when males had greater corrected mass than females, and by 26 April, when corrected mass of males was greater for adults than for juveniles. Late-winter rain had a positive effect on corrected body mass, corraborating previous Kirtland's Warbler studies that showed carryover effects on the breeding grounds and that survival in the following year was positively correlated with March rainfall in The Bahamas. Given that drought reduces the food resources and body condition of Kirtland's Warblers in The Bahamas, which negatively affects survival and breeding of Kirtland's Warblers in North America, conservation efforts in the Bahamas archipelago should focus on protecting the least-drought-prone early-successional habitats and sites with favored fruit species. *Received 23 September 2012, accepted 8 October 2013.*

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Key words: carryover effects, food resource tracking, Nearctic–Neotropical migrant, nonbreeding season, rainfall effects, *Setophaga kirtlandii*, site fidelity.

Diferencias de Sexo y Edad en la Fidelidad al Sitio, Evaluación de Recursos Alimenticios y Condición Corporal de Reinitas de Kirtland Invernando en las Bahamas

Resumen.—La distribución de aves migratorias no reproductivas en relación a la variación en la disponibilidad de alimento está siendo hipotetizada como un resultado de la interacción de las jerarquías de dominancia y las respuestas de movimientos variables, que conjuntamente pueden tener consecuencias especificas con la edad y sexo. Predecimos que la fidelidad al sitio de invernada, los movimientos y la abundancia de las reinitas de Kirtland (*Setophaga kirtlandii*) invernando en la isla de Eleuthera en las Bahamas podrían estar correlacionadas con la abundancia de alimento, pero varían por sexo y edad. Encontramos que la abundancia de recursos alimenticios de la especie (frutos y artrópodos) disminuyó durante un invierno, pero no entre inviernos (años) y sitios de estudio. La precipitación es un impulsor de la variación en la abundancia de frutos, como es indicada por la evaluación de la información teórica de los factores abióticos que influyen en la abundancia de alimento. A pesar de la variación en la disponibilidad de alimento, las proporciones de frutos y artrópodos en la dieta de las reinitas de Kirtland (88% de 90 muestras fecales con ambos tipos de alimentos) variaron poco dentro y entre inviernos, o con sexos o clases de edad. La persistencia al sitio durante el invierno fue baja y variable entre sitios (promedio = 43%, rango = 11–67%); tal como fue predicho en este estudio, la fidelidad al sitio dentro y entre inviernos vario entre sexos (machos > hembras) y clases de edad (adultos > juveniles). Sin embargo, el conocimiento de solo el sexo y edad fue insuficiente para predecir la persistencia al sitio en un esquema de selección de modelos en ausencia de otras variables de un grupo de modelos confiables (i.e., recursos alimenticios y/o estructura del hábitat) para dos grupos de modelos. Estos análisis además indicaron que las mediciones de recursos alimenticios, ya sean artrópodos de follaje o frutos fueron predictores positivos confiables, dada las respectivas confiabilidades de los modelos. Las aves que cambiaron entre sitios de estudio dentro de un invierno se movieron hacia sitios con mayor biomasa de frutos maduros y artrópodos del suelo, así que las densidades al final del invierno de reinitas Kirtland fueron positivamente correlacionadas con la biomasa de frutos y artrópodos del suelo. Las diferencias de sexo y edad en masa corporal corregida y grasa fueron significativas desde mediados hasta finales de invierno, consistente con los resultados esperados de dominancia y experiencia. Diferencias en masa corporal corregida fueron evidentes hacia el 16 de abril, cuando los machos presentaron mayor masa corporal corregida que las hembras, y el 26 de abril, cuando la masa corporal corregida de adultos fue mayor que los juveniles. La precipitación al final de invierno tuvo un efecto positivo sobre la masa corporal corregida, corroborando los estudios previos de la especie, que mostraron efectos de arrastre en los cuarteles de invierno, y que la supervivencia en el año siguiente fue positivamente correlacionada con la precipitación de marzo en las Bahamas. Dado que la sequía reduce los recursos alimenticios y condición corporal de las reinitas Kirtland en las Bahamas, este factor también afecta negativamente la supervivencia y reproducción de esta especie en Norteamérica. Los esfuerzos de conservación en el archipiélago de Bahamas deben enfocarse en la protección de los hábitats de sucesión temprana menos susceptibles a las sequias y los sitios con mayor riqueza de especies de frutos.

Introduction

Because spatial and temporal variation in food availability affects the distribution, abundance, behavior, and regulation of animal populations, knowledge of an animal's responses to variation in food resources is required to understand its population ecology and to devise appropriate conservation strategies (Andrewartha 1961, Sinclair et al. 2006). Evaluating the role of food resources in the behavior and ecology of migrant animals, such as migratory birds, can be especially challenging given the variety of habitats utilized during the annual cycle. Studies during one stage of the annual cycle, however, can facilitate assessment

of the importance of food abundance as a causative factor in population regulation, particularly in the nonbreeding period, when interpretations are not confounded by immediate reproductive requirements (Hutto 1985). Studies in the nonbreeding or wintering period have shown that migrant abundance is associated with food abundance (Hutto 1985, Martin and Karr 1986, Greenberg 1992, Lefebrve et al. 1994, Johnson and Sherry 2001, Kwit et al. 2004). This association suggests that food can be a limiting resource for wintering migrants (Hutto 1985, Sherry et al. 2005, Brown and Sherry 2006). Food shortages can also drive intraspecific competition that may be expressed by social dominance (Marra 2000), resulting in demographic and fitness consequences, which may lead to population limitation (Fretwell 1972, Sherry and Holmes 1996, Sherry et al. 2005). Thus, events on wintering grounds can affect migrants directly, by limiting populations, or indirectly, by influencing reproductive success (Marra et al. 1998, Studds et al. 2008, Reudink et al. 2009, Rockwell et al. 2012).

Late-winter droughts in the tropics or subtropics can be especially challenging for migrants prior to vernal migration, when increased energy intake is needed for premigratory fattening (Brown and Sherry 2006) and for molt in some species (van den Brink et al. 2000). Drought-induced food declines can constrain maintenance of adequate body condition (Studds and Marra 2005, 2007, 2011) and delay spring departure, which may reduce breeding-ground return rate, degrade body condition, and delay spring arrival time, thus reducing reproductive success (Marra et al. 1998, Gill et al. 2001, Bearhop et al. 2004, Norris et al. 2004, Saino et al. 2004, Studds and Marra 2005, Reudink et al. 2009, Rockwell 2013). Despite growing evidence of delayed responses to food conditions in winter and subsequent carryover to the breeding grounds, studies of these seasonal interactions have been limited to a few species (Sherry et al. 2005, Webster and Marra 2005).

Evidence of carryover effects from wintering-ground droughts has been found in Kirtland's Warbler (*Setophaga kirtlandii*; hereafter "warbler"), a Nearctic–Neotropic migrant whose wintering- and breeding-ground connectivity is increasingly well known (Mayfield 1992, Ewert et al. 2012, Rockwell 2013). The warbler winters in the Bahamas archipelago and breeds primarily in Michigan (Mayfield 1992), with smaller breeding colonies established recently in Wisconsin and Ontario (Richard 2008, Trick et al. 2008). Carryover effects in this species were first suggested by Ryel (1981), who found a positive relationship between winter rainfall in the Commonwealth of the Bahamas (hereafter "The Bahamas") and the number of singing males in Michigan during 1971–1980. Recently, Rockwell et al. (2012) found that following March droughts in The Bahamas, male warblers arrived later on their Michigan breeding grounds, where delayed arrival was associated with reduced fledging success. Second-year males showed greater sensitivity to March rainfall declines than adult males; later arrivals corresponded with lower March rainfall. In addition, apparent annual survival of male warblers was best explained by March rainfall in The Bahamas in a model-selection framework that included candidate models with summer, winter, or large-scale variables (Rockwell 2013, S. M. Rockwell et al. unpubl. data). Moreover, survival in the following year was positively correlated with March precipitation, which is consistent with the likelihood that rainfall in The Bahamas influenced survival probability in subsequent seasons. These carryover effects may be due to drought-induced food declines. Although the effects of rainfall on the warbler's food resources in The Bahamas are unknown, studies elsewhere in similar habitats indicate drought sensitivity in arthropods (Strong and Sherry 2000, Johnson and Sherry 2001) and fruits (Griz and Machado 2001, Ramírez 2002, Redwine et al. 2007).

Until recently, the warbler was poorly studied in the Bahamas archipelago, despite recognition that events on its wintering grounds could compromise breeding-ground recovery efforts for this federally listed endangered species and, hence, wintering ground studies were deemed a research priority (U.S. Fish and Wildlife Service 1985). Our study was initiated on the island of Eleuthera in the central Bahamas to determine whether warblers are susceptible to declines in food resources, given their use of habitats on drought-prone shallow soils on limestone substrates (Wunderle et al. 2010). The warblers use this habitat in October–April, which coincides with the dry season, and droughts can be especially severe in March and April (Sealey 2006),

immediately prior to spring migration. Drought stress may be particularly severe for the shallow-rooted shrubs that bear the high-water-content fruits (i.e., 60–70% water; J. M. Wunderle et al. unpubl. data) that are consumed by warblers (Wunderle et al. 2010). These early-successional shrub habitats can be more prone to seasonal fluctuations in food resources than older forests (Greenberg 1992, Levey and Stiles 1992, Smith and Robertson 2008).

Given the susceptibility of warblers' food resources to periodic droughts, we hypothesized that their site fidelity and distribution would vary among sites because of differences in food abundance due to differences in water-table depth or moisture availability (Byrne 1980, Sealey 2006, Smith et al. 2010) and the presence of shrub species bearing fruit. Spatial and temporal variation in food availability both within and among sites was expected to vary among winters with variation in rainfall (Studds and Marra 2007). The degree of site fidelity by warblers was expected to be highest where food was most abundant and predictable (Marra et al. 1998, Johnson and Sherry 2001, Latta and Faaborg 2002, Smith et al. 2011b). As with other species that use ephemeral resources, such as fruit, warblers are likely to move during the winter as food resources become more or less available (Morton 1971; Greenberg 1984, 1986; Sherry and Holmes 1996). Redistribution may occur as individuals abandon sites where food abundance declines and shift to food-rich sites (Levey 1988, Loiselle 1988, Blake and Loiselle 1991, Johnson and Sherry 2001), leading to the prediction that warbler abundance will be positively correlated with food abundance (Poulin et al. 1992, 1993; Johnson and Sherry 2001). Site fidelity and resource tracking, however, were expected to vary with sex and age as a result of competition (Fretwell and Lucas 1970, Fretwell 1972) and experience (Wunderle 1991) in the typical avian pattern, with males being dominant to females and adults dominant to juveniles (Wilson 1975, Balph 1977, Marra 2000). These sex and age differences were expected to result in corresponding differences in body condition (Marra and Holmes 2001), which by late winter could affect migration departure schedules (Marra et al. 1998; Studds and Marra 2007, 2011). Body condition was also expected to vary with rainfall (Katti and Price 1999, Studds and Marra 2007, Smith et al. 2010), given the likely effects of rainfall on food resources, especially in late winter, when drought conditions are most likely to occur. Finally, warblers in good body condition were expected to show higher annual return rates than those in poor body condition (Wolfe et al. 2013).

In the present study, we tested hypotheses related to the warbler's response to winter food variation as driven by variation in winter rainfall. We tested our hypotheses in several ways. (1) We determined the effect of rainfall on fruit abundance in three shrub species that produce fruits commonly consumed by the warbler. (2) We characterized the variation in the warbler's fruit and arthropod food resources by testing the effects of winter seasonality (i.e., periods within a winter), study site, and year (i.e., different winters) as factors affecting food-resource abundance. (3) We examined variation in the proportions of fecal samples with remains of arthropods or fruit to compare potential dietary changes in relation to winter period, winter, sex, and age. (4) We evaluated overwinter site persistence and annual return rate to quantify the warbler's use of space, including potential sex and age differences. (5) We characterized the relative contribution of the abundance of different food resource types and sex and age class to overwinter site persistence rates and abundance. (6) We analyzed corrected body mass and fat scores to test for effects of winter season and sex and age differences, which could lead to differences in spring departure schedules, which were also compared. (7) The effects of rainfall on body condition were also examined to test for effects of winter season and sex and age differences. (8) Finally, annual return rates were examined to determine whether birds with high corrected body mass were more likely to return to a site in the following winter than those with lower corrected body mass. Thus, our study documents the responses of wintering warblers to fluctuations in winter food availability as potentially driven by rainfall and identifies sex and age differences in site fidelity, resource tracking, and body condition that we hypothesize are likely to contribute to carryover effects demonstrated in models of annual survival and on the breeding grounds (Rockwell et al. 2012, Rockwell 2013).

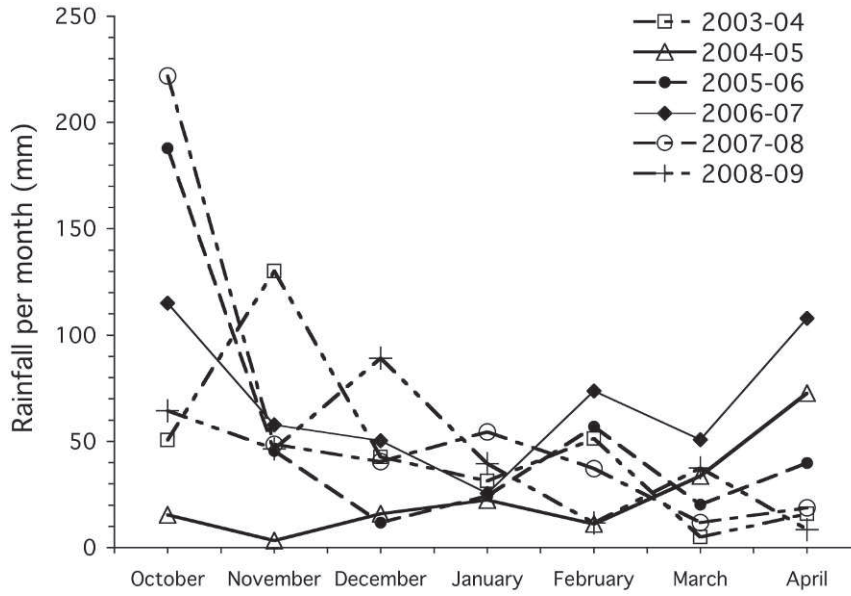

FIG. 1. Rainfall (mm) per month, October–April, for six winters of our study (2003–2004 through 2008–2009), as measured at the Nassau International Airport, located 96.6 km to the west of the Eleuthera study sites. Data are from the National Climatic Data Center of the National Oceanographic and Atmospheric Administration.

METHODS

Study area.—Our study was conducted on Eleuthera (25°15′N, 76°20′W), a low-elevation (51 m maximum) subtropical island of 518 km^2 in The Bahamas. The climate is characterized by annual wet and dry seasons, with most of the mean annual rainfall (1,090 mm year^{-1}) occurring in May–October (Sealey 2006). Although rainfall tends to decline in October–April (Sealey 2006), as it sometimes did during the six winters of our study, the winters varied considerably (Fig. 1).

Vegetation on Eleuthera includes evergreen and semi-deciduous broadleaf trees and shrubs, which form thick scrub or dense vegetation (locally known as "coppice") on poorly developed soils on limestone substrate (Correll 1979, Byrne 1980, Sealey 2006). Eleuthera's vegetation has been extensively disturbed by humans, principally for agriculture (Mooney 1905, Young 1966), most of which has ceased, resulting in a mosaic of abandoned sites with broadleaf habitats of different ages (Helmer et al. 2010, Larkin et al. 2012). Our study was conducted on southern Eleuthera (Tarpum Bay to 3 km south of Wemyss Bight and Green Castle). Warblers occurred in the early seral stages at 3–30 years after disturbance in sites where mean canopy was highly variable (range: 0.25–4.4 m; Wunderle et al. 2010, J. M. Wunderle unpubl. data).

Study sites were established at localities where at least four warblers were found within 200 m of each other. Trails, some placed in a grid pattern, and abandoned roads provided access through thick vegetation. Study sites were of different sizes because of access limitations or limited available habitat. The six study sites used for monitoring site fidelity and food resources had a mean (± SD) nearest-neighbor distance of 1.9 ± 0.8 km, and the distance between the two farthest study sites was 20.6 km. However, the number of study sites used each winter varied as a result of human disturbance or access limitations at any given study site. Therefore, given these accessibility and disturbance challenges, we were opportunistic in the use of study sites from one year to the next. Characteristics of the six study sites, including the winters each was monitored, as well as two-letter site acronyms, size, and other characteristics, are shown in Table 1. Additional sites (e.g., Gibson Estate [GE], 20 ha) were routinely monitored for dispersing birds and used to capture birds. For certain analyses, and unless otherwise specified, each winter was divided into

TABLE 1. Characteristics of study sites where Kirtland's Warblers and their food resources were monitored on Eleuthera, The Bahamas. "Period monitored" refers to the winters (1 October–30 April) that study sites were monitored. "*N* plots" is the number of 0.03-ha capture plots in which vegetation was measured. "Mean age" refers to the number of years after disturbance of the plots. "Mean canopy height" is the height (m) of canopy in the plots. "Mean number of stems" is the number of stems in the plots with a diameter at breast height (DBH) of 3.0–8.0 cm. "Mean percent foliage" is the percentage of foliage cover in the vertical foliage height class as designated for 0.0–0.5 m or 0.5–1.0 m above the ground. "Mean percent leaf litter" and "mean percent rock cover" refer to the respective groundcover types present at 20 points in the plot. Methods for sampling the vegetation are described in the text and in Wunderle et al. (2010).

Study-site acronym	Study site	Size (ha)	Period site monitored	*N* plots	Mean age	Mean canopy height (m)	Mean number of stems DBH 3.0–8.0 cm	Mean percent foliage 0.0–0.5 m	Mean percent foliage 0.5–1.0 m	Mean percent leaf litter	Mean percent rock cover
DD	DD Road	31.1	2004–2005 through 2007–2008	6	20.6	2.0	139.0	28.3	36.7	97.5	22.5
GF	Goat Farm	10.0	March–April 2006 through 2007–2008	17	11.3	1.3	18.5	40.3	47.9	95.9	73.8
MR	Madiera Road	50.5	2005–2006 through 2008–2009	22	16.0	2.3	69.5	36.6	45.0	77.5	51.6
OH	Ocean Hole	1.7	February–April 2004 through 2004–2005	17	6.0	0.8	12.9	41.5	41.5	80.3	76.5
RS	Rock Sound	18.7	2003–2004 through 2008–2009	13	18.7	2.2	80.4	23.1	39.2	95.4	27.7
WB	Wemyss Bight	11.7	2003–2004 through 2005–2006	9	17.7	2.6	86.0	17.8	36.1	99.4	37.8

three periods: early (1 October–23 December), middle (4 January–February), and late (March–April).

Habitat characterization.—Habitat in the six study sites was characterized by obtaining measurements in 0.03-ha circular plots placed at capture sites selected using a stratified random design in each study site, as described in Wunderle et al. (2010). Habitat variables were measured in plots placed at capture sites where birds were captured with or without playback (see below). No significant differences were found between habitat variables measured in the two types of capture plots within a study site; therefore, measurements from all capture plots, regardless of capture technique, were used to characterize each study site and to make comparisons among study sites. Within each plot, as described in detail in Wunderle et al. (2010), we measured diameter at breast height (DBH; i.e., 1.3 m above ground) for all trees ≥3 cm, counted stems <3 cm DBH, and determined foliage density at different height classes above ground, percent groundcover, mean canopy height, and age since disturbance. Mean canopy height per plot was determined by using the median value of the highest foliage height class measured at 20 equally spaced points along four 10-m transects radiating from the plot center in the four cardinal directions and dividing the total median height values by 20 (Wunderle et al. 2010). Variation in eight habitat variables measured in the capture plots (age since disturbance, canopy height, tree stems 3–8 cm DBH, stems <3.0 cm, foliage density at 0.5–1.0 m, foliage density at 0–0.5 m, rock groundcover, and

leaf-litter groundcover) was assessed with a principal component analysis (PCA) based on a correlation matrix.

Captures and banding.—Warblers were captured from March 2002 through April 2010, typically from 1 October through 30 April during each field season. Birds were captured in mist nets (30-mm mesh, 6 or 12 m length, 4 shelves) either with or without the use of tape-recorded playback of conspecific songs and chip notes. Playback was used with either a single net (target netting) or along a line of 11–20 mist nets; the latter were operated without playback (passive netting) in all winter periods. Net lines were operated from sunrise to 0930–1000 hours EST for at least two mornings and an afternoon (1600 hours–sunset) at a location before moving the net line elsewhere in a site. Efforts were made to capture all warblers on the study sites during each of the three winter periods.

Morphological measurements (unflattened wing chord, tail length, culmen length, and tarsus length to ±0.5 mm) and body mass (±0.1 g with a Ohaus digital scale) were obtained for all captured individuals. Subcutaneous furcular fat was scored after the method of Holmes et al. (1989), which included: 0 (no fat), 1 (trace), 2 (fat filling bottom of furculum), 3 (fat filling furculum), and 4 (fat mounded). Midlevel ratings were also used in assigning fat scores (i.e., 0.5, 1.5, 2.5, 3.5). Sex was determined by wing length and plumage, whereas age was determined by a combination of tail shape and other plumage traits (Goodman 1982, Pyle 1997). We classified age as either adult (AHY and ASY; >1 years) or juvenile (HY and SY; <1 year) (U.S. Fish and Wildlife Service 1977). All individuals were banded with a unique combination of three plastic color bands and an aluminum U.S. Geological Survey band and released near the capture site.

Site fidelity.—Our objective in quantifying site fidelity was to describe within-winter and between-winter space or patch use by warblers in relation to variation in food resources and to determine whether site fidelity differed with sex and age. The data from our study have been used in estimating apparent survival rates during the winter and annual survival using Cormack-Jolly-Seber (CJS) models (Rockwell 2013, S. M. Rockwell et al. unpubl. data). We compare survival estimates from the CJS models with our reported site-fidelity rates in the Discussion.

To document site fidelity and the number of warblers using a site, intensive area searches, supplemented with mist netting, were conducted during the early-, middle-, and late-winter periods to find banded warblers. Our area search methods were comparable to those of Holmes et al. (1989), Marra (2000), Strong and Sherry (2000), Johnson and Sherry (2001), and Latta and Faaborg (2001, 2002), to facilitate comparisons with their results. Searches were conducted primarily from sunrise to 1000 hours EST, during which time each observer traversed trails and roads independently to locate both banded and unbanded birds. Some searches were conducted in late afternoon (1600 hours to sunset) and opportunistically while netting and during visits to the site to sample food resources in the three winter periods. As resights and recaptures of different banded individuals accumulated at a site during each winter period, observers concentrated on locating missing birds (i.e., birds previously known from the site). Although playback was used extensively to initially capture and band birds, thereby establishing the presence of an individual on a study site in a specific winter period, it was not used to recapture birds to establish site fidelity. Most banded birds were detected visually, but we used nets to help document the presence of missing banded birds; once a specific banded individual was recaptured, we did not try to locate it again in the same period. The effort allocated to searching each study site during each winter period was related to the size of the study site and the number of warblers on the site. Generally, 5–9 mornings were spent searching a study site during each winter period (but see OH site, Appendix 8) by 2–5 observers searching independently on a site. A GPS unit (Garmin eTrex Vista) was used to obtain coordinates (±5 m) for all capture sites and sites where color-banded and unbanded birds were observed. To document late-winter departure date, we intensified searches for known individuals, which were assumed to have departed when they were not found for two consecutive days on a study site.

By the end of late winter, most warblers using the study sites were color-banded, which enabled us to determine the number of warblers using each study site. We related late-winter warbler abundance at each study site (based on area searches supplemented with mist netting)

with the biomass of food resources at the corresponding study site. For this analysis, all birds on the sites each late winter were color-banded, with the exception of two unbanded individuals in the OH site in late winter 2004 (total 16 birds), and one unbanded individual in the RS site in late winter 2009 (total 2 birds).

Measures of site fidelity included both overwinter site persistence during different periods of a winter (early to middle, or middle to late, or early to late) and annual return, which is the presence of an individual from one winter to the next at a study site. Site fidelity was established by detections at a site based on either resighting or recapturing birds at a study site, following Strong and Sherry (2000). Comparisons of site-fidelity values (birds present vs. birds absent) based on resights only with values based on both resights and passive net recaptures gave similar results when analyses were conducted by sex and age class within a study site (Fisher exact tests; $P > 0.10$).

A radiotelemetry study coincided with resighting efforts on the same study sites in early and late winter 2004–2005 and facilitated a comparison of the two methods to establish presence or use of a study site (details in Appendix 1). Thirteen warblers were radiotagged (8 early winter, 5 late winter) in different study sites and located daily until each transmitter battery expired (mean = 20.6 days). After each bird was color-banded, radiotagged, and released at the site of capture, six locations were obtained daily and georeferenced. In the same period, observers conducted their usual area searches for color-banded birds on the study sites without knowledge of the tagged birds' locations. The observers resighted 12 of the 13 radiotagged birds (Appendix 2). Only a juvenile female was not resighted in the WB site because it left the study site the day after it was radiotagged and before the next resight sample period. Three other birds departed from the study sites, but their presence was verified by resighting before departure to other locations. Although sample sizes were insufficient to compare radiotag and resight detections by sex and age class, our results suggest that missing birds had departed from the study sites. Subsequent telemetry studies (J. M. Wunderle et al. unpubl. data) and our resighting of banded birds at other locations (see Table 12 and Appendix 9) indicate that birds regularly emigrated from the study sites where initially detected.

We quantified between-year fidelity (i.e., annual return) of banded birds to the same study site in several different ways. These included noting the winter period in which the bird was present so that percent returns were tallied for returns to a study site between winters for early winter from previous early winter, midwinter from previous midwinter, late winter from previous late winter, and early winter from previous late winter. In addition, returns were also tallied on an aggregated basis over winter periods; that is, warblers were considered to be returning to a site from the previous winter regardless of the winter period in which they were detected.

Factors affecting fruit abundance.—To evaluate factors that influence abundance of fruits frequently consumed by warblers, we monitored fruit on marked shrubs of the three species that contribute 76% of the fruit consumed by the warbler: Snowberry (*Chiococca alba*), Blacktorch (*Erithalis fruticosa*), and Wild Sage (*Lantana involucrata*) (Wunderle et al. 2010). Shrubs were monitored monthly during October–April over three winters (2006–2007, 2007–2008, and 2008–2009) at six sites. The sites included DD, GF, RS, and MR. In addition, shrubs were marked on both sides of an unpaved road (Mingo Drive) on the southern border of the MR site, as well as in an abandoned citrus orchard adjoining Mingo Drive to the south (Leary's field). The six sites were located at a mean (± SD) nearest-neighbor distance of 1.6 ± 1.9 km, with the two most distant sites separated by 6.4 km. Three to seven reproductively mature plants were randomly selected and marked at each of our six sites, resulting in a marked total of 30 *E. fruticosa*, 25 *C. alba*, and 25 *L. involucrata* plants. We counted all unripe and ripe fruit on each of these "phenology plants" once each month. When marked plants died as a result of bulldozing (3 plants), cutting (1), flooding (2), or other causes (1), they were replaced by another nearby individual. In total, we monitored 86 individual plants and made an average of 10 visits to lost and replacement plants ($n = 10$) and 21 visits to other plants ($n = 76$). For numbers of marked individuals of each species monitored each winter, see Figure 3.

To evaluate factors that influenced shrub fruit abundance, we measured various plant-size and environmental variables at each marked plant (for details, see Appendix 3). Measurements

of height, width, stem number, and diameter were obtained from each plant. Environmental measurements obtained at each plant included soil moisture, canopy cover in late winter, and slope. Local rainfall and temperature were measured at the MR and RS sites (6.4 km apart) using a data-logging rain gauge and HOBO event rainfall logger and a HOBO TEMP H8 series logger (Onset, Bourne, Massachusetts). We used the rainfall sum for each month (rain) and the rainfall from the previous month (rain prev) as phenology covariates. During the first two months of the first year of the phenology study, we lacked local rain and temperature data; therefore, to fill in these missing values, we used data from Nassau International Airport (96.6 km to the west of the study sites) from the National Climatic Data Center of the National Oceanographic and Atmospheric Administration (www7.ncdc.noaa.gov/IPS/mcdw/mcdw.html). During some months, we missed rainfall data from either the MR site (n = 1 month) or RS site (n = 9 months) because of instrument failure; in these cases, we used the monthly rainfall data from the alternate site. We averaged the afternoon temperature for a monthly high-temperature estimate (temp hi), and potential evapotranspiration (pet) was calculated (Appendix 3) on the basis of the overall temperature average for each month by site (RS and MR).

Food availability per study site.—Food availability in study sites was determined during the three winter periods by counting fruit in transects and sampling arthropods in foliage and on the ground. We sampled fruit and arthropods from 10 November to 21 December (early), 24 January to 8 February (middle), and 23 March to 5 May (late) for the three winter periods. Arthropods were sampled in both the morning (0630–1200 hours) and afternoon (1430–1730 hours); regressions of ground-arthropod biomass or foliage-arthropod biomass with time of sample indicated that arthropod biomass did not vary with time of day (i.e., slopes not different from zero; $P > 0.10$).

Fruit abundance in each study site was monitored in belt transects (20 × 1 m) placed parallel to trails and unpaved roads. A stratified random design was used to space transects throughout study sites. The number of transects established varied among study sites, depending on disturbance levels: RS (7), DD (5), MR (13), OH (13), GF (4), and WB (7). Additional transects were added between winters to expand coverage in RS (+3, winter 2004–2005) and to replace transects lost to human disturbance (DD 2 lost after 2005–2006; +7 new, 10 total in 2006–2007; WB 1 lost after 2003–2004; 1 new, 7 total in 2005–2006). Comparisons of fruit abundance among winters was restricted to those transects sampled over the entire period, but we included new transects if they were sampled for each of the three periods within a winter for within-winter comparisons. We counted ripe and unripe fruit of all plant species, but analyses were restricted to the three most important to warblers: *C. alba*, *E. fruticosa*, and *L. involucrata*. Biomass for these three species combined is reported as dry mass (g) per transect (20 m^2) based on previous measurements of dried pulp mass for each species (J. M. Wunderle et al. unpubl. data). Some analyses were run separately for live fruit (both unripe and ripe) and ripe fruit, because for some species (*E. fruticosa* and *L. involucrata*) it was difficult to distinguish ripe from unripe fruit on the basis of color. Also, warblers consumed unripe as well as ripe fruit (J. M. Wunderle et al. unpubl. data).

A stratified random design was used to space sample stations for foliage and ground arthropods throughout each study site. Sample stations were located ≥15 m apart on grid trails, or on other tagged trails at the DD site, where a grid was unavailable. During each sampling visit to a station, a coin toss was used to determine the side of the trail for sampling, near the estimated midpoint between tagged locations on the trails. Once the side of the trail for sampling was determined, the quadrat frame for sampling ground arthropods was placed 0.5–2 m off the trail, taking care not to disturb vegetation or leaf litter in the plot. Quadrats were established on representative groundcover but required clear visibility from 50–75 cm height to ensure that no part of the ground in the quadrat was obscured by vegetation.

Abundance of ground arthropods was measured with a timed, direct search of the surface of the ground substrate within a 0.25-m^2 quadrat, following the methods of Strong and Sherry (2000). All substrates within the quadrat were scanned for arthropods during a 5-min period. Upon detection, attempts were made to remove the individual to eliminate the risk of recounting. Forceps, fingers, or aspirators were used

to capture ground arthropods in the quadrats, although the latter method (see Strong and Sherry 2000) was abandoned because of its ineffectiveness and disruption of the leaf litter. We estimate that we captured 50–70% of the arthropods in a plot during a timed scan.

Arthropods on shrubs and small trees were sampled using a modified version of the branch-clipping method of Schowalter et al. (1981) as adapted by Johnson (2000). Our method involved carefully placing an open cloth bag (53 × 78 cm), contained within a canvas sweep-sample insect net (38 cm diameter), over the end of a small branch of a shrub or small tree and then enclosing the branch and foliage within the bag by quickly closing the bag about the branch. Because of the irregular shape of branches of coppice shrubs, it was necessary for one person to carefully bunch together a group of branches while holding them together and taking care not to jar the intended sample as the bag was placed around it by an assistant. Once surrounded, the bag was quickly closed around the branch, sealing the enclosed clipping sample. In a few instances, when sample weight was insufficient (<200 g), it was necessary to obtain a second sample of the same plant species, either from the original plant or from another conspecific nearby within the specified sample area.

After cutting the sample branch, the bag and its enclosed clipping were weighed with a Pesola spring scale (±5 g) and the bag weight subtracted to obtain the sample clipping weight. Next the closed bag was vigorously shaken, then opened cautiously to allow inspection and capture of any arthropods visible on the bag or vegetation. Following inspection and capture of arthropods within the bag, a smaller clipping from the enclosed branch was made and the smaller cutting removed. This smaller clipping was placed on a light gray cloth on the ground to capture remaining arthropods. After inspection, the smaller sample was lightly beaten against the cloth on the ground to dislodge any remaining arthropods, and the process was repeated until the bag was emptied. The arthropods found on the smaller clippings and those found within the bag were combined to give the total value for arthropods for the original (larger) sample clipping. Two people worked together on each sample, with one searching the bag interior for arthropods and the other inspecting the smaller clippings after each was removed from the bag.

Foliage arthropod samples were obtained as close to the sampling-station midpoint as possible on the randomly selected side of the trail. Selection of foliage for sampling required that sample vegetation could be gathered into a suitably sized bunch to fit within the bag opening and that it not be heavily covered with vines (light vine cover was clipped and removed when necessary before bagging). A thorny plant species (*Zanthoxylum fraga*) and a poisonous species (*Metopium toxiferum*) were not sampled; both were rarely used as arthropod foraging substrates by the warbler (i.e., each was used in 2.3% of 86 arthropod foraging maneuvers; J. M. Wunderle et al. unpubl. data). Samples of branches or crown shoots were taken between 0.5 and 3 m, the higher samples obtained by bending the plant down to enable one person to hold the bunched foliage sample and another to bag it. The sample height range was similar to the vertical range used by foraging warblers when consuming arthropods (J. M. Wunderle et al. unpubl. data).

All arthropods (spiders and insects) were identified at least to the level of order (ants recorded separately from other Hymenoptera), and all captured specimens were preserved in alcohol to verify identifications in the first two winters. Afterward, however, only specimens that could not be identified in the field were collected for later identification. Length of arthropods was measured in the field with a ruler (±0.5 mm), except in instances when it was necessary to make estimates for individuals that escaped (<10%). Length was used to calculate biomass based on length–weight regressions of Jamaican arthropods (Johnson and Strong 2000) derived separately for taxa found above or on the ground. Biomass of foliage arthropods is reported as "mg/g foliage clip" and biomass of ground arthropods as "mg/5 min scan of 0.25 m^2." Although different observers were responsible for arthropod identifications and measurements (3 for foliage arthropods and 5 for ground arthropods), no significant differences ($P > 0.10$) were found among observers in arthropod identifications or measurements.

The branch-clipping method inadequately samples flying insects such as Dipterans (Johnson 2000), but combined with the ground-scan method, it accurately measures the abundance of the arthropod prey consumed by

warblers. Sampling arthropods both above ground in foliage (including twigs and small branches) and on the ground was required because the warbler forages for arthropods in both locations on Eleuthera (69% of 155 arthropod maneuvers occurred on the ground, the remainder above ground; J. M. Wunderle et al. unpubl. data).

Our analyses excluded stinkbugs (Pentatomidae) in foliage and fast-flying taxa of Diptera (Tabanidae and Muscidae) on the ground because of their absence in warbler fecal samples, foraging observations from Eleuthera (J. M. Wunderle et al. unpubl. data), and fecal samples from Michigan (Deloria-Sheffield et al. 2001). Analyses were restricted to arthropods with lengths <25 mm, the size range of prey most likely to be consumed by the warbler (J. M. Wunderle et al. unpubl. data).

Warbler fecal samples were collected from cotton holding bags or directly under the mist net where the bird was captured. Samples were placed in small paper envelopes and stored in a freezer. For the analyses, the stored fecal samples were placed in a small Petri dish and mixed with warm water, and samples were gently broken apart with a closed forceps tip. A dissecting microscope was used to identify remains of arthropods (mandibles, appendages, wing scales) and fruit (seeds, exocarp). We determined the percentages of fecal samples that contained the remains of arthropods, fruit, and remains of both arthropods and fruit. Assessing arthropod diet from fecal samples has several drawbacks, especially due to underestimation of soft-bodied arthropods that do not have distinctive sclerotized parts (Hartley 1948, Ralph et al. 1985). However, our analyses focused only on the presence or absence of the remains of arthropods (of any order) or fruit (any species) in the fecal samples, and similar analyses showed that variation in proportions of fecal samples with fruit or arthropods was consistent with variation in stable isotope signatures sampled from the same birds at the same time (Diggs et al. 2011). The most abundant taxa of arthropods found in fecal samples from Eleuthera (n = 96; J. M. Wunderle et al. unpubl. data) include Coleoptera (35.4%), Formicidae (30.2%), and Araneae (31.3%), all of which were well represented in foliage clip samples, whereas Formicidae was the most frequently encountered arthropod taxa in ground scans.

Ocean Hole space use and food resources.—Foraging observations were made while searching for birds in the OH site, most between sunrise and 1030 hours, but some also between 1600 hours and sunset. Once a foraging warbler was located, the observer waited 15 s after encountering the bird before recording its first foraging maneuver. Only one foraging maneuver was recorded per individual. Different observers occasionally encountered the same color-banded bird during the same day and independently obtained a foraging observation; only observations separated by >1 h were included in the analyses.

To test the prediction that warblers were concentrating in food-rich patches within the OH site in late winter 2004 (3 March–2 May), we compared the number of warbler home ranges overlapping fruit transects or ground arthropod quadrats with the quantity of fruit in the transects or ground-arthropod biomass in the quadrats. This was accomplished by determining the home ranges of 12 color-banded warblers observed within the 1.7-ha study site (see Appendix 8). The low-stature shrubs (most <1.5 m; Wunderle et al. 2010) on the site facilitated observations. Home range calculations for each individual within the OH site were based on repeated observations, which were >0.5 h apart. Banded birds were observed on that site over an average (± SD) of 22.9 ± 12.9 days (range: 3–39 days) at an average of 44.6 ± 36.8 locations bird^{-1} (range: 7–116). On the basis of these observations, we used CALHOME (Kie et al. 1996) to calculate the adaptive kernel home-range size (95%) and core area (50%; Worton 1989) for each bird. This program automatically sets the optimal bandwidths for adaptive kernel (AK) home-range calculations. Home range and core areas were then plotted in ARCVIEW, version 3.2 (ESRI, Redlands, California), along with the positions of 13 fruit transects and 13 ground-arthropod quadrats. We counted the number of individual AK home ranges and core areas that overlapped each fruit transect and each arthropod quadrat. The number of AK home ranges or core areas overlapping a transect or ground quadrat were compared with the fruit biomass in each transect or the arthropod biomass in each quadrat. Because all bird observations were restricted to the OH study site, and warblers regularly left the site, our home-range and core results describe only a portion of the

area used by the birds. Therefore, our determination of core and home range areas in relation to food resource plots within the OH study site provide only a measure of space use while the birds were in the study site.

Analyses and definitions.—Percent overwinter site persistence and percent annual return were summarized by pooling within or among the three winter periods (i.e., early, middle, late), which sometimes included using values from the same birds more than once. The pooled site-persistence values included the percentage of birds remaining through each winter pooled for the winters 2003–2004 through 2008–2009, and the pooled annual return percentages were based on values obtained between successive winters during this period. Pooling of all measures provided larger sample sizes for statistical analyses but violated assumptions of statistical independence because some individuals were included more than once. It is unlikely that minor violations biased results, because analyses conducted using independent measures (values from known individuals used only once) gave results consistent with those from pooled values. Moreover, we considered observations of the same individual in different periods or years to be independent because the environmental conditions encountered between periods or years were not constant. We pooled across study sites of different sizes for certain analyses of overwinter site persistence and for annual returns after establishing that there were no significant ($P > 0.20$) linear trends (i.e., slope = 0) in either overwinter site persistence rates or annual return rates with study-site size using the Cochran test of linear trend.

Body mass was corrected for structural size following Marra et al. (1998) by first reducing data on unflattened wing chord, tarsus, and tail onto a single axis using PCA. Next we regressed body mass against the factor scores from the PCA, and the resulting residual values provided an estimate of corrected body mass. Birds with negative residual values were considered to be in poor condition in relation to their structural size, whereas birds with positive values were considered to be in good condition in relation to their structural size. Our analyses of corrected body mass and fat scores included recaptured individuals. We included individual bird as a random effect in our mixed-model analyses (see below) and found that use of recaptures typically had no significant effect ($P > 0.15$) on either corrected body mass or fat scores; therefore, we dropped this effect from the models (unless noted otherwise).

Statistical tests.—Parametric analyses were conducted when assumptions of normality and homogeneity of variances were met, and nonparametric analyses were conducted when these assumptions were not met (Sokal and Rohlf 1995). To meet assumptions of normality for analyses of food resource biomass, we used different transformations (i.e., $\ln(x + 0.001)$ for foliage arthropods, $\ln(x + 0.01)$ for ground arthropods, and $\ln(x + 0.1)$ for both live and ripe fruit). Variation around the mean is reported with SE for comparisons of several means, and SD is provided for descriptive purposes when only a single mean value is reported.

Certain families of tests were adjusted for a set of hypotheses to be tested with a particular set of data. Although some hypotheses and data sets overlap, where adjustments were made they were made only in relation to a particular family of hypotheses and a single data set (no false-discovery control methods). For example, Bonferroni sequential adjustment (BSA; Rice 1989) was applied to individual P values for suites of statistical analyses (e.g., mixed effects models, penalized spline mixed-model analysis of covariance [ANCOVA] to prevent inflation of family-wise error rate). However, the Bonferroni adjustments are controversial because they are very conservative in that they control the Type I error rate at the expense of the Type II error rate and, therefore, can have negative consequences in exploratory studies such as ours (Hurlbert and Lombardi 2003, Moran 2003, Roback and Askins 2005). Because of conservation implications, failing to detect important potential responses associated with various variables is a much greater concern to us than identifying a potentially false association. Therefore, we report P values without application of BSA to analyses of various statistical tests (i.e., row × column test of independence, Fisher's exact test, Wilcoxon signed-ranks test) and accept as significant all values $P < 0.05$, but show values that approach significance for descriptive purposes.

Analyses of live-fruit biomass involved use of mixed effects models for repeated measures run in SAS, version 9.2 (SAS Institute, Cary, North Carolina), with winter period (early, middle, late) as the repeated measure, and fruit transects nested within study site. We compared

the logarithmic transformed biomass of live fruit at the site level across periods and winters. Because different combinations of study sites (the between-subject factors) were used in each winter, repeated-measures mixed models were run separately for each winter. However, two study sites (RS and WB) were consistently sampled over three winters (2003–2004 through 2005–2006), enabling comparison of live-fruit biomass across winters with a balanced repeated-measures mixed model. The repeated-measure covariance matrices considered included unstructured, compound symmetry, and Huyn-Feldt either with or without dependencies across winters, and the covariance matrix used to report results was chosen on the basis of Akaike's information criterion corrected for small sample sizes (AIC_c; Burnham and Anderson 2002). Post hoc least significant difference (LSD) tests were used to compare fruit biomass values between study sites, winters, and/or winter periods.

Biomass of foliage arthropods and biomass of ground arthropods were each analyzed separately with mixed effects models at the site level using Proc GLIMMIX (SAS) to compare biomass samples among study sites, winter periods, and winters. Study sites, winter, and winter period were treated as fixed effects, and transects were treated as a nested random effect. The dependent variables, biomass of foliage arthropods and biomass of ground arthropods, were log transformed. Because different study sites were surveyed each winter, models were run separately for each winter. However, we also used unbalanced-design models (P values denoted P_{unadj}) that included all sites and all winters to test specific contrasts that were not possible using balanced designs (e.g., OH site sampled only in late winter 2003–2004). Balanced-design models were based on the subsets of the data, which allowed specific tests of interactions (i.e., sites RS and WB sampled over three winters). Comparisons between the models were made to ensure that results were consistent across models. Structured and unstructured covariance matrices were compared using AIC_c, and as a result, foliage-arthropod biomass was treated as simple compound symmetry for winters 2003–2004 and 2004–2005 and Huyn-Feldt structure for winter 2005–2006, whereas ground-arthropod biomass was always treated as simple compound structure. In cases where adjustments for specific sets of multiple comparisons were made with SAS's simulation procedure, the adjusted P value is reported (P_{adj}).

Associations between variables were assessed with Pearson's correlation coefficient when normality assumptions were met (with or without transformations) or with Spearman rank correlation when normality assumptions were not met. Because fruit and arthropod transects differed within each site, possible pairwise correlations between food resources were based on the means of the transformed biomasses per study site, winter, and winter period. Log transformations of biomass were used for Pearson correlations of food resources. Spearman rank correlations were used to evaluate the association between the biomass of fruit in a transect or biomass of ground arthropods in a quadrat with the number of overlapping warbler home ranges or core areas at the OH site.

To test for sex and age differences in body size in relation to site fidelity among the different winter periods, we used two-factor analyses of variance in SPSS, version 20 (SPSS, Chicago, Illinois). Body size was based on the principal component factor scores of wing, tail, and tarsus measurements from the first capture of each bird (i.e., recaptures excluded). Analyses involved comparisons of body size for banded individuals that either stayed or disappeared during early to late winter, early to midwinter, or midwinter to late winter. Some individuals were used in more than one period of comparison.

Various categorical analyses were conducted in SYSTAT, version 10.2 (SYSTAT, Richmond, California). For example, log-linear models in three-way tables were used to test for the presence of three-factor interactions (Sokal and Rohlf 1995). In particular, log-linear models were used to test for interactions among sex (male vs. female), age (adult vs. juvenile), and capture method (playback vs. passive); overwinter site persistence (persist vs. absent), winter period (early, middle, late), and sex or age; and among annual return (return vs. absent), winter period, and sex or age. In the absence of three-factor interactions, log-linear models were then used to test for conditional independence and for two-factor interactions. Only significant interactions are reported. Row × column tests of independence with a G-statistic (Sokal and Rohlf 1995) were used to assess equality of site fidelity (stay vs. leave) between capture

methods (playback vs. passive), between winter periods, between sexes and ages, and among study sites. These tests also were used to evaluate equality of diet items (arthropod vs. fruit) in foraging observations at the OH site in the beginning and at the end of late winter and in remains in fecal samples among winters, among periods, and between sex or age classes. A chi-square goodness-of-fit test was used to compare sex ratios in net captures. Because of small sample sizes (<5) in the cells of 2 × 2 tables, we used Fisher's exact tests for comparisons of site persistence with female age (adult vs. juvenile), and absence of birds in midwinter (birds present all three periods vs. present only early and late) by sex or age class.

We used nonparametric Wilcoxon signed-ranks test to compare food abundance at study sites for individual birds that were followed from one study site (initial site) to another study site (new site) within the same winter. The comparisons of study-site food abundance were made individually for biomass of live fruit, ripe fruit, and ground arthropods (insufficient sample sizes for foliage arthropods) for the winter period in which the bird shifted study sites.

We compared Spearman partial correlation coefficients and significance levels to evaluate the relative strengths of their association with late-winter warbler abundance at a study site with transformed biomass (as with Pearson correlations) for each of the four food-resource measures. Within a winter, each study site was treated independently, given that warbler abundance and food-resource biomass differed across winters (denoted "site–winter"). We controlled for study-site size differences in all calculations of Spearman partial correlations and excluded cases list-wise for missing values. Spearman partial correlations were compared to overdispersed Poisson regression models of warbler abundance using site size and each of the four food-resource measures, which were obtained at 12 site–winters. The Poisson models were also compared to the *P* values for Spearman partial correlations in which study-site size and one of the food-resource variables was held constant while determining the association with another food-resource measure. Negative binomial (NB) regressions were compared to *P* values for the Spearman partial correlations for analyses of a single food resource (live fruit, ripe fruit, and ground arthropods) based on measurements at 15 site–winters. Both overdispersed Poisson regressions and negative binomial regressions allow for some degree of variation with mean and were fit using Proc GENMOD in SAS.

Corrected body mass and fat were modeled for change over winter using penalized spline mixed-model ANCOVAs in SAS. Models included bird group as identified by sex and age class (adult, juvenile) as fixed effects with winter (2003–2004 through 2009–2010) and study site and their interaction as random effects. Time of capture (based on time after sunrise) and days after 1 October were included as covariates. Recaptured birds were also included as a random effect but were not found to be a significant contributor to variation in preliminary analyses and were not included in subsequent models. We compared a cubic model, a fixed-effect spline model, and a penalized spline model to determine which model best captured trends. The cubic model best fit the data, but we report results from the penalized spline model because it fit the data almost as well as the cubic model and allows more flexibility in its interpretation. On the basis of the trend model, body mass and fat measurements taken on the following days after 1 October were assigned into the winter periods early (days 30, 45, 60, 75, 90), middle (days 105, 120, 135, 150, 165), and late (days 180, 195, 205). Multiple comparisons of *P* values were adjusted by the Holm-simulated procedure in SAS for each group. Random effects were tested using likelihood ratio tests, based on mixture distributions, where appropriate. We report the results of the penalized spline model, which for fat reduced down to a linear model with separate slopes for each sex and age class. Non-normal models were also fit to accommodate the ordinality of the fat scores; however, with nine levels, these models were similar to the reported normal-based penalized spline models.

Warbler departure schedules, pooled for all winters, were monitored from 15 to 31 April and were analyzed using Kaplan-Meier survivorship analysis in SPSS. Tarone-Ware χ^2 was used to test for departure schedule differences between males and females (ages pooled) and between adults and juveniles (sexes pooled).

The effects of prior rainfall (30 days, 60 days, 90 days) on corrected body mass or fat level were studied by use of linear mixed effects models run in SAS. Rainfall data were obtained for the

Nassau Airport station. Models included sex and age class as a fixed effect (four categories) along with three covariates, including days after 1 October, time after sunrise, and one of the rainfall periods prior to capture (i.e., 30, 60, or 90 days). The models initially also included random effects for study site, winter, site*winter, and individual birds (to determine effect of recaptures). Random effects that contributed the most to models containing all the fixed effects were included on the basis of minimal AIC_c. In midwinter, the contribution of random bird effects was dependent on the rainfall periods and varied from borderline significant to nonsignificant as determined with likelihood ratio tests, but were included in the models as determined by minimal AIC_c. We report the results only from the models that include the random effects determined to contribute the most to the linear models. Further tests of slopes (by sex and age class) were tested for differences from zero, and if so, to test whether they were common for the four bird classes. Post hoc tests on corrected body mass were used to compare the slopes between the different sex and age classes. In addition, corrected body masses were compared among the different sex and age classes at different prior rainfall amounts (75 mm, 150 mm, 225 mm) using Holm-Scheffe adjusted *P* values.

To evaluate the influence of corrected body mass on annual return, we used logistic regression (Proc LOGISTIC in SAS) in which annual return was treated as a binary response variable (present vs. absent anytime in following winter). Data included the individuals observed and captured in more than one year, and the study sites varied across years. For birds captured multiple times in the same winter, only the last corrected body mass was used for the analysis in that winter. The logistic regression of the binary response variable (return or absent) was run on the residuals of corrected body mass from the regression run with covariates including days since 1 October, time after sunrise, prior rainfall (30-day, 60-day, or 90-day), and group indicator (factors for sex*age), and with random adjustments for study*winter. The logistic regression was run separately for birds captured any time in the previous winter (i.e., October–April) and those captured only late (March–April) in the previous winter. The odds of returning compared with the odds of being absent are given by the odds ratio (OR), which shows how likely birds were to return, based on each additional unit of the residual of corrected body mass with adjustment for prior rainfall. The 95% confidence intervals (CIs) are provided for each OR to allow assessment of its significance (i.e., lower bound of CI > 1 suggests that the effect is significant).

Fruit abundance model selection.—We took the natural log of unripe fruit for the response variable (unripe) and the natural log of ripe fruit for the response variable (ripe). Each shrub species was analyzed separately using the same basic global models and submodels with the Proc Mixed procedure for longitudinal data run on SAS. We checked for multicollinearity between covariates using Proc Reg and used the criteria that there was no multicollinearity when the correlation coefficient was <70%, the tolerance was >0.4, and the variance inflation factor (VIF) was <2.5 (Allison 1999). Additional statistical details are provided in Appendix 3.

We developed 10 a priori models to determine whether environmental factors, plant characteristics, or temporal factors might best explain fruit abundance (Appendix 4). In addition to the environmental and plant predictor variables (all treated as fixed effects), we included winter (wi) and month (mo) as fixed-effect predictor variables to avoid convergence problems, and we included six interaction terms (Appendix 4). Phenology study site (6 sites) and individual marked plants were included as random-effect predictor variables to enable inferences to other sites and plants on the island. However, using study site as a random effect caused convergence problems for unripe *E. fruticosa*, so we treated site as a fixed effect for this set of models.

The "climate subglobal" model included all environmental measures; these environmental measures were further subdivided into a "winter-rain" model to determine whether rainfall throughout the winter influenced fruiting, an "evaporation" model to determine whether higher temperatures and relatively dry conditions influenced fruit production, and a "sunlight" model to determine whether canopy cover influenced fruit production (Appendix 4). We also included a model that combined predictor variables that we expected to be most important to fruit production for the "likely-combo" model. For *E. fruticosa*, we included site in the climate subglobal and sunlight models as a fixed factor, given that sites were of different

TABLE 2. Eigenvalues for the first three principal components (PC1–3) from a principal component analysis of seven habitat variables and age since disturbance measured in 0.03-ha circular plots at 84 Kirtland's Warbler capture sites in six study sites on southern Eleuthera, The Bahamas (for plot sample sizes and habitat traits at each study site, see Table 1). Variables are defined in the text and in Wunderle et al. (2010).

Variable	PC1	PC2	PC3
Rock groundcover	–0.848	0.089	–0.058
Tree stems 3–8 cm DBH	0.809	–0.107	0.377
Canopy height (m)	0.802	–0.020	0.279
Age since disturbance	0.797	0.221	0.100
Stems <3.0 cm DBH	0.709	0.084	–0.620
Foliage at 0.5–1.0 m	–0.108	0.879	–0.041
Foliage at 0–0.5 m	–0.511	0.644	0.287
Leaf-litter groundcover	0.643	0.569	–0.119
Eigenvalue	3.84	1.59	0.72
Percentage of variance accounted for	48.03	19.84	8.95

successional stages that might influence canopy cover of shrubs.

The "plant subglobal" model included height and width for *C. alba* and an interaction term between the two variables (Appendix 4). For *E. fruticosa* and *L. involucrata*, we included only the crown width variable because of multicollinearity between height and canopy cover. The plant subglobal model also included stem number and diameter and an interaction term between the two. Crown and stem variables were subdivided into a "crown" and "stem" model. A "temporal" model included the variables winter and month and an interaction term between the two. Lastly, we included a null model that did not contain fixed effect predictor variables.

We checked each of the six global models for goodness of fit using the likelihood ratio statistic (Appendix 5). We used AIC_c to identify the best-approximating model for each data set. We calculated the absolute difference between models (ΔAIC_c) and Akaike weights (w_i), which estimate the likelihood that a given model is the true Kullback-Leibler best model given the set of models (Burnham and Anderson 2002). Mixed models use restricted maximum likelihood (REML) to produce the least biased parameter estimates (Pinheiro and Bates 2000); however, they are inappropriate for ranking models using Akaike's weights (Pinheiro and Bates 2000, Littell et al. 2006). Therefore, to rank models and for model fit, we used the maximum likelihood (ML) method but used REML for parameter estimation.

Overwinter site persistence model selection.—To examine variation in overwinter site persistence, we created logistic regression models (Proc LOGISTIC and GLIMMIX in SAS) to predict presence or absence of birds and used AIC_c to analyze factors affecting site fidelity (Burnham and Anderson 2002). Site fidelity was represented as "0" when a bird was present on a study site in early winter that disappeared from the study site by late winter, and as "1" when a bird was still present on the same study site by late winter. Data included individuals found in more than one year, and the study sites varied across years along with our sampling. The probability of site fidelity was modeled as a function of sex (male = 1, female = 0; reference = females) and age (adult = 1, juvenile = 0; reference = juveniles), the biomass of food resources at the study site in late winter, a principal component habitat score, and rainfall 30 or 60 days prior to late-winter resource sampling. Scores for each study site from principal component 2 (PC2) of the principal component analysis conducted on eight habitat variables (Table 2) were used to characterize habitats at each study site; PC2 was used because it provided better discrimination of the older study sites than PC1 (Fig. 2). Food resources included biomass of dried live

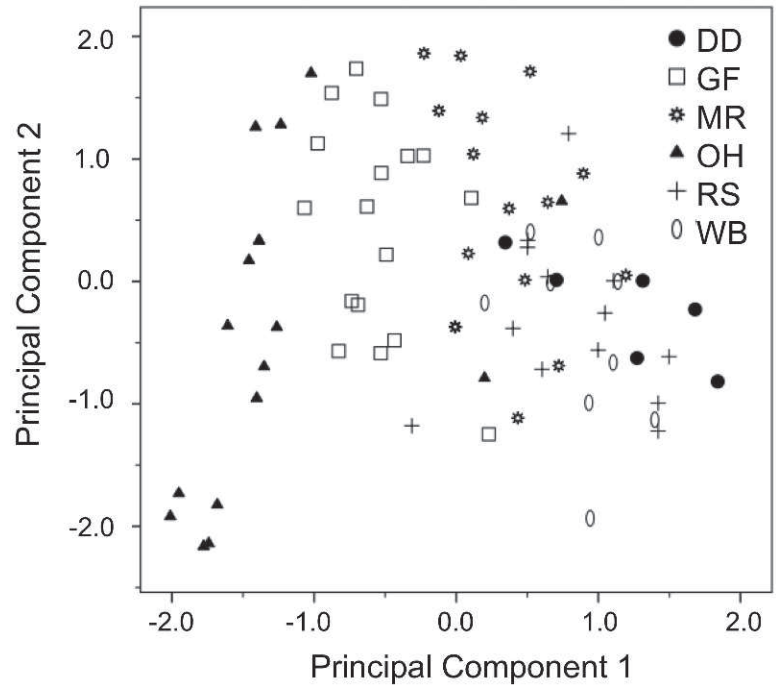

FIG. 2. Graph of the first two principal components (PC1 against PC2) based on eight habitat traits measured in 0.03-ha circular plots at 44 Kirtland's Warbler capture sites in six study sites on southern Eleuthera, The Bahamas. Upper right side of panel shows study-site symbols and acronyms (defined in Table 1). The eight habitat variables included in the principal component analysis were age since disturbance, canopy height, tree stems 3–8 cm DBH, stems <3.0 cm, foliage densities at 0–0.5 m and at 0.5–1.0 m, rock groundcover, and leaf-litter groundcover. Factor loadings for each of the eight habitat traits are given in Table 2, and measurement of habitat variables and capture methods are described in the text and in Wunderle et al. (2010).

fruit (g/20 m^2), dried ripe fruit (g/20 m^2), foliage arthropods (mg/g foliage clip), and ground arthropods (mg/5 min scan) collected from winters 2003–2004 through 2005–2006 at the following study sites: DD, MR, RS, and WB. Additional fruit data gathered in winters 2006–2007 through 2008–2009 allowed separate analyses of fruit response over more winters and included the following sites: DD, MR, OH, RS, and WB.

Because arthropod biomass was sampled for only three winters and fruit biomass for six winters, we ran two separate AIC_c analyses. In both analyses, we generated a priori models (Burnham and Anderson 2002) that we hypothesized could best explain variation in overwinter site fidelity. For the analyses based on three winters with both fruit and arthropod measures, each variable was used individually and in biologically plausible additive combinations. These included age (binary), sex (binary), biomass of food resources (live fruit, ripe fruit, foliage arthropods, ground arthropods), PC2 scores of habitat variables, and rainfall prior to date of late-winter resource sampling (30 days, 60 days). We limited the number of candidate models in the first analysis to a total of 28 by restricting candidate models to five or fewer predictor variables, with the exception of the global model that contained nine variables (Appendix 7). In the second analysis, which included fruit (ripe or live), but no arthropods, sampled for six winters, each variable was also used individually and in additive combinations as well as in two interaction parameters (age*habitat PC2 and sex*habitat PC2). The number of candidate models in this second (fruit only) analysis was restricted to a total of 20 by restricting candidate models to five or fewer predictor variables, with the exception of one model with six variables and the global model that contained 10 variables (Appendix 7). In both analyses, model averaging was used

to calculate parameter coefficients and SEs for models that were considered competitive if they occurred within two points of the lowest AIC_c score (Burnham and Anderson 2002). We report percent deviance for the top-ranked candidate models. Percent deviance for the fruit and arthropod models is based on McFadden's r^2. Percent deviance for the fruit models with a winter random effect was based on a Laplace approximation to the marginal likelihood. Random effects were determined not to be helpful in the fruit and arthropod models.

Results

Habitat variation among study sites.—Ordination of warbler capture plots in the six study sites (Table 1) with PCA indicated that the first three principal components accounted for 76.8% of the variation in habitat characteristics, with 48% contributed by PC1, 19.8% by PC2, and 9% by PC3 (Table 2). For PC1, the most influential negative loadings were rock groundcover and foliage density at 0–0.5 m, whereas total tree stems 3–8 cm DBH, canopy height, and age since disturbance had the highest positive loadings. Study sites were arrayed along the PC1 axis, with the OH site at the negative extreme, followed by the GF, MR, RS, WB, and DD sites at the positive extreme (Fig. 2). Therefore, PC1 indicates that capture plots at the OH site were situated on recently disturbed, rocky ground with abundant foliage <0.5 m, few tree stems with 3–8 cm DBH, and short canopy. At the other extreme, the WB and DD sites had less exposed rock, less foliage at <0.5 m, but numerous woody stems with 3–8 cm DBH and taller canopies, and were older. These older study sites (DD, WB, and RS) tended to have capture plots showing more overlap (i.e., more similar) along PC1 than the younger sites such as OH and GF, which had more distinctive capture plots. For PC2, the most influential negative loadings were canopy height and number of tree stems 3–8 cm DBH, whereas the most influential positive loadings were foliage density at 0.5–1.0 m and at 0–0.5 m and leaf-litter groundcover. In contrast to PC1, the capture plots in the older study sites (DD, WB, and RS) showed slightly greater separation along PC2, whereas capture plots in younger study sites, such as GF and especially the OH site, spanned much of the variation along PC2.

Fruiting phenology.—To evaluate factors affecting the abundance of fruits of importance to the warbler, we counted both ripe and unripe fruit on marked plants of *C. alba*, *E. fruticosa*, and *L. involucrata* during the last three winters of the study (2006–2007, 2007–2008, and 2008–2009; Fig. 3). Both ripe and unripe fruit of *C. alba* declined over the winter for the first two winters of the phenology study to a low of <1 ripe fruit plant^{-1} (Fig. 3). However, during the third winter, *C. alba* ripe fruit abundance continued to increase from October to January before declining; unripe fruit did not increase in early winter and declined after November. Both ripe and unripe fruit of *E. fruticosa* were at their lowest numbers from December to February but increased in number again in late winter (Fig. 3). During the third winter of the study, however, ripe fruit of *E. fruticosa* declined through late winter and unripe fruit stabilized. By contrast, *L. involucrata* ripe and unripe fruit amounts fluctuated throughout the winter, with more extreme lows often occurring during February and March.

Fruit abundance modeling.—The global model explained significantly ($P = 0.005$) more than the null model for each of six sets of models, which included ripe and unripe fruit abundance for *C. alba*, *E. fruticosa*, and *L. involucrata* (Appendix 4). The global model was the most supported model for ripe and unripe fruit for all shrub species. Because the global and temporal models received the most support (Table 3), we were unable to determine which abiotic factors most influenced the abundance of ripe and unripe fruit. Therefore, we conducted post hoc analyses and explored the subglobal models and reduced models (Appendix 4) separately and without the global model. In each case for the set of subglobal models, the temporal model was the most supported (Appendix 6). Temporal-model parameter estimates show greater fruit numbers in the third winter than the first two winters for *C. alba* and *E. fruticosa*, but not in the first winter for ripe and unripe *L. involucrata*. There was no monthly trend for *L. involucrata*. Unripe fruit of *E. fruticosa* and *C. alba* showed the expected trend of having greater fruit abundance in early winter than in midwinter and late winter (Fig. 3 and Appendix 6). Ripe *C. alba* fruit had peak numbers in December and January of the third winter of the study.

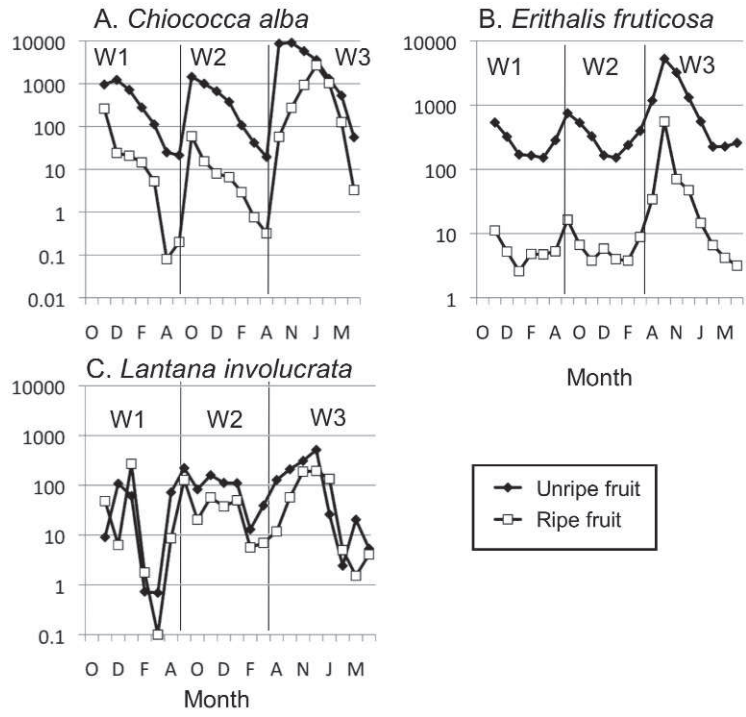

FIG. 3. Mean number of unripe and ripe fruit on marked shrubs by month during winters 2006–2007 (W1), 2007–2008 (W2), and 2008–2009 (W3) on southern Eleuthera, The Bahamas, for (A) *Chiococca alba*, (B) *Erithalis fruticosa*, and (C) *Lantana involucrata*. Numbers of marked individual shrubs monitored for each winter included 25 (W1), 29 (W2), and 25 (W3) individuals of *C. alba*; 30 (W1), 31 (W2), and 30 (W3) individuals of *E. fruticosa*; and 26 (W1), 25 (W2), and 25 (W3) individuals of *L. involucrata*.

Of the reduced environmental and plant models, the winter-rain model received the greatest support in five of six model sets, including all model sets for unripe fruit (Table 3). The likely-combo model had the most support for *C. alba* ripe and received some support for *L. involucrata* ripe, though the variables for *C. alba* ripe were in the direction opposite from expected (rain and late-winter canopy cover) or had confidence limits that included zero (Table 4). Likewise, all variables in the likely-combo model for *L. involucrata* had confidence limits that included zero.

The previous month's rain was important in five of the six models (*C. alba* unripe, *E. fruticosa* ripe and unripe, and *L. involucrata* ripe and unripe) and in the expected direction (Table 4). Rain also explained variation for unripe *C. alba*. Rain and late-winter canopy cover had the largest effects for ripe *C. alba*; however, both were in the direction opposite from expected. Rain explained variation for *E. fruticosa* unripe and ripe fruit, though there was an inverse relationship between rain and ripe fruit abundance (Table 4). There also was an interaction between soil moisture and rain for ripe *E. fruticosa* fruit, as well as for unripe fruit of *L. involucrata*, though coefficients were quite small for each interaction term (Table 4).

Variation in food availability.—Given the sensitivity of the warbler's food resources to rainfall, the food resources were expected to decline over the course of the winter dry season, although the presence and severity of the declines were expected to vary among study sites as a result of site differences in moisture availability. Moreover, differences in food-resource abundance were expected to vary among winters as a result of annual rainfall variation (Fig. 1).

Fruit.—Live-fruit (unripe and ripe) biomass decreased with winter period for all study sites in winter 2003–2004 (Fig. 4), but no significant differences in median live-fruit biomass were found between the two sites (RS and WB)

TABLE 3. Model-selection results for temporal, climate, and plant factors affecting unripe and ripe fruit abundance monitored over three winters (October–May, 2006–2009) on marked individuals of the shrubs *Chiococca alba*, *Erithalis fruticosa*, and *Lantana involucrata* on southern Eleuthera, The Bahamas. For description of all candidate models, see Appendices 3 and 4.

Species	Model	–2LL [a]	*K* [b]	ΔAIC_c [c]	w_i [d]
C. alba, unripe	Global	1,613.1	43	–	–
	Temporal	1,685.3	24	–	–
	Winter rain	2,353.1	8	0.0	0.999999999
	Likely combo	2,395.5	8	21.2	0.0000
	Crown	2,465.0	7	54.9	0.0000
	Sunlight	2,471.8	5	56.3	0.0000
	Evaporation	2,470.9	6	56.8	0.0000
	Stem	2,498.8	7	71.8	0.0000
	Null	2,592.8	2	113.7	0.0000
C. alba, ripe	Global	1,758.8	43	–	–
	Temporal	1,824.3	24	–	–
	Likely combo	2,168.1	9	0.0	1
	Evaporation	2,331.0	6	156.7	0.0000
	Crown	2,360.1	7	187.9	0.0000
	Winter rain	2,358.1	8	187.9	0.0000
	Sunlight	2,367.3	5	191.0	0.0000
	Stem	2,373.0	6	198.7	0.0000
	Null	2,397.5	2	215.1	0.0000
E. fruticosa, unripe	Global	2,275.3	45	–	–
	Temporal	1,824.3	24	–	–
	Winter rain	2,573.0	7	0.0	1
	Likely combo	2,635.1	7	62.1	0.0000
	Evaporation	2,675.3	5	98.2	0.0000
	Sunlight	2,737.0	9	168.1	0.0000
	Stem	2,744.6	6	169.5	0.0000
	Crown	2,752.8	4	173.7	0.0000
	Null	2,917.7	2	334.5	0.0000
E. fruticosa, ripe	Global	1,786.6	41	–	–
	Temporal	1,872.9	24	–	–
	Winter rain	2,095.6	8	0.0	0.999999966
	Likely combo	2,130.0	8	34.4	0.0000
	Evaporation	2,254.5	6	154.8	0.0000
	Stem	2,261.3	7	163.6	0.0000
	Sunlight	2,270.5	5	168.7	0.0000
	Crown	2,272.6	5	170.8	0.0000
	Null	2,400.3	2	292.4	0.0000
L. involucrata, unripe	Global	1,858.4	40	–	–
	Temporal	1,944.0	24	–	–
	Winter rain	2,211.1	8	0.0	1
	Evaporation	2,254.8	6	39.6	0.0000
	Likely combo	2,254.7	7	41.5	0.0000
	Crown	2,290.9	5	73.6	0.0000
	Sunlight	2,291.1	5	73.8	0.0000
	Stem	2,296.4	7	83.2	0.0000
	Null	2,415.7	2	192.3	0.0000
L. involucrata, ripe	Global	1,835.7	40	–	–
	Temporal	1,912.2	24	–	–
	Winter rain	2,179.9	8	0.0	0.9094
	Likely combo	2,186.7	7	4.7	0.0850
	Sunlight	2,197.5	5	11.4	0.0030
	Crown	2,198.5	5	12.4	0.0018
	Evaporation	2,198.2	6	14.1	0.0008
	Stem	2,202.5	7	20.5	0.0000
	Null	2,292.2	2	100.0	0.0000

[a] Negative two times the maximum log likelihood given by the Mixed procedure.
[b] Number of parameters in the model.
[c] Difference between AIC_c for the model and the lowest AIC_c score.
[d] Weight of evidence for the model given the other models in the set.

TABLE 4. Parameter estimates (± SE) and 95% confidence intervals (CI) for the most supported reduced models for unripe and ripe *Chiococca alba*, *Erithalis fruticosa*, and *Lantana involucrata* fruits monitored over three winters (October–May, 2006–2009) on Eleuthera, The Bahamas. For description of all candidate models, see Appendices 3 and 4.

Species	Model	Effect	β ± SE	95% CI
C. alba, unripe	Winter rain	intercept	3.3413 ± 0.3380	2.6653 to 4.0173
		sm mean	0.1892 ± 0.0952	–0.0011 to 0.3795
		rain	0.0072 ± 0.0010	0.0052 to 0.0092
		rain prev	0.0073 ± 0.0008	0.0058 to 0.0089
		sm mean*rain	–0.0008 ± 0.0004	–0.0016 to 0.0001
C. alba, ripe	Likely combo	intercept	3.4745 ± 0.5993	2.2759 to 4.6731
		sm mean	0.1747 ± 0.09640	–0.0181 to 0.3675
		rain	–0.0029 ± 0.0010	–0.0050 to –0.0009
		late canopy	–0.0387 ± 0.0066	–0.0518 to –0.0256
		sm mean *rain	0.0002 ± 0.0004	–0.0007 to 0.0010
E. fruticosa, unripe	Winter rain	intercept	3.5355 ± 0.2844	2.9667 to 4.1043
		sm mean	0.0660 ± 0.06242	–0.0588 to 0.1909
		rain	0.0083 ± 0.0008	0.0067 to 0.0099
		rain prev	0.0046 ± 0.0006	0.0035 to 0.0058
		sm mean*rain	–0.0011 ± 0.0003	–0.0017 to –0.0004
E. fruticosa, ripe	Winter rain	intercept	1.9521 ± 0.2445	1.4631 to 2.4411
		sm mean	0.0717 ± 0.0984	–0.1252 to 0.2685
		rain	–0.0027 ± 0.0011	–0.0048 to –0.0006
		rain prev	0.0033 ± 0.0008	0.0017 to 0.0049
		sm mean*rain	0.0002 ± 0.0004	–0.0006 to 0.0011
L. involucrata, unripe	Winter rain	intercept	1.6662 ± 0.3023	1.0616 to 2.2708
		sm mean	–0.0395 ± 0.0575	–0.1544 to 0.0754
		rain	0.0011 ± 0.0009	–0.0007 to 0.0030
		rain prev	0.0050 ± 0.0006	0.0037 to 0.0063
		sm mean*rain	0.0009 ± 0.0003	0.0002 to 0.0016
L. involucrata, ripe	Winter rain	intercept	1.3876 ± 0.2858	0.8160 to 1.9592
		sm mean	–0.0048 ± 0.0562	–0.1171 to 0.1076
		rain	0.0011 ± 0.0009	–0.0007 to 0.0029
		rain prev	0.0030 ± 0.0006	0.0017 to 0.0043
		sm mean*rain	0.0002 ± 0.0003	–0.0004 to 0.0009
	Likely combo	intercept	1.3706 ± 0.4018	0.5670 to 2.1742
		sm mean	0.0148 ± 0.0577	–0.1006 to 0.1303
		rain	0.0014 ± 0.0009	–0.0005 to 0.0032
		late canopy	0.0041 ± 0.0053	–0.0066 to 0.0148
		sm mean*rain	0.0002 ± 0.0003	–0.0005 to 0.0009

sampled across the three periods (early, middle, and late $P > 0.10$). For winter 2004–2005, live-fruit biomass was significantly different among winter periods, but there was an interaction between study site and winter period (Fig. 4), and together their median values decreased significantly (statistics in Table 5) from early to middle to late winter (Fig. 4). For most sites, the median fruit biomass decreased from early to late winter, with the exception of the OH site, where fruit (i.e., *Lantana* spp.) biomass increased as the winter progressed in 2004–2005 (simultaneous contrast of season difference for the OH site; $F_{2,66} = 21.06$, $P < 0.0001$).

Both RS and WB sites were sampled for three winters (2003–2004, 2004–2005, and 2005–2006), and median abundance of live fruit showed a significant interaction between winter period and winter, winter and site, and winter period and site (statistics in Table 6). Overall, median

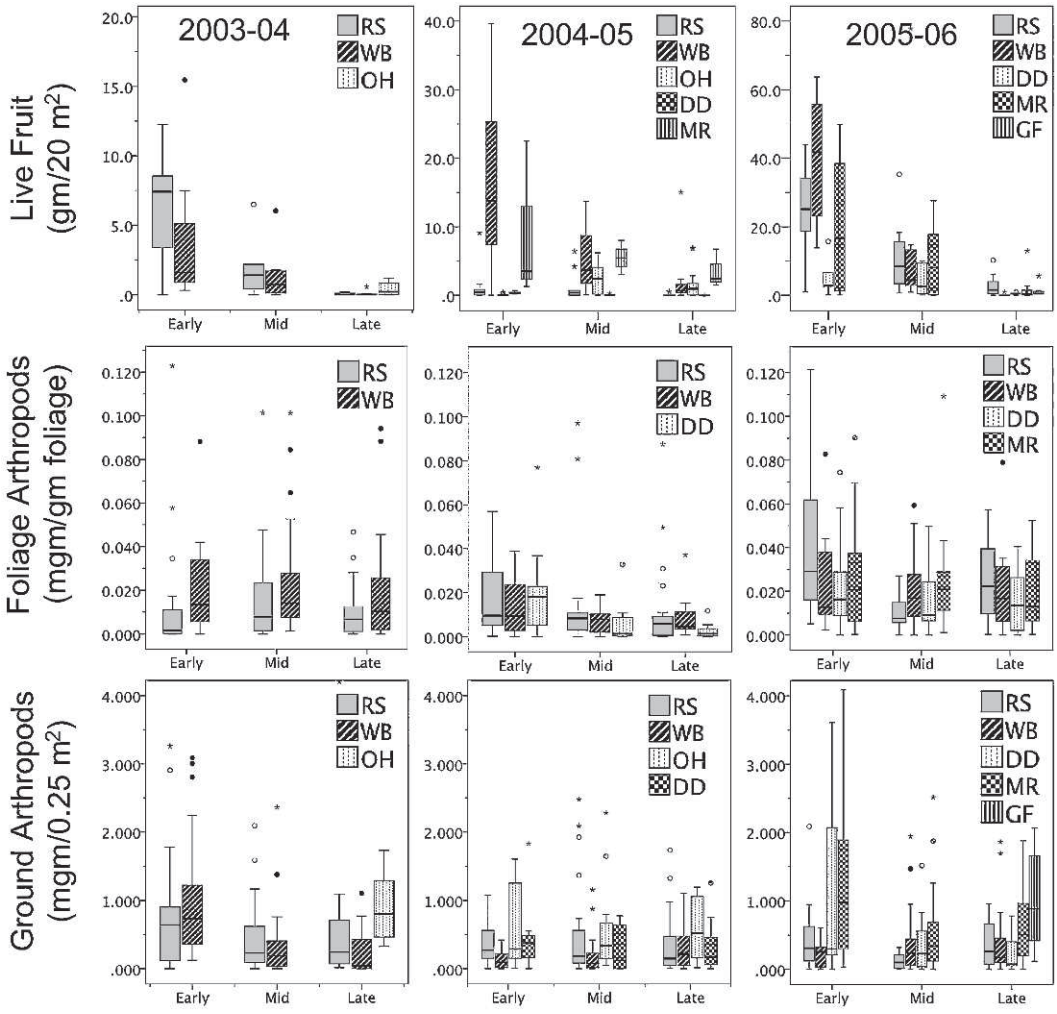

FIG. 4. Variation in median food-resource biomass in different Kirtland's Warbler study sites in early (October–December), middle (January–February), and late (March–April) winter periods for three winters on southern Eleuthera, The Bahamas. Box plots show the median (dark horizontal bar), interquartile range, and outliers (not all shown due to scale). (A) Median dry biomass of live fruit (unripe and ripe) per 20-m^2 transect (note that the *y*-axis scales are not equivalent among years). (B) Median dry biomass of foliage arthropod per gram of foliage clipping. (C) Median dry biomass of ground-surface arthropods per 5-min scan of 0.5 m^2. Study-site acronyms are shown in upper right side of each panel, and only RS and WB sites were sampled each winter. Study-site acronyms are defined in Table 1, and sampling details are given in the text.

live-fruit biomass was significantly greater in winter 2005–2006 than in 2003–2004 for both sites (Fig. 4). Live-fruit biomass was also significantly greater in 2005–2006 than in 2004–2005 at RS but did not differ between years for WB (P = 0.4155). Live-fruit biomass was not significantly different between 2003–2004 and 2004–2005.

Foliage arthropods.—Foliage-arthropod biomass did not vary significantly with period in winter 2003–2004 (P = 0.260) but varied with period in 2004–2005 and with an interaction between period and study site in 2005–2006 (Fig. 4 and Table 5). Foliage-arthropod biomass from the early to middle and early to late periods significantly declined in 2004–2005, but no difference was found between the middle and late periods. In winter 2005–2006, foliage-arthropod biomass was not different across three sites (P >

TABLE 5. Results of statistical analyses of the effects of winter period, study site, and interaction of period and site on food resources used by Kirtland's Warblers on Eleuthera, The Bahamas, during three winters. Because different study sites were sometimes used in different winters, as shown in Figure 4, analyses were run within winters. "Period" includes early (October–December), middle (January–February), and late (March–April) winter. Dry biomass of food resources is analyzed separately for live fruit (unripe and ripe), foliage arthropods, and ground arthropods, as shown in Figure 4 and described in the text. Transformed (ln(fruit + 0.1) biomass of live fruit per 20-m^2 transect was analyzed with repeated-measures mixed effects models with winter period as the repeated measure to determine effects of winter period and site. Transformed biomass of foliage arthropods (ln(biomass + 0.001) per branch clip and biomass of ground arthropods (ln(biomass + 0.01) per 5-min ground scan of 0.25 m^2 were analyzed separately using mixed effects models with samples nested within sites. Study-site acronyms used in the footnotes are defined in Table 1.

	Period		Site		Period × site	
Food type, winter	Test	*P*	Test	*P*	Test	*P*
Live fruit, 2003–2004	$F_{2, 20.23} = 16.29$	<0.0001				
Live fruit, 2004–2005					$F_{8, 66} = 8.34$	<0.0001
Live fruit, 2005–2006					$F_{6, 55.02} = 7.19$	<0.0001
Foliage arthropods, 2003–2004			$F_{1, 46.7} = 11.18$	0.0016		
Foliage arthropods, 2004–2005 [a]	$F_{2, 114} = 7.77$	0.0007	$F_{2, 57} = 2.58$	0.0844		
Foliage arthropods, 2005–2006 [b,c]					$F_{6, 158.4} = 2.19$	0.0464
Ground arthropods, 2003–2004 [d,e]					$F_{2, 140} = 5.66$	0.0043
Ground arthropods, 2004–2005 [f]			$F_{3, 69} = 6.20$	0.0009		
Ground arthropods, 2005–2006 [g,h]					$F_{6, 100.3} = 2.52$	0.0259

[a] Period effect, early > mid, $t = 2.88$, df = 114, $P_{adj} = 0.0125$; early > late, $t = 3.77$, df = 114, $P_{adj} = 0.0009$; mid = late, $P_{adj} = 0.636$.
[b] Period effects in RS ($F_{2, 158.6} = 10.19$, $P < 0.0001$), early > mid, $t = 4.49$, df = 155.8, $P_{adj} < 0.0001$; late > mid, $t = 2.60$, df = 160.5, $P_{adj} = 0.0244$.
[c] Site effects in midseason, RS < MR, $t = 2.71$, df = 85, $P_{adj} = 0.0366$; RS < WB, $t = -2.68$, df = 85, $P_{adj} = 0.04$.
[d] Period effect in WB, early > mid, $t = 4.32$, df = 140, $P_{adj} < 0.0001$; early > late, $t = 5.53$, df = 140, $P_{adj} < 0.0001$.
[e] Late winter, site effect, RS > WB, $t = 2.92$, df = 140, $P_{adj} = 0.0044$; OH > RS, $t = 2.47$, df = 152, $P_{unadj} = 0.0146$; OH > WB, $t = 4.99$, df = 152, $P_{unadj} < 0.0001$; early, site effect, RS < WB, $t = 1.76$, df = 140, $P_{adj} = 0.0838$.
[f] Site effect, OH > WB, $t = 4.15$, df = 69, $P_{adj} = 0.0004$.
[g] Period effect in RS ($F_{2, 78.44} = 5.48$, $P = 0.0059$), early > mid, $t = 3.13$, df = 80.43, $P_{adj} = 0.0067$; late > mid, $t = 2.91$, df = 81.13, $P_{adj} = 0.0139$.
[h] Early winter, site effect ($F_{3, 78.31} = 5.51$, $P = 0.0017$), MR > WB, $t = 4.06$, df = 78.55, $P_{adj} = 0.0008$; midwinter, site effect, MR > RS, $t = 2.98$, df = 78.11, $P_{adj} = 0.0179$.

0.77 for all three sites), but there was an interaction between winter period and site, reflecting a significant period effect in RS, where biomass was lower in the middle than in the early or late periods (Table 5).

A site effect on foliage-arthropod biomass was significant in winter 2003–2004 but not significant in 2004–2005. In winter 2005–2006, as mentioned above, biomass varied with a site*period interaction, in which the RS site had significantly lower biomass than MR and WB sites (Table 5).

Over the three winters that the RS and WB sites were sampled, foliage-arthropod biomass showed a significant three-way interaction with winter, period, and site (Fig. 4 and Table 6). For both sites, foliage-arthropod biomass varied significantly among winters in the early and late periods, but only among sites in midwinter at WB. Foliage-arthropod biomass differed significantly between the two sites only in early winter 2003–2004 and in midwinter 2005–2006.

Ground arthropods.—Biomass of ground arthropods did not vary directly with period in any winter, but it varied with the interaction of period and study site in winters 2003–2004 and 2005–2006 (Fig. 4 and Table 5). In winter 2003–2004, differences between periods were found only in the WB site, where ground-arthropod biomass in early winter was significantly greater than that in the middle and late periods. In winter 2005–2006, differences between periods occurred only in the RS site, where ground-arthropod biomass in early and late winter were both significantly greater than in midwinter.

TABLE 6. Results of statistical analyses of the effects of winter, winter period, study site, and their interactions on food resources used by Kirtland's Warblers on Eleuthera, The Bahamas. The study sites WB and RS were sampled over three winters (2003–2004, 2004–2005, 2005–2006) in three winter periods (early, October–December; middle, January–February; late, March–April). Dry biomass of food resources are analyzed separately for live fruit (unripe and ripe), foliage arthropods, and ground arthropods as shown in Figure 4 and described in the methods. Transformed (ln(fruit + 0.1) biomass of live fruit per 20-m^2 transect was analyzed in a balanced repeated-measures mixed model with winter period as the repeated measure to determine the effect of winter period, study site, and winter. Transformed biomass of foliage arthropods (ln(biomass + 0.001) per branch clip and biomass of ground arthropods (ln(biomass + 0.01) per 5-min ground scan of 0.25 m^2 were analyzed separately using balanced mixed effects models with samples nested within sites to determine the effect of winter, winter period, and study site. All analyses resulted in interactions between factors; hence, values for single factors are not shown. Study-site acronyms used in the footnotes are defined in Table 1.

	Fruit [a]		Foliage arthropods [b]		Ground arthropods [c]	
Variable and interaction	Test	*P*	Test	*P*	Test	*P*
Period*site	$F_{2, 95.79} = 3.95$	0.0225				
Period*winter	$F_{4, 95.82} = 6.79$	<0.0001				
Site*winter	$F_{2, 95.26} = 20.33$	<0.0001				
Period*site*winter			$F_{2, 204.4} = 2.62$	0.0358	$F_{4, 416} = 5.93$	0.0001

[a] Winter effect by site, post hoc LSD: 2005–2006 > 2003–2004, RS, $P < 0.0001$; WB, $P < 0.0001$; 2005–2006 > 2004–2005, RS, $P < 0.0001$, WB, $P = 0.4155$; 2004–2005 < 2003–2004, RS, $P = 0.0159$; 2004–2005 > 2003–2004, WB, $P < 0.0001$.

[b] Winter effect by period for sites: early, RS, $F_{2, 273.1} = 18.66$, $P < 0.0001$; early, WB, $F_{2, 273.2} = 3.97$, $P = 0.0199$; late, RS, $F_{2, 273.6} = 8.93$, $P = 0.0002$; late, WB, $F_{2, 274.2} = 3.66$, $P = 0.0270$; mid, WB, $F_{2, 273.5} = 6.58$, $P = 0.0016$; site effect by winter for periods: 2003–2004 early, $F_{1, 138.9} = 7.89$, $P = 0.0057$; 2005–2006 mid $F_{1, 138.4} = 5.26$, $P = 0.0233$; 2003–2004 mid, $F_{1, 138.9} = 3.43$, $P = 0.0661$; 2005–2006 early, $F_{1, 138.4} = 3.05$, $P = 0.0829$.

[c] Winter effect by period for sites: early, WB, $F_{2, 416} = 16.85$, $P < 0.0001$; late, WB, $F_{2, 416} = 3.17$, $P = 0.0431$; mid, RS, $F_{2, 416} = 3.84$, $P = 0.0222$; site effect by winter for periods: 2003–2004, late, RS > WB, $t = 2.98$, df = 416, $P_{adj} = 0.0031$; 2004–2005, early, RS > WB, $t = 2.83$, df = 416, $P_{adj} = 0.0044$; 2004–2005, mid, RS > WB, $t = 2.15$, df = 416, $P_{adj} = 0.0305$; 2005–2006, early, RS > WB, $t = 2.27$, df = 416, $P_{adj} = 0.0236$; 2003–2004, early, WB > RS, $t = -1.80$, df = 416, $P_{adj} = 0.0721$; 2005–2006, mid, WB > RS, $t = -1.83$, df = 416, $P_{adj} = 0.0711$.

Ground-arthropod biomass varied with site in winter 2004–2005 and, as stated above, in an interaction with period in winters 2003–2004 and 2005–2006. In winter 2003–2004, site had a significant effect in late winter, when RS had greater ground-arthropod biomass than WB, and OH had significantly greater biomass than RS and WB. In winter 2005–2006, site had a significant effect on ground-arthropod biomass in early winter, when biomass in MR was significantly greater than in WB, and in midwinter, when MR was significantly greater than RS (Table 5).

Over the three winters, ground-arthropod biomass at RS and WB varied significantly in a three-way interaction of winter, season, and site (Table 6). Biomass of ground arthropods varied significantly with winter at WB in the early- and late-winter periods and at RS in midwinter. Significant differences between RS and WB in ground-arthropod biomass occurred in winter 2003–2004 in the late period, in 2004–2005 in the early and middle periods, and in 2005–2006 in the early period.

Seasonal change in food resources within a winter.—As expected, the percent change in mean biomass of live fruit per study site and mean ripe fruit per study site decreased from early to late winter (Table 7) in all study sites and winters, with the exception of the OH site that showed a substantial increase in live and ripe-fruit biomass from early to late winter of 2004–2005. By contrast, seasonal changes in arthropod biomass were less consistent among study sites and winters, as shown by both decreases and increases in ground- and foliage-arthropod biomass.

Correlation of food-resource measures.—Mean transformed foliage-arthropod biomass per study site was weakly, but significantly, correlated with mean transformed live-fruit biomass at the site level for the three winters and three winter periods combined (Pearson $r = 0.517$, $P = 0.006$, $n = 27$). The correlation increased across periods and was highest in late winter (Pearson $r = 0.582$, $P = 0.100$, $n = 9$) and increased as the winter proceeded from the early period (Pearson $r = 0.458$, $P = 0.215$, $n = 9$) to the middle period (Pearson $r = 0.511$, $P = 0.160$, $n = 9$). Mean transformed ground-arthropod biomass per study site was not correlated with mean transformed live-fruit biomass or transformed ripe-

TABLE 7. Percentage change in mean dry biomass of live fruit (unripe and ripe), ripe fruit, ground arthropods, and foliage arthropods from early winter (October–December) to late winter (March–April) in different study sites during three winters (Fig. 4) on southern Eleuthera, The Bahamas. Study-site acronyms used in the footnotes are defined in Table 1, and the techniques used to measure food resources are described in the text. NA = not available.

	Study site				
Winter and food type	RS	WB	OH	DD	MR
2003–2004					
Live fruit	–99.1	–97.9	NA	NA	NA
Ripe fruit	–97.5	–99.4	NA	NA	NA
Ground arthropods	–12.2	–77.7	NA	NA	NA
Foliage arthropods	+11.7	+14.5	NA	NA	NA
2004–2005					
Live fruit	–91.7	–83.4	+2,105.0	–99.4	NA
Ripe fruit	–97.0	–99.8	+6,273.1	–100	NA
Ground arthropods	–1.7	+283.4	–8.4	+11.7	NA
Foliage arthropods	–64.4	+2.9	NA	–86.6	NA
2005–2006					
Live fruit	–88.9	–99.7	NA	–91.3	–89.6
Ripe fruit	–93.5	–100	NA	–95.8	–97.9
Ground arthropods	–25.6	+71.9	NA	–78.7	–55.5
Foliage arthropods	–59.9	–69.3	NA	–5.3	–46.0

fruit biomass per study site for the combined three winters and three winter periods; Pearson $r = 0.002$, $P = 0.994$, $n = 32$; $r = –0.008$, $P = 0.965$, $n = 32$, respectively). There were no significant correlations between transformed biomass of ground arthropods and transformed live-fruit biomass at the site level with any of the winter periods ($P > 0.12$ in all nine winter periods). By contrast, transformed ground-arthropod biomass showed a significant correlation with transformed ripe-fruit biomass in the late-winter period ($r = 0.755$, $P = 0.005$, $n = 12$), but a marginally negative relationship in the early period ($r = –0.555$, $P = 0.096$, $n = 10$) and no relationship in the middle period ($r = 0.168$, $P = 0.643$, $n = 10$).

Diet composition.—Despite variation in availability of food resources among winter periods, study sites, and winters, the composition of the warbler's diet in terms of arthropods and fruit was relatively consistent, based on remains in fecal samples collected over seven winters (2003–2004 to 2009–2010). For samples with identifiable remains ($n = 90$), an average of 95.7 ± 0.63% had arthropods, 92.0 ± 0.92% had fruit, and 87.7 ± 1.23% had both arthropods and fruit. Variation among winters (2005–2006 to 2008–2009) in proportion of arthropods in relation to fruit in samples was not significant ($G = 0.459$, df = 3, $P = 0.928$). When pooled across winters, little variation occurred among samples from early ($n = 20$), middle ($n = 23$), and late ($n = 47$) periods for percentages of samples with arthropods (90.0%, 100%, 91.5%), fruit (80.0%, 91.3%, 91.5%), or both (70.0%, 91.3%, 83.0%). This variation among winter periods in percentage of arthropods and fruit in samples was not significant ($G = 0.111$, df = 2, $P = 0.946$). Sex differences also were not significant for the percentage of arthropods and percentage of fruit remains in samples pooled across winters and winter periods ($G = 0.163$, df = 1, $P = 0.687$). Samples from females ($n = 29$) and males ($n = 58$) had similar percentages with arthropods (96.3% vs. 100%), with fruit (100% vs. 90.6%), and with both (88.9% vs. 84.9%). Samples from adults and juveniles also did not differ significantly in the percentage of arthropods in relation to fruit in samples pooled across all winters, periods, and sexes ($G = 0.064$, df = 1, $P = 0.801$). Samples from adults ($n = 50$) and juveniles ($n = 28$) had similar percentages with arthropods (94.0% vs. 89.3%), with fruit (86.0% vs. 89.3%), and with both (80.0% vs. 78.6%).

Sex and age differences in captures.—We captured 224 individuals and recaptured 73 of

these birds one or more times,resulting in a total of 373 captures. Individuals included 50 adult females, 29 juvenile females, 83 adult males, and 62 juvenile males. Playback captures were biased toward males, as found previously (Wunderle et al. 2010). For example, given bird age, there was a significant interaction of sex with capture method (conditional independence; $G = 7.099$, df = 2, $P = 0.028$). The male bias in captures with playback versus passive netting was more pronounced in adults (71.4% of 77 playback captures vs. 50.0% of 56 passive captures) than in juveniles (72.0% of 50 playback captures vs. 63.4% of 41 passive captures). Although both age classes (sexes pooled) were more likely to be captured by playback than passively, significantly more adults were captured by playback (57.9% of 133 adult captures) than juveniles (54.9% of 91 juvenile captures; test of independence, $G = 7.880$, df = 3, $P = 0.0485$). Within passive captures, there was a slight but not significant bias toward males in total passive captures (55.7% of 97 captures; $\chi^2 = 0.623$, df = 1, $P = 0.430$).

Neither sex nor age ratios varied significantly among study sites, based on passive mist-net captures (initial passive captures plus passive recaptures of birds initially captured with playback). For example, sex ratios of passively captured birds did not differ significantly among the four study sites with adequate sample sizes (percent male: MR 62.5%, $n = 40$; OH 68.8%, $n = 16$; RS 57.9%, $n = 19$; GF = 47.1%, $n = 51$; row × column test of independence, $G = 3.448$, df = 3, $P = 0.328$). Similarly, age ratios from passive captures did not differ significantly among the study sites (percent adult: MR, 67.5%, $n = 40$; OH, 50.0%, $n = 16$; RS, 52.6%, $n = 19$; GF, 45.1%, $n = 51$; $G = 2.361$, df = 3, $P = 0.501$).

Overwinter site persistence.—To test the prediction that playback biased captures toward behaviorally dominant or territorial individuals with high site fidelity, we first compared overwinter site persistence of birds captured with playback or captured passively. In contrast to this prediction, however, no significant differences in overwinter site persistence were found between the two capture methods for all birds captured in early winter and found (i.e., observed or captured) in midwinter, captured in midwinter and found in late winter, or captured in early winter and found in late winter (G tests, $P > 0.10$). In addition, no significant differences (G tests, $P > 0.10$) in overwinter site-persistence values were found between the two capture methods over any periods compared separately for females, males, adults, or juveniles. Given the absence of a significant effect of capture method on overwinter site persistence, we pooled all birds, regardless of capture method, for subsequent analyses of site fidelity.

To further test the prediction that behavioral dominance contributed to site persistence, we compared body size of birds that remained on a study site with that of birds that disappeared after initial presence in early winter, with the expectation that larger birds would displace smaller birds and, hence, show greater site persistence (i.e., stay vs. leave). Although body size differed with sex (i.e., males > females; $F_{1, 184} = 91.296$, $P < 0.0001$), but not age ($F_{1, 184} = 2.492$, $P = 0.116$), based on factor scores of the first principal component of body characteristics, including measurements of wing, tail, and tarsus, we found no evidence that body size varied with site persistence. For instance, mean body size was unrelated to overwinter site persistence from early to late winter ($F_{1, 64} = 0.435$, $P = 0.512$), early winter to midwinter ($F_{1, 64} = 2.096$, $P = 0.153$), or midwinter to late winter ($F_{1, 71} = 1.180$, $P = 0.281$) in samples with sexes and ages pooled across winters. Similarly, within a sex, there were no significant differences between mean body size of individuals that remained on a site and that of individuals that disappeared between any of the winter periods ($P > 0.10$).

Overall, less than half (42.5%) of the banded individuals (sexes and age classes) encountered on a study site in early winter were found again on the same study site late in the same winter (Table 8). For sexes and ages combined, site persistence from early winter to midwinter was 58.5%, which was not significantly different from the 54.8% present from midwinter to late winter ($G = 0.309$, df = 1, $P = 0.579$). Samples of banded birds at individual study sites were insufficient to test for winter (i.e., year-to-year) effects. However, differences in site persistence existed among sites late in the winter for four sites with adequate sample sizes pooled across winters (sites MR, RS, DD, and GF). The four sites differed in persistence levels (sexes and ages pooled; Table 8) only in the middle to late period ($G = 8.121$, df = 3, $P = 0.044$; MR > GF > RS > DD), with no differences in the early to middle period ($G = 1.202$, df = 3, $P = 0.752$) and

TABLE 8. Overwinter site persistence of Kirtland's Warblers in six study sites on Eleuthera, The Bahamas, during the winters of 2003–2004 through 2008–2009, based on resightings supplemented with passive net captures of individuals color-banded in early winter or midwinter and subsequently observed or captured on the same study site in the same winter. Shown are the percentages of color-banded individuals that remained on the study site in which they were initially sighted or captured (number in parentheses). Study-site acronyms are defined in Table 1, and details of the specific winters in which observations were made are provided in the text. Winter periods were defined as "early" (October–December), "middle" (January–February), and "late" (March–April).

	Male	Male	Male	Female	Female	Female	Both sexes
Study site	Adult	Juvenile	All	Adult	Juvenile	All	Total
			Percentage that persisted from early winter to midwinter				
MR	80.0 (25)	28.6 (7)	68.8 (32)	37.5 (8)	0.0 (4)	25.0 (12)	56.82 (44)
WB	83.3 (6)	50.0 (2)	75.0 (8)	50.0 (2)	0.0 (1)	33.3 (3)	63.6 (11)
RS	76.9 (13)	33.3 (3)	68.8 (16)	57.1 (7)	60.0 (5)	58.3 (12)	64.2 (28)
OH	100.0 (1)	0.0 (0)	100.0 (1)	50.0 (2)	0.0 (0)	50.0 (2)	66.7 (3)
DD	80.0 (5)	0.0 (0)	80.0 (5)	0.0 (2)	0.0 (2)	0.0 (4)	44.4 (9)
GF	50.0 (4)	100.0 (1)	60.0 (5)	50.0 (4)	50.0 (2)	50.0 (6)	54.5 (11)
Total	77.8 (54)	38.5 (13)	70.2 (67)	44.0 (25)	28.6 (14)	38.5 (39)	58.5 (106)
			Percentage that persisted from midwinter to late winter				
MR	70.9 (31)	50.0 (6)	67.6 (37)	20.0 (5)	0.0 (0)	20.0 (5)	61.9 (42)
WB	100.0 (5)	0.0 (1)	83.3 (6)	0.0 (1)	0.0 (0)	0.0 (1)	71.4 (7)
RS	38.5 (13)	33.3 (6)	36.8 (19)	60.0 (5)	50.0 (2)	57.1 (7)	42.3 (26)
OH	100.0 (4)	50.0 (2)	83.3 (6)	100.0 (4)	0.0 (0)	80.0 (5)	81.8 (11)
DD	20.0 (5)	0.0 (2)	14.3 (7)	0.0 (1)	0.0 (0)	0.0 (1)	12.5 (8)
GF	33.3 (9)	0.0 (1)	30.0 (10)	100.0 (8)	0.0 (3)	72.7 (11)	52.4 (21)
Total	59.7 (67)	33.3 (18)	54.1 (85)	66.7 (24)	16.7 (6)	56.7 (30)	54.8 (115)
			Percentage present during entire winter				
MR	72.0 (25)	71.4 (7)	71.9 (32)	12.5 (8)	25.0 (4)	16.7 (12)	56.8 (44)
WB	83.3 (6)	0.0 (2)	62.5 (8)	0.0 (2)	0.0 (1)	0.0 (3)	45.5 (11)
RS	30.8 (13)	0.0 (3)	25.0 (16)	42.9 (7)	20.0 (5)	33.3 (12)	28.6 (28)
OH	100.0 (1)	0.0 (0)	100.0 (1)	50.0 (2)	0.0 (0)	50.0 (2)	66.7 (3)
DD	20.0 (5)	0.0 (0)	20.0 (5)	0.0 (2)	0.0 (2)	0.0 (4)	11.1 (9)
GF	50.0 (4)	0.0 (1)	40.0 (5)	50.0 (4)	0.0 (2)	33.3 (6)	36.4 (11)
Total	57.4 (54)	38.5 (13)	53.7 (67)	28.0 (25)	14.3 (14)	23.1 (39)	42.5 (106)

a suggestive but nonsignificant difference over the entire winter ($G = 6.412$, df = 3, $P = 0.093$).

Sex differences in overwinter site persistence (with age classes pooled) were complex, as evidenced by a significant three-way interaction of persistence, sex, and winter period ($G = 7.561$, df = 2, $P = 0.0228$; Table 8). For instance, sex differences in persistence occurred only in early winter to midwinter, when males had greater persistence than females (70.1% vs. 38.5%; row × column test of independence, $G = 10.195$, df = 1, $P = 0.001$), but not in midwinter to late winter (54.1% vs. 56.7%; $G = 0.058$, df = 1, $P = 0.809$). Persistence over the entire winter was greater in males than in females (53.7% vs. 23.1%; $G = 9.879$, df = 1, $P = 0.002$), reflecting the higher persistence of males from the early to middle period.

Within a winter, adults were more likely to be faithful to a study site than juveniles in samples with the sexes pooled. For example, we found a significant interaction between age and persistence given winter period (conditional independence, $G = 21.752$, df = 3, $P = 0.00007$). In this case with sexes pooled (Table 8), adults had higher persistence than juveniles from early winter to midwinter (67.1% vs. 33.3%; $G = 9.444$, df = 1, $P = 0.002$), from midwinter to late winter (61.5% vs. 29.2%; $G = 8.034$, df = 1, $P = 0.005$), and over the entire winter (i.e., early to late winter, 48.1%

vs. 25.9%; $G = 4.216$, df = 1, $P = 0.04$). Similarly within males, adults showed greater overwinter site persistence than juveniles given winter period (conditional independence, $G = 12.669$, df = 3, $P = 0.0054$). Differences between adult and juvenile males in persistence was greater from early winter to midwinter (77.8% adults vs. 38.5% juveniles) than from midwinter to late winter (59.7% adults vs. 33.3% juveniles), reflecting significantly higher adult male persistence from the early to the middle period than from the middle to the late period ($G = 4.473$, df = 1, $P = 0.034$). This contrasted with juvenile males, whose persistence did not vary significantly between the two periods ($G = 0.768$, df = 1, $P = 0.768$). For females, age trends in persistence were similar to those in males (adults > juveniles); however, small samples limited statistical analyses, and only a marginally significant (Fisher's exact test, $P = 0.061$) difference in persistence with age was found between the middle and late periods.

Annual return to a study site.—Percent annual return, calculated on the basis of an individual's presence in a study site in a specific winter period and its return to the same study site in the same period in the following winter, varied from 34.9% for late-winter birds detected again in the following late-winter period (range among sites: 20% to 60%) to 41.7% for midwinter birds detected in the following midwinter period (range among sites: 0–66.7%). However, regardless of how calculated (i.e., early to early, middle to middle, or late to late), percent annual return did not differ significantly among the three winter periods (row × column test of independence, $G = 1.002$, df = 2, $P = 0.606$). Overall, for birds detected again in any period in the following winter, 43.7% were found in the following winter on the same study site (Table 9). Annual return rates, based on birds detected again in any period in the following winter, did not differ among sites, at least for the four sites (DD, MR, GF, and RS) with adequate sample size ($G = 4.601$, df = 3, $P = 0.203$).

Sex and age differences in annual return (Table 9) were consistent with differences in overwinter site persistence when analyses were based on birds detected again in any period in the following winter in a three-way model (presence*sex*age). For example, given sex, there was an age difference (conditional independence; $G = 8.354$, df = 2, $P = 0.0153$) in annual return; and given age, there was a sex difference in annual return (conditional independence; $G = 8.6472$, df = 2, $P = 0.0133$). Thus, annual returns were higher in males than in females and were higher in adults than in juveniles.

Not only did females have lower annual return rates than males, but females were also less likely to return in the following winter to study sites that had high male annual return rates (detected in any period). For instance, female annual return rates showed a significant negative correlation with male annual return rates to the six study sites (Pearson $r = –0.844$, $P = 0.035$, $n = 6$; Table 9). The inverse relation was strongest, but only marginally significant for annual returns of males (all ages) versus juvenile female returns to the same study site (Pearson $r = –0.847$, $P = 0.070$, $n = 5$). Juvenile females, however, were less likely to return in the following year to sites with high adult male return rates, as evidenced by a strong and significant negative correlation between annual return rates of juvenile females and of adult males (Pearson $r = –0.947$, $P = 0.015$, $n = 5$).

Site persistence in relation to food abundance and sex and age.—To test the hypothesis that overwinter site persistence (early to late winter) was related to a site's late-winter food abundance (biomass separately for live fruit, ripe fruit, foliage arthropods, and ground arthropods) and sex and age of the birds ($n = 48$), we stratified the birds according to whether or not they disappeared from the site where they were observed in early winter for each of three winters (2003–2004, 2004–2005, 2005–2006). We then compared late-winter food abundance for birds that remained on a study site with that for birds that disappeared. Study sites where birds remained through late winter, in contrast to study sites where birds disappeared, had significantly higher mean biomass of live fruit (1.517 ± 0.33 g/20 m^2 vs. 0.524 ± 0.167 g/20 m^2), ripe fruit (0.014 ± 0.004 g/20 m^2 vs. 0.004 ± 0.001 g/20 m^2), and foliage arthropods (0.024 ± 0.002 mg/g foliage vs. 0.0151 ± 0.002 mg/g foliage) (likelihood ratio tests, all $P < 0.01$); and a higher, albeit not quite significant, ground-arthropod biomass (0.997 ± 0.129 mg/0.25 m^2 vs. 0.736 ± 0.069 mg/0.25 m^2; $P = 0.0577$). Age differences in fidelity were evident, in that adults (14 present, 18 absent) showed significantly ($P = 0.0082$) greater fidelity than juveniles (1 present, 15 absent), although fidelity did not differ significantly

TABLE 9. Percentage annual return of color-banded Kirtland's Warblers to six study sites on southern Eleuthera, The Bahamas, during different winter periods over the winters 2003–2004 through 2008–2009. Percentage annual return was recorded for banded birds present in a given winter period out of the total banded birds present during that period (number in parentheses) and subsequently found in the following winter at the same study site. These percentage returns include birds present in early winter (October–December) and found in the following early winter; present in midwinter (January–February) and again in the following midwinter; present in late winter (April–March) and again in the following late winter; present in late winter and again in the following early winter; and present in the first winter and again in the following winter, regardless of period. Study-site acronyms are defined in Table 1, and details of the specific winters in which observations were made are provided in the text.

Site	Male Adult	Male Juvenile	Male All	Female Adult	Female Juvenile	Female All	Male and female Total
Present early winter from previous early winter							
MR	62.5 (24)	16.7 (6)	53.3 (30)	20.0 (5)	0.0 (1)	16.7 (6)	47.2 (36)
WB	66.7 (3)	0.0 (0)	66.7 (3)	0.0 (1)	0.0 (0)	0.0 (1)	50.0 (4)
RS	46.2 (13)	0.0 (3)	37.5 (16)	33.3 (6)	0.0 (5)	18.2 (11)	29.6 (27)
OH	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)	0.0 (0)
DD	66.7 (6)	0.0 (2)	50.0 (8)	33.3 (3)	0.0 (3)	16.7 (6)	35.7 (14)
GF	0.0 (1)	0.0 (1)	0.0 (2)	0.0 (0)	0.0 (1)	0.0 (1)	0.0 (3)
Total	57.4 (47)	8.3 (12)	47.5 (59)	26.7 (15)	0.0 (10)	16.0 (25)	38.1 (84)
Present midwinter from previous midwinter							
MR	63.3 (30)	25.0 (4)	58.8 (34)	0.0 (4)	0.0 (0)	0.0 (4)	52.6 (38)
WB	100.0 (2)	0.0 (0)	100.0 (2)	0.0 (1)	0.0 (0)	0.0 (1)	66.7 (3)
RS	50.0 (14)	20.0 (5)	42.1 (19)	33.3 (6)	0.0 (3)	22.2 (9)	35.7 (28)
OH	0.0 (2)	0.0 (0)	0.0 (2)	0.0 (2)	0.0 (0)	0.0 (2)	0.0 (4)
DD	50.0 (4)	50.0 (2)	50.0 (6)	100.0 (1)	0.0 (0)	100.0 (1)	57.7 (7)
GF	12.5 (8)	0.0 (1)	11.1 (9)	25.0 (4)	66.7 (3)	42.9 (7)	25.0 (16)
Total	51.7 (60)	25.0 (12)	47.2 (72)	22.2 (18)	33.3 (6)	25.0 (24)	41.7 (96)
Present late winter from previous late winter							
MR	65.5 (29)	0.0 (9)	50.0 (38)	0.0 (2)	0.0 (1)	0.0 (3)	46.3 (41)
WB	60.0 (5)	0.0 (0)	60.0 (5)	0.0 (0)	0.0 (0)	0.0 (0)	60.0 (5)
RS	37.5 (8)	0.0 (2)	30.0 (10)	60.0 (5)	0.0 (2)	42.9 (7)	35.3 (17)
OH	14.3 (7)	33.3 (3)	20.0 (10)	0.0 (2)	100.0 (1)	33.3 (3)	23.1 (13)
DD	100.0 (1)	0.0 (1)	50.0 (2)	0.0 (1)	0.0 (0)	0.0 (1)	33.3 (3)
GF	22.2 (9)	28.6 (7)	25.0 (16)	16.7 (12)	0.0 (2)	14.3 (14)	20.0 (30)
Total	49.2 (59)	13.6 (22)	39.5 (81)	22.7 (22)	16.7 (6)	21.4 (28)	34.9 (109)
Present early winter from previous late winter							
MR	62.1 (29)	22.2 (9)	52.6 (38)	0.0 (2)	100.0 (1)	33.3 (3)	51.2 (41)
WB	60.0 (5)	0.0 (0)	60.0 (5)	0.0 (0)	0.0 (0)	0.0 (0)	60.0 (5)
RS	62.5 (8)	0.0 (2)	50.0 (10)	40.0 (5)	0.0 (2)	28.6 (7)	41.2 (17)
OH	14.3 (7)	0.0 (3)	10.0 (10)	50.0 (2)	0.0 (1)	33.3 (3)	15.4 (13)
DD	0.0 (1)	0.0 (1)	0.0 (2)	0.0 (1)	0.0 (0)	0.0 (1)	0.0 (3)
GF	22.2 (9)	0.0 (7)	12.5 (16)	25.0 (12)	0.0 (2)	21.4 (14)	16.7 (30)
Total	49.2 (59)	9.1 (22)	38.3 (81)	27.3 (22)	16.7 (6)	25.0 (28)	34.9 (109)
Present any time from presence anytime in previous winter							
MR	76.5 (34)	27.3 (11)	64.4 (45)	12.5 (8)	0.0 (1)	11.1 (9)	55.6 (54)
WB	50.0 (6)	0.0 (0)	50.0 (6)	0.0 (1)	0.0 (0)	0.0 (1)	42.9 (7)
RS	52.6 (19)	12.5 (8)	40.7 (27)	30.0 (10)	16.7 (6)	25.0 (16)	34.9 (43)
OH	14.3 (7)	33.3 (3)	20.0 (10)	50.0 (2)	100.0 (1)	66.7 (3)	30.8 (13)
DD	57.1 (7)	25.0 (4)	45.5 (11)	50.0 (4)	0.0 (3)	28.6 (7)	38.9 (18)
GF	46.2 (13)	50.0 (8)	47.6 (21)	33.3 (12)	40.0 (5)	35.3 (17)	42.7 (38)
Total	58.1 (86)	29.4 (34)	50.0 (120)	29.7 (37)	25.0 (16)	28.3 (53)	43.4 (173)

TABLE 10. The best-supported models describing overwinter site persistence in Kirtland's Warblers on Eleuthera, The Bahamas. Two separate analyses were conducted using Akaike's information criterion (AIC_c): the first included dry biomass of fruit and arthropods (winters 2003–2004 through 2005–2006) and involved 28 candidate models, and the second included dry biomass of fruit without arthropods (winters 2003–2004 through 2008–2009) and involved 20 candidate models (Appendix 7). For model details, see text. Models are ranked by decreasing support, separately for fruit and arthropod models, and fruit-only models with $\Delta AIC_c < 4$ are shown. w_i = Akaike weight.

Model	K [a]	ΔAIC_c	w_i	Percent deviance explained [b]
Fruit and arthropod models				
Age + sex + live fruit + habitat PC2	5	0.0 [c]	0.34	38.3
Age + sex + foliage arthropods	4	1.5	0.16	31.6
Age + sex + live fruit	4	1.9	0.13	31.0
Global model	9	2.2	0.11	53.6
Age + sex + foliage arthropods + rain 30-day	5	2.9	0.08	33.5
Age + sex + live fruit + rain 30-day	5	3.3	0.06	32.7
Fruit models				
Age + sex + live fruit	4	0.0 [d]	0.31	16.0
Age + sex + habitat PC2 + age*habitat PC2 + sex*habitat PC2	6	0.6	0.23	19.6
Age + sex + live fruit + rain 30-day	5	2.1	0.11	16.2
Age + sex + live fruit + habitat PC2	5	2.3	0.10	16.0
Age + sex + rain 30-day	4	3.6	0.05	10.9
Global model	10	3.9	0.04	25.6

[a] Number of fixed effect parameters (fruit models also had random effect for winters).
[b] For the fruit and arthropod models, calculations are based on McFadden's r^2. For fruit models with a winter random effect, calculations are based on a Laplace approximation to the marginal likelihood.
[c] Minimum value of AIC_c = 48.21.
[d] Minimum value of AIC_c = 106.12.

(P = 0.3928) between sexes (males: 11 present, 20 absent; females: 4 present, 13 absent).

Modeling overwinter site persistence: *Models with arthropod and fruit biomass*.—The model with age + sex + live fruit + habitat PC2 was the most supported model for overwinter site persistence and had 34% of the model weight (Table 10). However, two additional models were competitive with this top model, and together the three models had a combined AIC_c weight of 0.63. These top three models all included age and sex and a food measure (live fruit or foliage arthropods), but only the top model included habitat PC2. The combined weights for the top three models containing these four variables indicate that values were highest for age (0.63) and sex (0.63), followed by live fruit (0.47), habitat PC2 (0.34), and foliage arthropods (0.16). Among the reduced set of models, age and sex were 1.34× more plausible explanations for site persistence than live fruit, 1.87× more plausible explanations than habitat PC2, and 3.96× more plausible explanations than foliage arthropods. There was comparatively little support for ground arthropods or for 30-day or 60-day prior rain as predictors of variation in site persistence. The global model explained 54% of the deviance in the data, whereas the top three models explained 32–38% of the deviance.

Although the signs of the parameter coefficients (Table 11) indicated that overwinter site persistence was positively associated with live fruit, foliage arthropods, and age (adult > juvenile), the reliability of these parameter estimates was low, as indicted by the 95% CIs that overlapped zero, except for the estimate for foliage arthropods. Only sex (male > female) and habitat PC2 had negative coefficients, but the reliability of these parameter estimates was low, given that 95% CIs for both overlapped zero.

Modeling overwinter site persistence: *Models with fruit biomass*.—The model with age + sex + live fruit was the most supported model for overwinter site persistence and had 31% of the model weight (Table 10). A second model was competitive with this top model, and together

TABLE 11. Model-averaged parameter coefficients, standard errors, and 95% confidence intervals (CI; $n \geq 30$) for the top models explaining overwinter site persistence of Kirtland's Warblers on Eleuthera, The Bahamas, among models with fruit and arthropods (winters 2003–2004 through 2005–2006) and models with fruit but no arthropods (winters 2003–2004 through 2008–2009). Models within two AIC points of the top model were averaged; therefore, three top models were averaged among models with fruit and arthropods and two top models among the fruit models.

Parameter	β	SE	95% CI
Fruit and arthropod models			
Intercept	–8.873	6.559	–21.728 to 3.982
Age [a] = adult	6.349	5.416	–4.267 to 16.965
Sex [b] = male	–0.106	0.881	–1.822 to 1.620
Live fruit	2.474	2.097	–1.635 to 6.584
Foliage arthropods	159.270	60.304	41.077 to 277.463
Habitat PC2	–5.186	4.553	–14.109 to 3.737
Fruit models			
Intercept	–3.288	1.238	–5.714 to –0.862
Age [a] = adult	1.274	0.783	–0.261 to 2.808
Sex [b] = male	1.687	1.094	–0.458 to 3.832
Live fruit	0.735	0.342	0.065 to 1.406
Habitat PC2	–4.230	4.429	–12.910 to 4.451
Age*habitat PC2	–0.889	2.016	–4.840 to 3.063
Sex*habitat PC2	6.514	4.166	–1.651 to 14.679

[a] Binary variable: reference was for juveniles (= 0).
[b] Binary variable: reference was for females (= 0).

the two models had a combined AIC_c weight of 0.54. These top two models both contained age and sex, the top-ranked model also contained live fruit, and the second-ranked model contained habitat PC2 and the interaction of habitat PC2 with sex and with age. The combined weights of all models containing the six variables indicate that values were highest for age (0.54) and sex (0.54), followed by live fruit (0.31), habitat PC2 (0.23), habitat PC2*age (0.23), and habitat PC2*sex (0.23). Based on the reduced set of models, age and sex were 1.75× more likely to explain site persistence than live fruit, and 2.33× more likely than the variables with habitat PC2 alone or with an interaction with age or sex. Live fruit was 1.33× more plausible an explanation for site persistence than habitat PC2 or habitat PC2*age or habitat*sex. There was comparatively little support for 30- or 60-day rain, all food, ripe fruit, or age*sex. The global model explained 26% of the deviance in the data, whereas the top two models explained 16–20% of deviance.

The signs of the parameter coefficients (Table 11) indicated that overwinter site persistence was positively associated with age, sex, and sex*habitat PC2, but the 95% CIs for each of these estimates overlapped zero, indicating low reliability of the coefficients. Site persistence was also positively associated with live fruit, and the 95% CI did not overlap zero. Although habitat PC2 and age*habitat PC2 both had negative coefficients, suggesting that site persistence was negatively associated with the two parameters, both had 95% CIs that overlapped zero. The global model explained 26% of the deviance in the data, whereas the top two models explained 16–20% of deviance.

Study-site shifts in relation to food abundance.—To test the hypothesis that individuals that abandoned sites were shifting from low- to high-food-abundance study sites within a winter, we compared food abundance from an individual's initial study site of occupancy with that of its subsequent occupied study site by following shifts between study sites by 10 color-banded birds (pooled for 2003–2003, 2004–2005, and 2005–2006; Table 12). Consistent with this hypothesis was our finding that ripe-fruit biomass was significantly more abundant at an individual's new site (median = 0.173 g/20 m^2) than at its abandoned site (median = 0.037 g/20 m^2; Wilcoxon

TABLE 12. Summary of individual Kirtland's Warblers that shifted between study sites within a winter, and mean food-resource measurements at original study site (old site) and subsequent study site (new site) following study-site shift, on southern Eleuthera, The Bahamas. Shown are the color-band combinations for each bird, winter, winter period (early, October–December; middle, January–February; late, March–April), study sites, distance between sites, and mean ripe fruit, live fruit (unripe and ripe), and ground arthropods measured at original and second study site. Study-site acronyms are defined in Table 1, and measurements of food resources are described in the text. NA = not available.

					Ripe fruit (mg/20 m^2)		Live fruit (mg/20 m^2)		Ground arthropods (mg/0.25 m^2)	
Bird	Winter	Winter period	Study sites	Distance (km)	Old site	New site	Old site	New site	Old site	New site
RR-XR	2003–2004	Late	WB to OH	2.7	0.002	0.209	0.102	0.463	0.223	0.778
WX-RR	2004–2005	Early	RS to DD	1.3	0.077	0.015	1.350	0.398	0.637	0.434
YR-XY	2004–2005	Early	RS to DD	1.2	0.077	0.015	1.350	0.398	0.637	0.434
OB-XO	2004–2005	Middle	MR to RS	6.0	0.128	0.077	5.468	0.876	NA	NA
RX-YY	2005–2006	Early	DD to RS	1.4	0.250	0.635	5.623	22.649	1.057	0.798
BB-BX	2005–2006	Late	RS to GF	4.7	0.037	0.173	2.773	1.235	0.594	1.119
OO-RX	2005–2006	Late	RS to GF	4.8	0.037	0.173	2.773	1.235	0.594	1.119
OO-XO	2005–2006	Late	RS to GF	5.1	0.037	0.173	2.773	1.235	0.594	1.119
XY-RY	2005–2006	Late	MR to GF	1.9	0.005	0.173	1.907	1.235	0.884	1.119
YX-RY	2005–2006	Late	MR to GF	2.2	0.005	0.173	1.907	1.235	0.884	1.119

signed-ranks test, $Z = -2.200$, $P = 0.028$). By contrast, median (but not mean) live fruit showed the opposite trend, with live fruit at the new site less than at the abandoned site (median = 1.235 g/20 m^2; median = 2.340 g/20 m^2, respectively), although the difference was only marginally significant ($Z = 1.688$, $P = 0.091$). Ground arthropod abundance showed only a marginally significant increase from an individual's abandoned site (median = 0.637 mg/0.25m^2) to its new site (median = 1.119 mg/0.25m^2; $Z = -1.727$, $P = 0.084$).

Late-winter warbler abundance at the fruit-rich OH site.—The late-winter abundance of warblers in the OH site in winter provided an opportunity to further test the hypothesis that the warblers were shifting from low- to high-food-resource sites. In late winter of 2003–2004, the OH site had significantly higher live-fruit biomass than was found at RS or WB (Fig. 4; simultaneous contrast, $F_{2, 28.33} = 4.55$, $P = 0.0194$; OH vs. RS, post hoc LSD, $P = 0.0222$; OH vs. WB, post hoc LSD, $P = 0.0171$). Similarly, ground-arthropod biomass in this period was also higher at the OH site than at RS or WB (Fig. 4; $F_{2, 152} = 12.98$, $P < 0.0001$; OH vs. WB, $t = 4.99$, df = 152, $P < 0.001$; OH vs. RS, $t = 3.01$, df = 152, $P = 0.0080$). Associated with the OH site's higher food abundance was a higher abundance of warblers, as initially demonstrated by four captures during 9–11 February 2004 and subsequently verified with observations and captures of 10 additional individuals. Overall, 14 color-banded individuals (11 males, 3 females) and two unbanded birds occurred on the OH site in late winter 2003–2004, including a color-banded male that had shifted 2.7 km from the WB site (details of observations in Appendix 8). This midwinter to late-winter increase in warblers resulted in an unusual abundance of warblers in the small (16 birds in 1.7 ha) OH site, in contrast to midwinter to late-winter declines in warbler numbers in the larger RS (8 to 2) and WB (5 to 4) sites in that same winter.

While in the OH site, warblers fed primarily on fruit (82.5% vs. 17.5% arthropods), based on 217 foraging observations between 4 January and 28 April 2004. Of the 179 fruit-foraging observations, most involved consumption of *Lantana* spp. (98.3%), although *Cassytha filiformis* (0.6%), *Bourreria ovata* (0.6%), and *Trema lamarckianum* (0.6%) were also consumed. Most of the 38 arthropod-foraging maneuvers occurred on the ground (89.5%), and the remainder were near the ground (5.3% at >0 to 0.5 m; 2.6% at >0.5 to 1.0 m; 2.6% at >1.0 to 1.5 m). Within the OH site, warblers concentrated in areas with high *Lantana* fruit

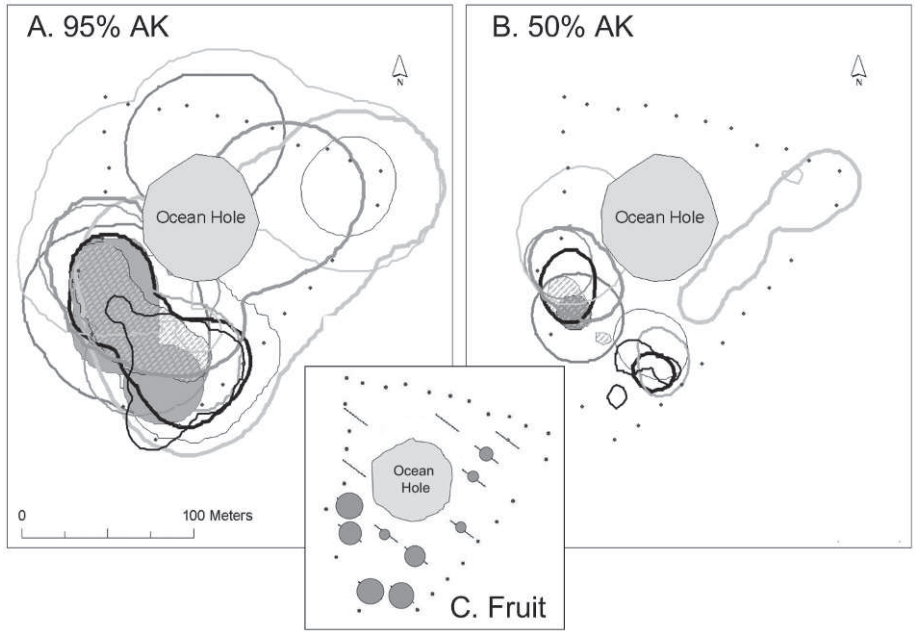

FIG. 5. Home ranges of 11 color-banded Kirtland's Warblers, based on (A) the 95% adaptive kernal and (B) the 50% adaptive kernal, in relation to dry biomass of live (unripe and ripe) fruit of *Lantana* spp. sampled in (C) 20-m^2 transects in the 1.7-ha Ocean Hole study site on southern Eleuthera, The Bahamas. Color-banded birds were observed from 10 March through 2 May 2004 in the study site but were not followed outside the study site's boundary (indicated by small black points in panels); therefore, home ranges and core areas depict only the area used by birds when in the study site and do not represent the full areas used by the birds. Because of space limitations, areas used by two additional color-banded birds are not shown. Fruit biomass per transect in panel C is depicted by circles of different diameters, which vary in size depending on the quantity of dry biomass of live fruit per transect (largest circle in lower right bottom of study site is equivalent to dry weight of 1.2 g of live fruit per 20-m^2 transect). The 13 fruit transects are indicated by lines. Details of sampling are provided in the text, and summaries of birds using the site are in Appendix 8.

biomass, as evidenced by a positive rank correlation between the number of warbler home ranges overlapping a transect and the transect's biomass of *Lantana* spp. fruit. For instance, the number of home ranges (95% AK) or number of core areas (50% AK) overlapping a transect were significantly correlated with the biomass of live *Lantana* fruit in the transect (Spearman $r = 0.728$, df = 13, $P = 0.005$, and $r = 0.700$, df = 13, $P = 0.008$, respectively) and ripe fruit in the transect (Spearman $r = 0.716$, df = 13, $P = 0.006$, and $r = 0.708$, df = 13, $P = 0.007$, respectively). By contrast, there was no significant correlation between ground-arthropod biomass per quadrat and number of overlapping 95% AK home ranges (Spearman $r = –0.355$, df = 13, $P = 0.235$) or 50% AK home ranges (Spearman $r = –0.339$, df = 13, $P = 0.257$). Both home ranges (95% AK) and core areas (50% AK) of the color-banded warblers using the OH site in late winter 2003–2004 overlapped extensively, indicating that the birds were not occupying exclusive areas while in the OH study site (Fig. 5).

In marked contrast in the following 2004–2005 late-winter period, the OH site had a warbler density of only half (7 birds or 4.1 birds ha^{-1}) the previous late-winter density, yet fruit and ground-arthropod biomass levels were comparable to levels found in the previous late winter (Fig. 4). Also, the warblers continued to feed heavily on fruit there (83.4% of 30 late-winter foraging observations) as in the previous late winter. However, the OH site's fruit- and ground-arthropod biomass levels of late winter 2004–2005 were not significantly different from the levels found in the RS and WB sites (Table 5), in contrast to the previous late winter, when levels of live fruit and ground-arthropod biomass were lower in both sites.

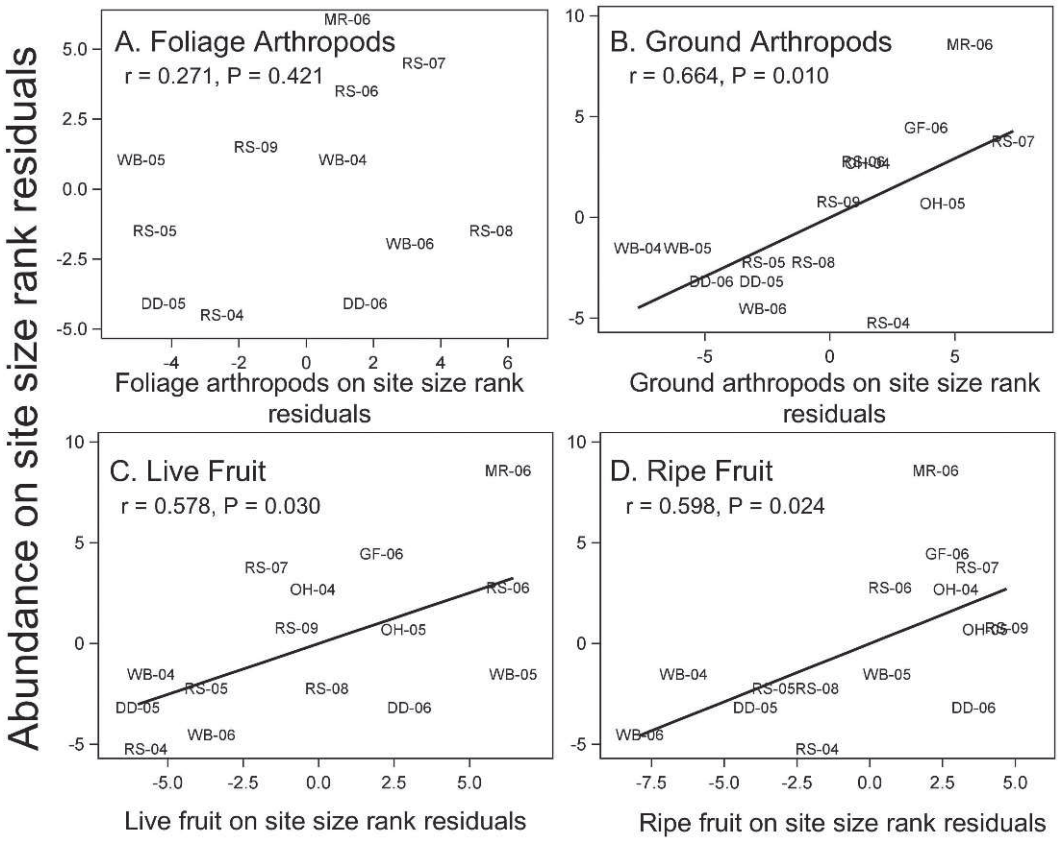

FIG. 6. Residuals for late-winter (March–April) abundance of Kirtland's Warblers, ranked on study-site size plotted against residuals for various food biomass measures ranked against study-site size, for late winters 2003–2004 through 2005–2006 on southern Eleuthera, The Bahamas (using the ranks for abundance, food biomass, and study-site size). Food dry biomass measures include (A) foliage arthropods, (B) ground arthropods, (C) live fruit (unripe and ripe), and (D) ripe fruit. Study sites are denoted by a two-letter acronym, followed by two digits indicating the late winter in which they were sampled. Study-site acronyms are defined in Table 1, and methods used to sample warbler abundance and measure food biomass are provided in the text.

Late-winter warbler abundance and food-resource biomass.—Given evidence that warblers were tracking food-resource changes over the course of a winter by shifting locations, we expected that by late winter, warbler abundance would be greatest in study sites with the highest food abundance. To test this prediction, we compared the total number of warblers per study site with the biomass of each of the four food-resource measures per study site in late winter while controlling for study-site size (Fig. 6). This analysis indicated a borderline marginal rank correlation but significant Poisson regression relationship with ground arthropods (Spearman partial $r = 0.519$, df = 9, $P = 0.1019$, Poisson $P = 0.0280$) and a marginally significant correlation with live fruit (Spearman partial $r = 0.535$, df = 9, $P = 0.0898$; Poisson $P = 0.0894$). Inclusion of three additional observations (i.e., sites where arthropods sampled on the ground but not on foliage) by dropping foliage arthropods from the comparisons indicated significant correlations of abundance with ground arthropods (Spearman partial $r = 0.664$, df = 12, $P = 0.0096$; NB $P = 0.0033$), ripe fruit (Spearman partial $r = 0.598$, df = 12, $P = 0.0239$; NB $P = 0.0067$), and live fruit (Spearman $r = 0.578$, df = 12, $P = 0.0304$; NB $P = 0.0124$). Given that transformed biomass of ripe fruit and ground arthropods at a study site were significantly correlated (Spearman partial $r = 0.582$, df = 12, $P = 0.0289$), we reran the correlations, controlling for both

study-site size and one of the food measures to determine the correlation of warbler abundance with the biomass of the other food measures. For example, controlling for study-site size and live fruit indicated a significant correlation with ground arthropods and warbler abundance (Spearman partial $r = 0.662$, df = 12, $P = 0.0138$; NB $P = 0.0065$). Controlling for study-site size and ripe-fruit biomass indicated only a weaker and not-quite-significant correlation with ground arthropods (Spearman partial $r = 0.484$, df = 12, $P = 0.0935$; NB $P = 0.0759$). Controlling for study-site size and ground-arthropod biomass indicated no significant correlations with ripe fruit (Spearman $r = 0.348$, df = 12, $P = 0.2442$; NB $P = 0.1727$), but a significant correlation with live fruit, at least for the Poisson regression (Spearman $r = 0.575$, df = 12, $P = 0.1072$; NB $P = 0.025$).

Changes in physical condition.—As a consequence of intraspecific competition, we expected that the sex and age classes that showed the most site fidelity (i.e., males and adults) would also have the highest corrected body mass and fat levels and that these differences would become most pronounced in late winter as birds prepared for spring migration. Detecting these patterns, however, may require controlling for changes in physical condition during the day, because condition is known to change during the day in other wintering migrants (e.g., Katti and Price 1999, Townsend et al. 2012).

Changes in corrected body mass.—Corrected body-mass values increased over the course of a day (time after sunrise) and were consistently higher in afternoon than in morning captures, including at the end of the winter as corrected body mass increased prior to migration (penalized spline model, $F_{1, 216} = 30.79$, $P < 0.001$; Fig. 7A). Captures of birds in January, February, and March displayed mean corrected body-mass scores in the morning of –0.152 ± 0.834, which increased to 0.319 ± 0.665 in the afternoon. During these 3 months, the daily increase in corrected body mass occurred at a rate of 0.047 units h^{-1}, based on the significant regression of condition against time after sunrise, pooled for all winters ($F_{1, 150} = 12.63$, $P = 0.001$). However, in April, corrected body mass averaged 0.455 ± 1.427 in the morning and increased to 0.618 ± 1.388 in the afternoon, increasing at a rate of 0.092 units h^{-1} with hours after sunrise (pooled for all winters; $F_{1, 90} = 12.07$, $P = 0.001$).

As expected, changes in corrected body mass with capture date (days after 1 October) were dependent on sex and age class (Fig. 7C), as evidenced by a significant interaction between capture date and sex–age class (penalized spline model, $F_{4, 281.5} = 15.35$, $P < 0.0001$). Although significant ($P_A = 0.0151$) corrected body-mass differences between juvenile females and juvenile males were observed as early as 120 days after 1 October (1 February), it was not until 195 days (16 April) that highly significant corrected body-mass differences between sex and age classes occurred (with the exception of the 120-day difference mentioned, no other significant differences for comparisons at 30, 45, 60, 75, 90, 105, 120, 135, 150, 165, or 180 days). By 16 April, males had significantly higher corrected body-mass scores than females in all comparisons within and between age classes (all $P_A < 0.05$), as also observed 10 days later, on 26 April (all $P_A \leq 0.001$), with the exception of a marginal difference between juvenile males and adult females; $P_A = 0.064$). Within a sex, age-class differences in corrected body mass were detected only within males and only on 26 April, when adult males had significantly ($P_A < 0.001$) higher corrected body-mass scores than juvenile males. The variation attributed to different capture sites and winters was significant for corrected body mass ($\chi^2 = 13.26$, $P < 0.0001$).

The percent differences in corrected body mass between the sex and age classes were substantial by late winter. For example, at 190 days after 1 October (11 April), at 1 h after sunrise, the percent increase in corrected body mass in relation to juvenile females was 46% for adult females, 133% for juvenile males, and 192% for adult males. Greater increases in corrected body mass in relation to juvenile females occurred at 11.5 h after sunrise, when adult females increased by 291%, juvenile males by 833%, and adult males by 1,209%. Thus, by the end of the day, percentage differences in corrected body mass between sex and age classes were substantially greater than those observed in the morning, which suggests that daily rates of increase in corrected body mass differed with sex and age class.

Changes in fat scores.—In contrast to corrected body mass, fat levels were not consistently higher in afternoon than in morning captures during the course of the entire winter (Fig. 7B) and showed a nonsignificant (penalized spline

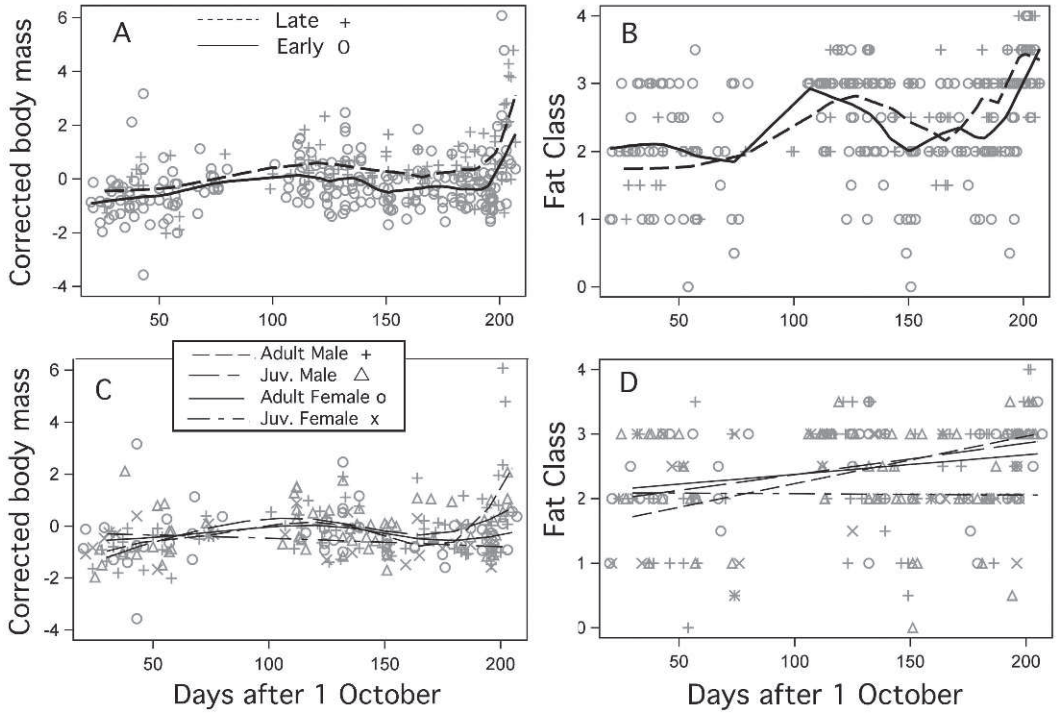

FIG. 7. Change in corrected body mass and furcula fat scores (0–4) in Kirtland's Warblers, in relation to captures after 1 October and through April (50 days = 19 November; 100 days = 8 January; 150 days = 27 February; 200 days = 18 April), based on captures (n = 324 for corrected body mass; n = 323 for fat) during winters 2003–2004 through 2009–2010 on southern Eleuthera, The Bahamas. Shown are loess smoothed graphs for corrected (A) body mass and (B) fat score measured in morning (dashed line; sunrise to sunrise + 6 h) and afternoon (solid line; sunrise + 6 h to sunset) during winter. Model graphs for (C) corrected body mass and (D) fat score for different sex and age classes sampled early in the day during the winter. Key shown in panel C depicts the different pattern of spline smoothed lines in front of the corresponding sex and age classes, which are followed by corresponding symbols for each individual value plotted on the graph. The key in panel C also applies to D. Corrected body-mass values represent the residuals of body mass regressed against principal component score of wing chord, tarsus, and tail measurements. See text for details.

model, $F_{1, 308}$ = 2.79, P = 0.0959) increase with time after sunrise. Mean morning and afternoon fat scores were similar (2.44 ± 0.739 and 2.531 ± 0.594, respectively) during January–March, when fat levels did not increase significantly during the day (0.009 units h^{-1}; $F_{1, 149}$ = 0.586, P = 0.445). By contrast, April fat scores (all birds) increased significantly ($F_{1, 91}$ = 5.217, P = 0.025) at a rate of 0.028 units h^{-1} during the day. Fat in April averaged 2.74 ± 0.699 in the morning and 3.05 ± 0.602 in the afternoon.

As with corrected body mass, change in fat score with capture date depended on sex and age class (Fig. 7D), as shown by a significant interaction between capture date and sex–age class (penalized spline model, $F_{4, 308}$ = 13.45, P < 0.0001). Much of this interaction is attributable to differences in fat scores of juvenile females, which were consistently and significantly lower than those of adult females, adult males, and juvenile males from 135 days after 1 October (16 February) through the end of the winter (sample dates 1 and 16 March, 1 and 16 April; all P_A < 0.02). Consistent with corrected body-mass differences on 1 February, fat scores of juvenile females were also significantly lower than those of juvenile males (P = 0.028). However, fat scores did not differ significantly between adult males and females or between adult and juvenile males, as found for corrected body-mass comparisons.

Departure schedules.—Given sex and age differences in mean corrected body mass and fat

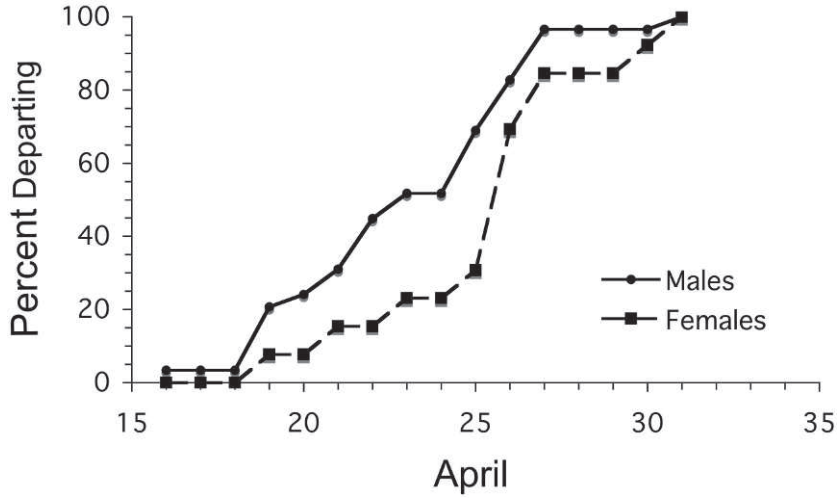

FIG. 8. Departures of color-banded male (n = 29) and female (n = 21) Kirtland's Warblers after 15 April, pooled for winters 2003–2004 through 2008–2009, from various study sites on southern Eleuthera, The Bahamas. Birds were assumed to have departed from the first date when they were not found for 2 consecutive days on a study site. See text for details.

scores in April, we expected that birds in better condition would depart from study sites earlier than those in poorer condition. Consistent with expectations (based on birds pooled over years and study sites), the mean departure date of males (24 April) was significantly earlier than that of females (26 April) (based Kaplan-Meier estimates for departures after 15 April; Tarone-Ware $\chi^2 = 3.929$, df = 1, $P = 0.047$; Fig. 8). However, differences in mean departure times between adults (25 April) and juveniles (26 April) in pooled samples of both sexes were not significant (Tarone-Ware $\chi^2 = 1.483$, df = 1, $P = 0.233$).

Changes in physical condition with rainfall.—Given the positive effect of prior rainfall on fruit abundance, we expected that the warbler's corrected body-mass and fat levels would correspondingly vary with prior rainfall. We also expected that rainfall effects on corrected body mass and fat levels would be most evident in the late-winter dry season, when food abundance was potentially lowest, but energy needs highest, as the birds prepared for migration. Because the warbler's physical condition changed with date and with time after sunrise, as previously demonstrated, we treated both variables as covariates, along with prior cumulative rainfall, in all models below.

Effect of rainfall on corrected body mass in different periods.—Rainfall had a marginally significant negative effect on corrected body mass in midwinter in the prior 30 days ($P = 0.0654$; Fig. 9A), no significant effect in the prior 60 days ($P = 0.2434$), and a significant negative effect in the prior 90 days (slope = –0.00607 ± 0.002597, df = 45.1, $t = -2.34$, $P = 0.0238$) in models with winter and individual birds as random effects (winter, all significant at $P < 0.001$; birds, $P = 0.0532$, 0.1310, and 0.0486, for 30-day, 60-day, and 90-day rain models, respectively). In addition, corrected body mass did not differ significantly with sex or age class in the midwinter period (all tests, $P > 0.05$). In late winter, however, rainfall had a significant positive effect on corrected body mass in the prior 30 days (slope = 0.008219 ± 0.003504, df = 133.1, $t = 2.35$, $P = 0.0205$; Fig. 9B) and 90 days (slope = 0.005172 ± 0.00249, df = 87.95, $t = 2.08$, $P = 0.0408$). The effect of rainfall 60 days prior to late-winter capture was not quite significant (slope = 0.006297 ± 0.003159 SE, df = 56.76, $t = 1.99$, $P = 0.0511$). All late-winter models included a site*winter random effect, which in all cases was significant ($P < 0.002$).

Regardless of the prior rainfall period (30, 60, or 90 days) before capture in late winter, corrected body mass varied significantly ($P < 0.0005$) with sex and age class, as previously demonstrated. In models with the 30-day prior-rainfall covariate, corrected body mass (i.e., slope) was significantly greater for adult males than for adult females ($P < 0.01$) and for adult males than for juvenile males ($P < 0.05$), but not

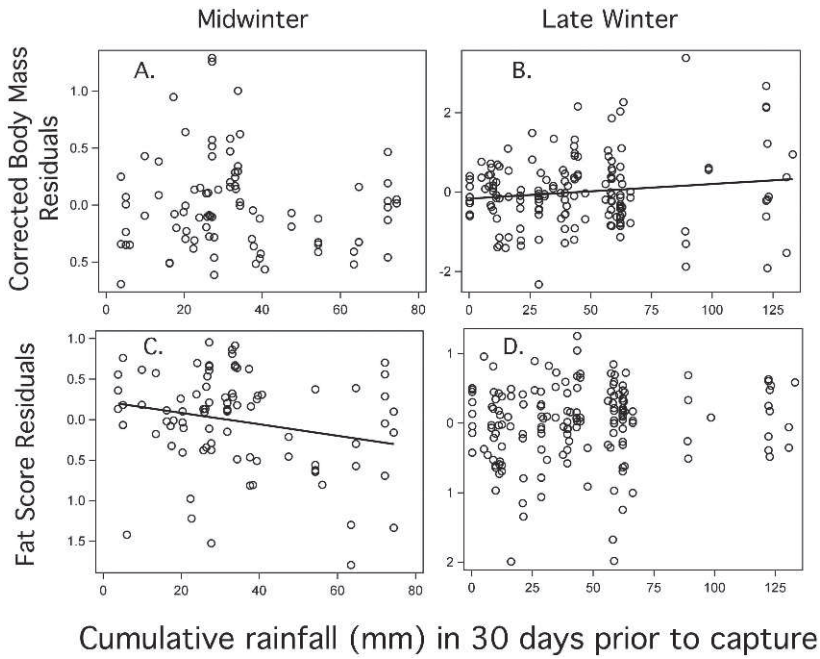

FIG. 9. Conditional residuals for corrected body mass of Kirtland's Warblers against rainfall 30 days prior to capture in (A) midwinter and (B) late winter, and residuals for fat scores of Kirtland's Warblers against rainfall 30 days prior to capture in (C) midwinter and (D) late winter on southern Eleuthera, The Bahamas. Residuals were based on linear models with body condition (corrected body mass or fat score) fit to bird sex and age class, random effects (winter*site for body mass, winter and individual for fat score), and with covariates of days after 1 October, time, after sunrise. Data are pooled for winters 2002–2003 through 2009–2010 and separated for midwinter (January–February) and late winter (March–April). Because mixed effects models were used, these only show general trends indicating the relationship between body condition (corrected for other measures) and rainfall. See text for methods, rain coefficient estimates, and *P* values from mixed effects models.

quite significantly greater for adult males than for juvenile females ($P < 0.10$). In some cases, these sex and age differences in corrected body mass varied with the amount of rainfall in the prior period. For example, corrected body mass of adult males was significantly (Holme-Scheffe adjusted $P < 0.05$) higher than that of juvenile females when 30-day prior rainfall was 75 mm or 150 mm, but not at 225 mm. However, the corrected body mass of adult males remained significantly (Holme-Scheffe adjusted $P < 0.05$) higher than that of adult females when comparisons were made at 30-day prior-rainfall levels of 75 mm, 150 mm, or 225 mm. In contrast to that of adult males, the corrected body mass of juvenile males did not differ significantly from the other sex and age classes at any of the three different levels of 30-day prior rainfall.

Effect of rainfall on fat levels during different periods.—In midwinter, rainfall in the prior 30 days had a significant ($P = 0.0200$; Fig. 9C) negative effect on fat levels in a similar model (winter random effect, $P = 0.0173$). However, no significant effects of rainfall on midwinter fat levels were detected in the prior 60 days ($P = 0.104$) or 90 days ($P = 0.1138$) in similar models with winter as a random effect ($P < 0.03$). In late winter, rainfall had no significant effect on fat levels in any of the prior rainfall periods (30 days, $P = 0.0925$; 60 days, $P = 0.3457$; 90 days, $P = 0.2177$) in models with winter as a random effect ($P < 0.01$). Thus, fat levels were less sensitive to rainfall than corrected body mass, and when fat levels were affected by rainfall, they declined with an increase in 30-day prior rainfall in midwinter.

Annual return in relation to corrected body mass.—We expected that warblers with higher corrected body mass would have a greater likelihood of surviving and returning to their study

site in the following winter than those with lower corrected body mass. This prediction was supported by our logistic regression of annual return as the binary response variable run on the residuals of corrected body mass. Residuals of the earlier regressions of corrected body mass were used to adjust for the covariates of days after 1 October, time after sunrise, prior rainfall, and a group variable (sex*age) and site*winter as random effects. The odds of annual return were consistently and significantly higher for birds with high residuals of corrected body mass than for those with low residuals of corrected body mass, regardless of the adjustment used for prior rainfall or period in which bird mass was measured. For example, for birds in which body mass was measured in any period of the prior winter, the odds of annual return were greater for those with higher than for those with lower residuals of corrected body mass when adjusted for rainfall in the prior 30 days (OR = 1.826, with 95% CI: 1.091–3.055; LR, $P = 0.0154$), 60 days (OR = 1.802, with 95% CI: 1.086–2.989; LR, $P = 0.0159$), or 90 days (OR = 1.822, with 95% CI: 1.093–3.037; LR, $P = 0.0147$). Similarly, when analyses were restricted to birds weighed only in the previous late-winter period, the odds for annual return were greater for birds with higher residuals of corrected body mass than for those with lower values, regardless of whether models were adjusted for rainfall in the prior 30 days (OR = 2.360, with 95% CI: 1.149–4.845; LR, $P = 0.0101$), 60 days (OR = 2.291, with 95% CI: 1.137–4.617; LR, $P = 0.017$), or 90 days (OR = 1.123, with 95% CI: 1.123–4.575; LR, $P = 0.0124$). Thus, the odds of annual return were significantly increased for birds in higher body condition compared with those in poorer body condition.

Discussion

Factors affecting fruit abundance.—Although rainfall is believed to be a primary influence on fruit abundance in seasonal dry forests (Lieberman 1982, Guevara de Lampe et al. 1992, van Schaik et al. 1993, McLaren and McDonald 2005), our global model was the most supported model for ripe and unripe fruit abundance in each of the three shrub species. These results may not be surprising, given factors—such as canopy cover, shrub size, and soil moisture, in addition to rainfall—that are known to affect fruit abundance (van Schaik 1986, Levey 1988, Bullock and Solis-Magallanes 1990, Reich 1995), some of which were included in our global model. Our post hoc analyses revealed that temporal effects had the largest influence on ripe and unripe fruit abundance within a winter for each of the three shrub species. These temporal-effect findings were consistent with our results from comparisons of live fruit (unripe and ripe combined) biomass from various study sites, which showed that winter period had either a direct effect or an effect through interaction with study site or winter on live-fruit biomass. Nevertheless, winter rainfall was the best explanatory factor of the reduced models for fruit abundance throughout the winter. Winter rain was the most supported reduced model for five of six model sets (including unripe fruit for all species), and in each case rainfall in the month prior to fruit counts was important. Similarly, short-duration rains late in the dry season (Opler et al. 1980) or rain during the 21 days preceding fruiting (Lieberman 1982) were found to be important for fruit abundance in seasonal dry forests elsewhere. Thus, our findings were consistent with expectations that rainfall in the previous month is an important factor for predicting fruit abundance in the three shrub species, at least for unripe fruit.

The relationship between ripe fruit and rainfall in the previous month was important in *E. fruticosa* and *L. involucrata*, but not in *C. alba*. For *C. alba*, the lack of congruence in the response to prior rainfall between unripe and ripe fruit may result from the fact that ripe fruits are more likely than unripe fruits to be consumed by frugivores or to fall off the shrub (J. D. White et al. unpubl. data). Therefore, the standing crop of ripe fruit may not accurately represent the quantity of fruits actually ripened by the plant. In addition, not all unripe fruits ripened, especially in *C. alba*, which in late winter frequently bore unripe fruit that never ripened, even in the wettest winters.

Variation in study-site food abundance.—We did not find consistent seasonal declines in the fruit and arthropod biomass at study sites as expected; biomass varied annually and across study sites. Biomass of fruit in relation to arthropods showed the greatest variation among winters, and fruit generally also showed the most consistent declines in biomass during a winter. Within-winter declines in fruit biomass were

most evident in the RS and WB sites, primarily reflecting the fruiting phenology of *C. alba*, the dominant fruit plant at both sites. *Chiococca alba* was the most consistently seasonal of the fruiting plants; its fruiting typically peaked in early winter (or rarely in midwinter) and declined thereafter, as observed elsewhere (Acevedo-Rodríguez and Woodbury 1985). However, *C. alba* fruit crop size varied considerably among winters. In contrast to the late-winter fruit decline and low abundance at RS and WB sites was the high late-winter fruit biomass in the OH site in winter 2003–2004. Here *L. involucrata* predominated, and its fruiting cycle was asynchronous with other sites. Thus, variation in fruit availability at a site depends not only on the presence and abundance of plants with fruits used by frugivores such as the warblers, but also on the fruiting phenology of those plants, which together with crop size may be affected by rainfall (Bancroft et al. 2000, present study).

Although arthropod biomass declined over the course of the winter, the effect of winter period on biomass was also complex, as evidenced by the three-way interaction of period, site, and winter for both foliage and ground arthropods at the RS and WB sites. Overall, winter seasonality of foliage and ground-arthropod biomass was not consistent and varied among winters and sites, as expected for resources sensitive to temporal and spatial variation in moisture.

We found expected positive correlations between arthropod and fruit abundance at a site, given that sites with higher moisture levels are expected to have greater fruit and arthropod abundance than sites with lower moisture availability (Karr and Freemark 1983, Levings and Windsor 1984, Murphy and Lugo 1986, White 2008), assuming the presence of fruit plants. Although arthropods may respond directly to moisture availability, they may also respond directly to the presence of fruit (Brown and Sherry 2006), as supported by our observations of ants, cockroaches, and beetles foraging on fallen fruit on the ground (J. M. Wunderle et al. unpubl. data). Support for a fruit–arthropod abundance relationship was found in the positive correlation ($r = 0.51$) of biomass of live fruit with foliage arthropods per study site pooled across winters and periods. Although slightly stronger, the correlation among sites for biomass of live fruit with foliage arthropods in late winter ($r = 0.58$) was only marginally significant. Stronger support, however, was found in late winter with the positive correlation among sites for biomass of ground arthropods with ripe fruit ($r = 0.76$). Correlations became increasingly stronger across the three winter periods for biomass measures of ground arthropods and ripe fruit, as well as for foliage arthropods and live fruit.

The higher late-winter correlation of arthropod and fruit biomass at a site is consistent with the likelihood that as the winter becomes drier, the landscape becomes patchier in terms of moisture availability and food resources (Smith et al. 2010). This may occur because of localized rainfall or because certain locations retain moisture or have shallower water tables (Sealey 2006). Shallow water tables were evident in both the OH and GF sites, where water levels in ponds and canals were within ~1.5 m of the surface, even in the driest winters, potentially contributing to availability of fruit and arthropod prey at these sites in late winter.

Habitats with low arthropod biomass.—Eleuthera arthropod biomass samples were comparable to those obtained with similar methods in dry limestone habitats on Jamaica; the latter were among the lowest arthropod values sampled from ground and foliage in various Jamaican habitats (Strong and Sherry 2000, Johnson and Sherry 2001). For instance, mean ground-arthropod biomass (i.e., Hymenoptera, Coleoptera, holometabolous larvae, snails, spiders, and Orthoptera) from Jamaican dry limestone in late winter ranged from 0.44 to 0.70 mg 0.25 m^{-2} (Strong and Sherry 2000) in comparison to our late-winter means (0.55–0.64 mg 0.25 m^{-2}) using similar methods, except that we excluded Diptera and arthropods >25 mm. By contrast, higher mean biomass of ground arthropods occurred in Jamaican second growth and shade coffee (range: 2.4–3.5 mg 0.25 m^{-2} and 1.5–2.6 mg 0.25 m^{-2}, respectively) in late winter. Strong and Sherry (2000) proposed that a biomass of 2.5–3.0 mg ants 0.25 m^{-2} was the threshold below which ground-foraging Ovenbirds (*Seiurus aurocapilla*) were unable to maintain their body condition in Jamaica, which suggests that the similar-sized warblers on Eleuthera may have difficulty subsisting on ground arthropods alone, especially in late winter.

Our foliage-arthropod biomass samples were also comparable to or slightly lower than Jamaican dry limestone foliage samples, which were also among the lowest obtained in Jamaican

habitats (Johnson and Sherry 2001). Although foliage samples from Jamaica excluded arthropods >10 mm (except Lepidoptera) and early, middle, and late samples were combined, the values obtained by Johnson and Sherry (2001) were slightly higher than those for our combined samples (Pentatomidae and arthropods >25 mm excluded). For example, mean arthropod biomass in Jamaican dry limestone for the three winter periods was 0.052 ± 0.007 mg g^{-1} clipping, compared with 0.013–0.034 mg g^{-1} clipping on Eleuthera for the three periods. In their study, foliage-arthropod biomass in dry limestone was significantly lower than in samples from shade coffee (= 0.166 mg g^{-1} clipping ± 0.003) and thorn scrub (= 0.169 mg g^{-1} clipping ± 0.002). Similarly, foliage-arthropod biomass sampled from Jamaican dry limestone habitat in January through March (= 0.066 mg g^{-1}) was significantly lower than in samples from coffee and citrus plantations (Johnson 2000).

Given the low arthropod biomass in habitats on drought-prone limestone substrates in our Bahamian sites, fruit may provide supplemental energy and water required by warblers to forage for unpredictable and sparse arthropod prey. In this case, fruit may facilitate use of sites with low arthropod abundance; similarly, nectar consumption may facilitate persistence of Cape May Warblers (*Setophaga tigrina*) in arthropod-poor sites (Latta and Faaborg 2002). Although ant colonies may provide warblers with predictable locations with abundant prey on dry limestone substrates (Strong 2000), ants are unprofitable prey because of their high chitin content and low mass (Zach and Falls 1978). Therefore, ants are profitable only in high densities (Zack and Falls 1976, 1979; Strong 2000). Given these limitations, it was not surprising that ants were found only in a third of the warbler's fecal samples, although the 30% of samples with ant remains further suggests a paucity of food resources. Additional evidence for the likelihood of sparse winter food resources comes from our observations from radiotagged warblers that indicate continuous foraging activity throughout the day (J. M. Wunderle et al. unpubl. data). This continuous diurnal foraging activity coincides with the observed increase in corrected body mass over the course of the day, suggesting that during the night the warblers lose energy, which can not be quickly replaced in the early morning hours (e.g., Katti and Price 1999). By late winter, the occurrence of the warbler's pre-alternate molt (Pyle 1997) further contributes to energetic demands when birds are storing fat for migration and food resources may be low.

Fruit may provide water as well as carbohydrates and lipids adequate for energy production, possibly facilitating the warbler's use of sites where arthropod prey alone are insufficient to maintain or increase body mass. Nonetheless, fruit often lacks protein and nitrogen needed to maintain muscle mass (Blem 1990), and some omnivorous passerines are unable to maintain body mass on a high-fruit diet (Levey and Karasov 1989, Long and Stouffer 2003, Pearson et al. 2003). Although the three fruit species most commonly consumed by warblers had moderate sugar content (range: 37–63% by weight), both crude fat (1.6–2.7%) and crude protein (3.7–9.0%) values were relatively low (J. D. White et al. unpubl. data). Thus, fruit may provide the warblers with calories to help sustain foraging for the more protein- and fat-rich arthropod prey. Despite being low in fat and protein, however, fruit was consistently consumed by the warblers, as evidenced by remains in fecal samples and by foraging observations. Moreover, fruit consistently remained an important food item through the end of winter, as documented in our foraging observations at the OH site and elsewhere. Fecal samples further indicated that both sex and age classes of the warbler consistently fed on a mixed fruit and arthropod diet throughout the winter. This mixed diet may be especially important for pre-migratory weight gain, because some birds on a mixed diet may gain weight faster than those on an insect-rich diet (Bairlein and Gwinner 1994; Parrish 1997, 2000; but see Long and Stouffer 2003, Diggs et al. 2011).

Overwinter site persistence.—Because food availability in habitats on drought-prone limestone substrates was expected to decline in winter, we expected warblers' overwinter site persistence to be low as birds abandoned sites in response to diminishing food resources as the winter became drier. Although overwinter site persistence varied among study sites (range: 11.1–66.7%), the overall 42.5% value fell within the range of lower persistence values known for other Nearctic–Neotropic parulids wintering in drought-prone Caribbean habitats. For example, Prairie Warblers' (*Setophaga*

discolor) overwinter persistence was lower in desert thorn scrub (42%) than in more mesic pine forest (65%) and desert wash (67%) in the Dominican Republic (Latta and Faaborg 2001). Similar low persistence occurred in Cape May Warblers in dry forest (28%) and desert thorn scrub (33%), which contrasted with 75% persistence in the mesic pine forest in the Dominican Republic (Latta and Faaborg 2002). On Jamaica, overwinter persistence of warblers in dry limestone habitat was usually lower than in other, more mesic, Jamaican habitats. There, Ovenbird persistence of 37.5–38.7% on dry limestone was lower than in other Jamaican habitats, except for a winter in which ground-ant biomass in second-growth scrub decreased in relation to other habitats, resulting in correspondingly lower persistence (34.2% vs. 50.0% in the previous winter; Strong and Sherry 2000). Similarly, American Redstarts (*Setophaga ruticilla*) had lower persistence in Jamaican dry limestone sites (52%) than in mangroves or coastal scrub or palm forests (74–76%; Sherry and Holmes 1996). Even without drought, lower persistence (42%) occurred in a highly frugivorous Black-throated Blue Warbler (*S. caerulescens*) population in a Puerto Rican lower montane wet forest where fruit declined, in contrast to a lowland site (68%) where birds were mostly insectivorous (Wunderle 1995). Thus, low overwinter site persistence of the warblers is consistent with patterns observed in other areas with wintering migrants where food availability declines, often in response to late winter droughts.

Although warbler site persistence from early to midwinter and from midwinter to late winter was similar in pooled samples, individual study sites differed in persistence levels, especially from the middle to the late period. Site persistence from early winter to midwinter did not differ among four sites (MR, RS, DD, and GF), in contrast to persistence from the middle to the late period, which differed among the sites, with low values for RS (42.3%) and DD (12.5%). The latter two sites, especially DD, were prone to late-winter declines in food resources. Much of the coastal DD site was on sandy substrate that had higher soil percolation rates than the other sites (J. M. Wunderle et al. unpubl. data) and, hence, was exceptionally drought prone. Birds routinely disappeared from DD by late winter, and in the first three winters we found no warblers there in late winter, although some marked DD birds were encountered elsewhere. A similar middle-to-late-winter decrease in persistence occurred in Prairie Warblers in Dominican desert thorn scrub as drying intensified and insect abundance declined (Latta and Faaborg 2001). Despite late-winter drought, however, Cape May Warblers' site persistence from the middle to the late period was similar in Dominican thorn scrub (67% vs. 64%) and increased in dry forest (39% vs. 86%), in response to drought-tolerant food resources (nectar in thorn scrub and Homopteran honeydew in dry forest; Latta and Faaborg 2002). This latter case of stable or increasing midwinter to late-winter fidelity at a site(s), despite declining food resources and fidelity elsewhere, is consistent with results for the OH site, where warblers showed 81.8% persistence from the middle to the late period of 2003–2004.

Site fidelity and survival.—Although site fidelity has been used as a measure of minimal survival (Holmes et al. 1989, Sherry and Holmes 1996), its utility for estimating survival is limited, given difficulties in differentiating emigration from mortality (Webster et al. 2002). For wintering warblers, however, we attribute most disappearances within a winter or between winters to emigration from a study site rather than to mortality. Although our intensive study-site searches found birds that had disappeared from one study site and reappeared at another, our search efforts outside of study sites were less intensive, but we still encountered missing birds (Appendix 9). Some of these missing birds were found at a considerable distance (e.g., maximum within-winter site shift from early to late winter of 14.8 km; maximum between-winter shift of 7.1 km from late-winter site to a new site in the following late winter), which suggests a low likelihood of our finding missing birds outside our study sites. Further supporting the likelihood of emigration is the estimated 90 ± 6% apparent winter survival for adult male warblers, averaged across mark–recapture models based on our data (Rockwell 2013, S. M. Rockwell et al. unpubl. data), compared with our mean overwinter site persistence for adult males of 57% (range: 20–72%). A similar disparity applies to adult females, for which Rockwell (2013) estimated apparent winter survival of 88 ± 10% for females, compared with our mean overwinter site persistence for females of 28% (range: 0–50%). As noted by Rockwell

(2013), the estimate of winter survival from the Cormack-Jolly-Seber methods is likely a minimum estimate of winter survival, given that not all surviving birds are detected and permanent emigration can not be distinguished from mortality (DeSante et al. 1995, Sandercock and Jaramillo 2002).

Annual return.—Annual return rates of warblers to the same study site in the following winter differed by sex and age in a pattern consistent with differences in overwinter site persistence. The overall annual return rate (43.4%; range for sites: 30.8–55.6%) fell within the range of parulid return rates to their wintering sites. For example, the annual return rate of Prairie Warblers in Dominican habitats ranged from 56% in desert thorn scrub to 42% in pine (Latta and Faaborg 2001) and was 48–49% in dry scrub and wooded pasture in Puerto Rico (Staicer 1992, Baltz 2000). Annual return rates ≥50% for wintering parulids are not unusual; for some species, rates of return to the wintering grounds may be higher than to the breeding grounds (Holmes and Sherry 1992).

Warblers' annual return rates to breeding sites in Michigan tend to be higher than the overall annual return rates to Eleuthera, although returns to certain study sites by some demographic classes exceeded the overall breeding-ground return rates. For example, 77% of adult males at the MR site returned in the following year (any period), although the overall value for all adult males pooled across sites was 58% (range: 14–77%). This annual return rate for adult males was identical to the estimated apparent annual survival rate of 58 ± 11% for adult males (Rockwell 2013), suggesting that few adult males permanently shift sites between winters. Although apparent annual survival of adult females was not estimated by Rockwell (2013) because of low sample size, the annual return rate of adult females to the Eleuthera study sites (total all sites = 29.7%, range: 0–50%) was lower than the 41.3% return of adult females to Michigan (Walkinshaw 1983). This disparity in adult female annual returns likely reflects site shifts between winters. Lower annual return rates of females than of males may also reflect the difficulties of finding females on the breeding (Walkinshaw 1983) and wintering grounds.

Role of dominance.—Some of our observations suggest that dominance influences settlement and site fidelity of wintering warblers in a manner consistent with the ideal free despotic model (Fretwell and Lucas 1970, Fretwell 1972). With the exception of the situation on the OH site in late winter 2003–2004, we rarely witnessed chases between individuals, although chip notes were occasionally heard when two or more conspecifics were near each other, as well as in response to playback. Moreover, early-winter spatial distributions based on observations of color-banded and radiotagged warblers indicate that their core areas rarely overlap, at least in early winter, although the outer portions of their home ranges, excluding core areas, frequently showed substantial overlap (about 30–60%; J. M. Wunderle et al. unpubl. data), even in early winter. This overlap of neighboring home ranges in early winter was not surprising, given the dense vegetation often frequented by the warbler (Wunderle et al. 2010). The home-range overlap suggests that only the area around an individual's current location is defended, and not its home range boundary, in the absence of an intruder (but see OH-site explanation below). This pattern of space use is consistent with the definition of spatial–temporal territories (Wilson 1975), as found in Ovenbird winter territories (Strong and Sherry 2000).

Our findings of sex and age differences in behavior and site fidelity are consistent with the typical pattern of avian dominance hierarchies in which males are dominant to females and adults are dominant to juveniles (e.g., Marra 2000). The larger body size of male warblers and their stronger response to playback (i.e., male-biased captures) fit expectations of male dominance. Although both sexes give chip notes, males vocalize more frequently than females, whether in response to playback or in its absence (J. M. Wunderle et al. unpubl. data). Given these sex differences in behavior, our findings that males showed higher early-winter to midwinter site persistence than females fits with the likelihood that males displace females or that their presence discourages females from initially settling at a site in early winter. Further supporting the likelihood of male dominance is the trend in apparent winter survival of adults, which suggests that winter survival may be slightly higher for males than for females (Rockwell 2013, S. M. Rockwell et al. unpubl. data). Moreover, our finding that female annual return rates to study sites were negatively correlated with male

annual return rates provides further evidence for male despotism in site use. From midwinter to late winter, however, both sexes showed equivalent levels of site fidelity, presumably a result of declining food resources, resulting in movement by both sexes.

Age differences in dominance were supported by our findings that adults were more likely to be captured by playback than juveniles, indicating greater adult aggressiveness. Moreover, the higher overwinter site persistence of adults in relation to juveniles in the early to middle and middle to late periods is consistent with the pattern expected from adult dominance in interference competition. Scramble competition, however, may also contribute to age differences in site fidelity due to expected greater foraging efficiency of experienced adults (Wunderle 1991). Experience, perhaps due to familiarity with a food source or shrub species and their locations, may enable adults to obtain asynchronously produced fruit shortly upon ripening more consistently than juveniles, while reducing the standing crop available to less experienced birds. In addition, familiarity with locations of widely scattered rich food patches obtained in the previous winter(s) may also give experienced birds an advantage (Smith et al. 2011a), especially in late winter of dry years. Consistent with this scenario was an instance in which an individual (OO-XO) used the same disjunct site each winter (DD site in early winter and midwinter, and then shifted 5.1 km to the GF site in late winter in both 2005–2006 and 2006–2007), which suggests year-to-year stability of movement patterns, at least while resources varied consistently within winters.

Although sex and age differences in site fidelity occurred as predicted for outcomes of behavioral dominance, there was little evidence of sex or age habitat segregation as expected from dominance interactions (Lynch et al. 1985, Greenberg 1986). Given the size differences between male and female warblers, it is reasonable to expect body-size-mediated dominance interactions between the sexes to result in sexual habitat segregation via despotic interactions (Marra 2000, Marra and Holmes 2001) or sex-specific habitat preferences (Morton et al. 1987). Nevertheless, despite these expectations, our comparisons of sex ratios in passive captures yielded no significant differences among study sites. Only a suggestive ($P = 0.09$) skew toward males (71% of 14 birds) was found at the OH site in late winter 2003–2004, which weakened in the following winter (when 55% of 9 birds were male). Earlier analyses of sex differences in habitat-structure and groundcover traits and in age of previous disturbance of capture sites indicated only that the sexes differed ($P = 0.05$) in foliage density <3 m above the ground, but with no evidence that distribution of foliage density varied with an interaction of sex and study site (Wunderle et al. 2010). In addition, we found no evidence to support age-related habitat segregation, given that age ratios sampled from passive net captures did not differ significantly among study sites.

The absence or rarity of habitat segregation in warblers on Eleuthera may reflect the constraints imposed by the seasonal and spatial unpredictability of the warbler's food resources, especially fruit. This unpredictability makes it difficult for birds initially settling on a site in early winter to assess the site's late-winter suitability, given unpredictable phenological changes that may occur as the winter proceeds (e.g., sites DD or OH). Habitat segregation may be further constrained by the warbler's use of early-successional habitats, which may limit the range of structural variation across which segregation might occur. This relatively limited range of variation in available structural habitat contrasts with the broader range of structural variation across which segregation occurs in other migrant species (e.g., early-succession site to mature forests; Lynch et al. 1985, Wunderle 1992, Parrish and Sherry 1994). If habitat segregation occurs in wintering warblers, it may be episodic or much more subtle than has been reported for other wintering parulids (Lynch et al. 1985; Lopez Ornat and Greenberg 1990; Wunderle 1992; Parrish and Sherry 1994; Latta and Faaborg 2001, 2002). Although it is possible that geographic segregation occurs within the archipelago, the available data are insufficient to test this hypothesis.

Warbler distribution in relation to food availability on Eleuthera was expected to result from the interaction of dominance hierarchies, with variable movement strategies used by birds responding to food-resource variation at different spatial scales, as hypothesized for wintering warblers by Johnson and Sherry (2001). Although the warblers' sex and age differences in site fidelity are consistent with outcomes

expected from behavioral dominance, the role of experience (e.g., age differences) likely also affects site fidelity. This interaction of dominance or experience with food abundance, as well as with habitat structure, occurred in overwinter site persistence, as is evident in our model-selection framework. Sex and age were included in all models of our confidence set of candidate models for both the fruit and arthropod model set and the fruit model set. In addition, the combined weights for all candidate models in the confidence set containing sex and age had the highest weight values of all the variables in both model sets. Nonetheless, when including model-selection uncertainty, knowledge of only sex and age was insufficient to predict site persistence without knowledge of other contributing variables from the confidence set of models (i.e., food resources and/or habitat structure) for both model sets.

In contrast to sex and age, knowledge of one of the food-resource variables alone was sufficient to predict site persistence without knowledge of other contributing variables from the confidence set of models. This was evident in the fruit and arthropod models, in which the parameter estimate for foliage arthropods alone was sufficiently reliable to predict site persistence, given the confidence set of models. However, comparing the combined weights for all candidate models in the confidence set containing sex and age, live fruit, habitat PC2, and foliage arthropods, it was live fruit that had the second-highest weight after sex and age, whereas foliage arthropods had the lowest weight. Live fruit also had the second-highest weight after sex and age, based on the combined weights for all candidate models in the confidence set from the fruit models, which also included habitat PC2 and the interaction of habitat PC2 with sex and with age. Moreover, the live-fruit parameter estimate was sufficiently reliable alone to predict site persistence, given the confidence set of fruit models. Thus, a food-resource measure, either foliage arthropods in the fruit and arthropod model set or live fruit in the fruit model set, was found to be a reliable positive predictor of site fidelity, given the respective confidence set of models. No other variables alone were found to be reliable predictors of site fidelity, given the respective confidence set of models.

Although habitat structure alone, as condensed in PC2, was an unreliable predictor of site fidelity given the confidence set of models for either model set, habitat PC2 contributed to the ability of the confidence set of models to predict site fidelity for both the fruit and arthropod and fruit model sets. Models that directly looked at the relationship between site fidelity and habitat had nonsignificant, but positive, trends in both model sets, with lower site fidelity in sites with less foliage, low canopy height, few stems 3–8 cm DBH, but many stems <3 cm (e.g., RS, DD, and WB), and higher site fidelity in sites with abundant foliage in height classes spanning 0–1.0 m and high leaf-litter groundcover (e.g., MR). However, in the confidence sets, the trend appears to be more complicated. In the fruit and arthropod model set, site fidelity is increased for adults and when there is more fruit available at the site, but increases in those adjustments are tempered by a negative adjustment for habitat to further characterize the adults that leave habitats similar to MR and adults that stay at sites similar to RS and WB. The confidence set of models for the fruit model set also included the interactions of habitat PC2 with sex and with age. The interaction with habitat PC2 and sex suggested that females were most likely to leave a site with habitat traits similar to the MR site, whereas males were more likely to leave a site with traits similar to the RS and DD sites. The age interaction with habitat PC2 suggested that adult males were more likely to stay in a site with traits similar to the MR site. Thus, the ability of habitat PC2 to help predict site fidelity in the confidence sets of the two model sets depended on sex and age information, a food-resource variable, and, for the fruit model set, also the interaction of habitat PC2 with sex and with age.

Birds disappeared from study sites at any time during the winter, although certain sites (DD and RS) were more prone to emigration during the middle to the late period. The marked emigrants we relocated at other study sites after site shifts within a winter were found to have moved from sites with low food resources to sites with higher food resources (i.e., significant for ripe fruit, marginally significant for ground arthropods), as expected for birds tracking ephemeral food resources (Sherry and Holmes 1996). These site shifts in response to food-resource declines are similar to the itinerant movements of Northern Waterthrushes (*Parkesia noveboracensis*) as they

track changes in food resources at different sites associated with differential changes in moisture as the winter becomes drier (Smith et al. 2010, 2011a). Although the moisture gradients among habitat patches used by warblers on Eleuthera are not as steep as the gradients encountered by wintering Northern Waterthrushes (i.e., dry forest to mangroves) and fruiting phenology may be out of phase with moisture availability (e.g., fruiting phase terminates as rainfall arrives), the itinerant patterns of response to habitat change in a heterogeneous landscape appear to be similar in the two species.

Late-winter warbler abundance and food resources.—Consistent with the hypothesis that warblers were shifting from low- to high-food-resource sites was the disappearance in late winter 2003–2004 of marked warblers from two study sites (RS, WB) with low fruit and ground-arthropod biomass while warbler numbers simultaneously increased in the OH site, where fruit and ground-arthropod biomass were higher. This pattern was typical of the opportunistic food-resource-tracking behavior of many overwintering Neartic–Neotropic migrants (Karr 1976, Morse 1989, Levey and Stiles 1992, Johnson and Sherry 2001, Latta and Faaborg 2002). The warblers in the OH site foraged primarily on *Lantana* fruit and concentrated their activities in localized fruit-rich areas of OH, as demonstrated by strong positive correlations between fruit biomass and number of home ranges or core areas overlapping our fruit transects. This small fruit-rich patch was likely not economically defensible (sensu Brown 1969), given the numbers of warblers and other species, such as the Bahama Mockingbird (*Mimus gundlachii*) and Greater Antillean Bullfinch (*Loxigilla violacea*), visiting it; hence, birds were not using exclusive areas within the site as expected for territorial behavior. Instead, individuals overlapped extensively in their use of space in the OH study site, and territorial behavior (chips and chases) was infrequent. However, most warblers did not spend the entire day in the OH site, as individuals frequently made extended forays (about 1–3 h) to the surrounding taller vegetation, where arthropods may have been more abundant but fruit was absent (J. M. Wunderle et al. unpubl. data).

In contrast to the OH site in late winter 2003–2004, OH in the following 2004–2005 late-winter period had a warbler density of only half the previous late-winter density, yet levels of fruit and ground arthropods were equivalent to those of the previous late winter, and the warblers continued to feed heavily on fruit there. However, late-winter levels of OH fruit and ground-arthropod biomass did not differ significantly from those at the other sites (RS and WB) as in the previous winter, likely a result of the higher rainfall in late winter 2004–2005 (161.6 mm vs. 25.7 mm). With abundant food resources elsewhere, fewer birds used OH in late winter 2004–2005, and few returned to the site (31% from the previous winter), most likely because resource abundance was no longer exceptional in OH compared with the other sites, as occurred in the previous late winter. Thus, late-winter habitat suitability of a warbler site may vary in relation to other sites, depending on food-resource availability elsewhere, as well as on a site's intrinsic suitability.

As demonstrated in other wintering migrant species (e.g., Poulin et al. 1992, 1993; Johnson and Sherry 2001), the abundance of warblers at study sites was positively correlated with food abundance at a site, at least in late winter. However, distinguishing between the relative importance of fruit versus arthropod biomass for potentially attracting warblers to a site was difficult, given that biomass measures of fruit and arthropods at sites were positively correlated, especially in late winter. Moreover, the warbler routinely feeds on a mixed diet of fruit and arthropods, as apparent in fecal samples, and, thus, sites with an abundance of both fruit and arthropods may be utilized most frequently. The importance of arthropods in attracting the warblers to study sites in late winter was suggested by slightly higher partial correlations of warbler abundance at a study site with ground-arthropod biomass than with fruit (live or ripe). This suggests that sites with little or no fruit, but with sufficiently high arthropod biomass, may also be used by the warbler. In addition, the importance in the warbler's diet of arthropods compared with fruit might be more apparent in a study in which food resources were specifically sampled within individual home ranges rather than at the level of the study site, as here.

Differences in corrected body mass and fat.—Sex and age differences in corrected body mass or fat corresponded with differences in site fidelity, as might be expected from outcomes of dominance and experience, at least by late winter. The first indication of differences in

body condition appeared on 1 February, when juvenile males had more fat and higher corrected body mass than juvenile females. By 16 April, however, males had higher corrected body mass than females; and by 26 April, adult males had significantly greater corrected body mass than juvenile males, just as males were departing on migration. Although corrected body-mass differences were not found between adult and juvenile females, fat score differences were evident by 16 February, when juvenile females had consistently lower fat scores than those of the other demographic classes through the end of the winter. The lower fat levels and corrected body mass of juvenile females may be indicative of their subordinate status, placing them at an energetic disadvantage should late-winter drought conditions intensify. Thus, by late winter, differences in corrected body mass or fat became apparent in a temporal sequence, with improved condition apparent first in juvenile males compared with juvenile females, followed by all age and sex classes compared with juvenile females, then by adult males compared with adult females, and finally by adult males compared with juvenile males.

We expected that warblers in late winter that delayed fat deposition or corrected body-mass improvement would also depart later than birds that improved corrected body mass more quickly, as demonstrated in American Redstarts (Marra et al. 1998, Studds and Marra 2011). Our findings that males departed before females was consistent with expectations that birds in better condition departed earlier than those in poorer condition. These results are also consistent with observations that males arrive a few days before females on the Michigan breeding grounds (Mayfield 1992, S. M. Rockwell et al. pers. comm.). Despite earlier improvement in corrected body mass in adults than in juveniles in April, however, we found no significant age differences in departure schedules. Small sample sizes may have been a factor in our inability to statistically demonstrate age differences in departure schedules, along with the necessity of pooling departures over several winters, which may have obscured departure differences that occur only during the driest winters. Age differences in departure schedules may occur only in drought years, resulting in age differences in male arrivals observed in Michigan (Rockwell et al. 2012).

Rainfall and body condition.—We expected that body condition would be affected by prior rainfall, given evidence of positive rainfall effects on the warbler's food resources and evidence from other species (Strong and Sherry 2000; Brown and Sherry 2006; Studds and Marra 2007, 2011; Smith et al. 2010). However, rainfall was found to have a negative effect on corrected body mass in midwinter, at least for 90-day prior rainfall (and suggestive for 30 days prior, $P = 0.065$), and a negative effect on fat scores for 30-day prior rainfall in midwinter. These results are consistent with previous findings (Gosler 1996, Katti and Price 1999, Strong and Sherry 2000) and theory (Houston and McNamara 1993, McNamara et al. 1994, Rogers 2005) that birds may increase fat stores and body mass in response to uncertain food availability. As uncertainty of food availability subsides, as a result of wetter conditions in this case, birds may reduce their fat stores and body mass because of the costs of fat-reserve maintenance resulting from metabolic costs or predation risk (McNamara et al. 1994). Although increased mass may increase predation risk (Lima 1986, Rogers 1987), it is unlikely that predation contributes appreciably to winter mortality in warblers. The warbler's frequent use of dense vegetation undoubtedly limits exposure to Merlins (*Falco columbarius*) and American Kestrels (*F. sparverius*), which infrequently occur in the warbler's habitat on Eleuthera and elsewhere in the archipelago. Boas (*Epicrates* spp.) and feral cats (*Felis domesticus*) also occur in the warbler's winter habitat and represent threats of unknown risk to the warbler population.

By late winter, as warblers accumulated fat in preparation for migration, prior rainfall had no significant effect on fat scores. By contrast, corrected body mass in late winter showed a significant positive response to rainfall 30 and 90 days prior to capture, and a marginally significant ($P = 0.0511$) positive effect of 60-day prior rainfall. The decrease in corrected body mass with decrease in rainfall, while fat scores remained unchanged, suggests that the birds may have had a negative protein balance while maintaining fat reserves to compensate for food shortages (e.g., Riddington and Gosler 1995).

The negative effects of late-winter droughts on corrected body mass in warblers are consistent with observations of delayed male arrival on the breeding grounds after March droughts

in The Bahamas (Rockwell et al. 2012). Besides delaying departure or transit during spring migration, poorer body condition after late-winter droughts may contribute to higher mortality during migration (Sillett et al. 2000, Sillett and Holmes 2002, Studds and Marra 2005). This appears to be the case in the warblers, as demonstrated in a model-selection framework with March rainfall in The Bahamas as the best-supported model of survival (Rockwell 2013, S. M. Rockwell et al. unpubl. data). Even the second- and third-ranked models in this analysis contained variables that are closely associated with late-winter rainfall in The Bahamas (February–April rainfall and mean Southern Oscillation Index of prior year, respectively). Thus, late-winter rainfall in The Bahamas could have population consequences for the warbler (Rockwell 2013), as found in other migrant species in which winter conditions influence population dynamics (Peach et al. 1991, Szép 1995, Sillett et al. 2000, Sillett and Holmes 2002, Mazerolle et al. 2005).

Changes in the amount of prior rainfall might be expected to influence late-winter sex and age differences in body condition by changing the intensity of intraspecific competition for food resources. For instance, as increasing rainfall increased food availability, competition for food would diminish, resulting in a reduction in body-condition differences between dominant and subordinate birds. Conversely, with a decrease in food availability with decreasing rainfall, competition would intensify, resulting in greater differences in body condition among dominant and subordinate birds. Consistent with expectations that increased rainfall might reduce late-winter competition was our finding that corrected body mass of adult males was only significantly greater than that of juvenile females when 30-day prior rainfall was 75 mm or 150 mm, but not at 225 mm. However, corrected body mass of adult males remained significantly greater than that of adult females at each of the three rainfall amounts for the prior 30 days. Although corrected body mass of adult males was significantly greater than that of juvenile males for the prior 30-day rainfall, insufficient sample size of juvenile males precluded comparisons at the different rainfall amounts. Therefore, expectations of changes in differences in corrected body mass with amounts of prior rainfall were met in one comparison at the potential extremes of dominance or experience (adult male vs. juvenile female). However, predictions were not met in the other comparisons, perhaps because of sample sizes and/or because the range in amounts of prior rainfall was insufficient for a response to occur.

Annual return and corrected body mass.—Results from our analysis of the likelihood of annual return in relation to corrected body mass (adjusted for covariates) were consistent with expectations that birds with higher corrected body mass were more likely to return in the following winter to the study site where found previously than birds with lower corrected body mass. The effect was reasonably strong, especially in late winter (and adjusted for 30-day prior rainfall), when the likelihood of annual return was more than twice as high for birds with high corrected body mass than for those with low corrected body mass. This positive relation of annual return with body condition may indicate higher mortality in birds with poor body condition, but we can not rule out the possibility that some birds in poor body condition return to The Bahamas and shift to sites with higher food resources than the site occupied in the previous winter. However, our results are consistent with findings that annual survival is increased with greater mass in Prothonotary Warblers (*Protonotaria citrea*) wintering in Costa Rica (Wolfe et al. 2013). The reduced likelihood of annual return by warblers in poor body condition is also consistent with findings that birds in poor body condition in late winter may be less likely to survive spring migration (Sillett et al. 2000, Sillett and Holmes 2002, Studds and Marra 2005). Although survival of male warblers during migration (75%) was found to be less than during the stationary periods (86% summer, 90% winter), it was not possible to determine whether mortality was higher during spring than during fall migration (Rockwell 2013, S. M. Rockwell et al. unpubl. data). Nonetheless, given our finding that late-winter rainfall positively affected body condition and the demonstration that March rainfall is an important influence on annual survival (Rockwell 2013, S. M. Rockwell et al. unpubl. data), mortality is potentially higher during spring than during fall migration.

Conservation implications.—As emphasized previously (Wunderle et al. 2010), wintering warblers rely on early-successional habitats created by periodic disturbances. Disturbances such as fires and hurricanes, including effects

of salt spray on coastal scrublands, may have naturally produced habitat prior to extensive anthropogenic forest loss (Lee et al. 1997, Haney et al. 1998, Wunderle et al. 2007). However, with loss of natural cover due to increased development, the potential for these disturbances to create habitat has been reduced. In addition, the abandonment of agricultural lands that produced much of the current warbler's habitat will likely result in less suitable habitat in the future if Bahamian agriculture continues to decline (Byrne 1980). Localized, small-scale slash-and-burn agriculture is unlikely to produce sufficient habitat. Anthropogenically altered fire regimes, especially recurring large-scale wild fires during winter, may also reduce available winter habitat (Lee et al. 1997, Haney et al. 1998). Thus, there will be a need for management to produce the periodic disturbances required for the warbler's winter habitat.

Adding further to the conservation challenge is the warbler's reliance on fruit, especially *L. involucrata*, *E. fruticosa*, and *C. alba*, which requires the warbler to respond to spatial and temporal variation in these and other food resources by moving from resource-poor to resource-rich sites. Despite the large extent of early-successional habitat of the appropriate age on southern Eleuthera (Helmer et al. 2010), the warbler's primary fruit species are locally distributed within early-succession habitat, and fruit production is asynchronous and patchy across the landscape (J. M. Wunderle et al. unpubl. data). Because species-specific differences in fruiting phenology contribute strongly to variation in fruit availability, sites with several fruiting plant species with asynchronous fruiting phenologies are more likely to have fruit available for a longer duration and, hence, higher warbler site fidelity than sites with few fruiting plant species. For this reason, efforts should be made to encourage a diversity of fruiting plant species used by the warbler, especially at sites with frequently used fruit species. Because wintering warblers track food-resource fluctuations across landscape mosaics of fruit and arthropod abundance at scales of more than a kilometer, management at a landscape scale will be required to ensure availability of sufficient habitat patches.

Because late-winter droughts reduce food resources for warblers, wintering-ground conservation efforts should focus on protecting the least drought-prone habitats to ameliorate the effects of droughts. Early-successional habitats with favored fruit species situated on sites where the freshwater table is near the surface, as is often found beneath young porous limestone (Sealey 2006), should receive high priority for protection. In addition, because the gradient in annual rainfall declines from northwest to southeast through the archipelago and the gradient in evapotranspiration increases along the same axis (Sealey 2006), habitats in the wetter northern and central islands should receive high conservation priority. Furthermore, given the reduced survival of warblers during the migratory period compared with the stationary breeding and nonbreeding periods (Rockwell 2013, S. M. Rockwell et al. unpubl. data), efforts should focus on identifying (Petrucha et al. 2013) and protecting key stopover sites, and perhaps especially those used during spring migration that might help ameliorate negative carryover effects from late-winter droughts. The importance of conserving the least drought-prone winter habitats is further emphasized by evidence of rainfall declines during 1959–1990 in The Bahamas (Martin and Weech 2001) and climate change models that predict increased droughts in the Caribbean region (Neelin et al. 2006). These recommendations take on added urgency as sea level continues to rise (IPCC 2007) and habitats are lost on these low-lying islands.

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Appendix 1: Radiotelemetry Methods Used to Study Kirtland's Warbler Movements

Kirtland's Warbler movements were studied for an average of 20.6 days with use of 0.43-g transmitters (LB-2N; Holohil Systems, Carp, Ontario), which represent ~3% of the warbler's body mass. Transmitters were attached to the backs of birds using a harness that consisted of two cotton thread loops attached to the transmitter and wrapped around the base of the legs, thereby positioning the transmitter on the back, over the synsacrum (following Rappole and Tipton 1991).

Radiotagged birds were located using a handheld three-element Yagi antenna and Wildlife Materials TRX-2000S receivers operating at frequencies between 164.001 and 164.999 MHz. So as not to disturb radiotagged birds, we determined location by triangulation from fixed points with known coordinates (i.e., fixed bearing points) plotted on study-site maps. We took a pair of compass bearings on a tagged individual from two fixed bearing points on the study sites every hour. The predicted location of individuals from each set of bearings was determined using ARCVIEW, version 3.2, with the intersection of the two bearings providing the position of the radiotagged bird. To minimize errors, we used only bearing pairs from fixed bearing points that were >40° apart. Because time delays between triangulated bearings may reduce data accuracy (Schmutz and White 1990), we took bearing pairs an average of 3.5 min apart and rejected any pairs >5 min. We retook the bearings from other fixed bearing points if the angles to the tagged bird were <40° or if the bird had moved between the two bearing readings. Six positions were obtained for each radiotagged bird per day, every hour between 0600–1200 hours or 1200–1800 hours on alternate days.

Appendix 2. Resight detections of color-banded radiotagged Kirtland's Warblers compared at the same study sites and in the same winter periods on Eleuthera, The Bahamas. Shown are the unique color-band combinations of each bird, sex (M = male, F = female), age (A = adult, J = juvenile), and study-site acronym, whether the radiotagged bird was resighted in the study site, capture date, date of resight independent of radiotelemetry detections, winter period (early, October–December; late, March–April), number of days the bird was tracked, and number of locations where the bird was found before the transmitter battery expired. Radiotelemetry indicated that radiotagged birds were located in the specified study site, unless specified under the resight column as departed, with the date of departure from the study site as determined by telemetry. None of the radiotagged birds departed a study site and returned during the period of radiotracking. Details of the telemetry and resight methods are given in Appendix 1 and in the text. Study-site acronyms are defined in Table 1.

Bird	Sex	Age	Study-site acronym	Resight independent of telemetry study	Capture date	Resight date in capture study site	Period	Days	Number of locations
BY-WX	F	A	RS	Resight RS	4 Nov 2004	9 Nov	Early	23	113
WX-RR	F	J	RS	Resight RS, departed RS 7 Nov	25 Oct 2004	3 Nov	Early	22	112
XB-WW	F	J	WB	No resight, departed WB 24 Nov	23 Nov 2004	Not seen in WB (departed before resight effort)	Early	21	115
YR-XY	M	A	RS	Resight RS, departed RS 7 Nov	03 Nov 2004	5 Nov	Early	18	98
BB-BX	M	A	RS	Resight RS	07 Nov 2004	19 Nov	Early	20	110
PX-GO	M	A	WB	Resight WB	21 Nov 2004	7 Dec	Early	21	114
BW-XW	M	J	DD	Resight DD	13 Nov 2004	11 Dec	Early	20	96
YB-YX	M	J	WB	Resight WB	25 Nov 2004	1 Dec	Early	20	114
BW-BX	F	A	OH	Resight OH	14 Mar 2005	6 Apr	Late	21	127
XB-BW	F	J	OH	Resight OH	14 Mar 2005	1 Apr	Late	20	115
XY-RW	M	A	OH	Resight OH, departed OH 31 Mar	14 Mar 2005	20 Mar	Late	21	124
BB-XR	M	J	OH	Resight OH	14 Mar 2005	25 Mar	Late	21	126
YW-XY	M	J	OH	Resight OH	14 Mar 2005	26 Mar	Late	20	117

Appendix 3: Details of Methods Used to Study Fruit Abundance and Phenology

Statistics.—There was no evidence of multicollinearity between covariates for *Chiococca alba*, the highest correlation coefficient (r) was between plant height and width (0.66), and the tolerance and VIF were within acceptable limits. There was evidence of multicollinearity between late-winter canopy cover (defined below) and plant height for *Erithalis fruticosa* (r = –0.72, late canopy tolerance = 0.33, VIF = 3.05) and for *Lantana involucrata* (r = –0.69, height tolerance = 0.36, VIF = 2.8). In both of these cases, we dropped height from the global and subglobal models because we were more interested in the effect of late-winter canopy cover on fruit abundance and because we used width as a size estimate for these species.

We checked normality of the residuals for the global models for ripe and unripe fruit for each species, using normal probability plots in Proc Mixed (SAS). Normal probability plots did not indicate deviations from normal. There was no evidence of influential data points or points with high leverage for any of the global models using leverage and Cook's D.

Plant measures.—To determine how much plant size accounted for fruit abundance, we measured the plant height and crown width of each marked plant in the spring (February–March 2007 and March 2008; we averaged 2007 and 2008 for the third winter) and used these values as explanatory variables "height" and "width" (Appendix 4). We also measured the diameter of the stem where it emerges from the ground (stem diam) and counted the number of stems at 10 cm above ground (stem no) during the first two winters and averaged these for the third winter. We took one diameter measurement per shrub, selecting the largest stem for measurement.

Environmental measures.—During each monthly phenology census, we measured soil moisture at each marked plant using a soil moisture meter (Lincoln Irrigation, Lincoln, Nebraska). After rain, we waited 3 days to measure soil moisture. For each measurement, we inserted the soil meter probe 1.5–2.0 cm into the soil in four quadrats (NE, NW, SE, SW) around each plant and under the canopy of the shrub and took an average of the four measurements for the explanatory variable mean soil moisture (sm mean) for analysis. The soil moisture meter broke during the last 2 months of the first year's field season; therefore, we used mean soil moisture for May (by site and species) from years 2 and 3 in order to avoid exclusion of observations due to missing data. In a few cases, we missed a measurement for one quadrat for a plant or one plant at a site, so for these we took the mean from the plant's other quadrats or for the plot at that month to fill in the missing value. We measured canopy cover using a spherical densiometer, in each of the four quadrats around the shrub and within a meter of the shrub in late winter (April 2007, March 2008, March 2009) after leaf fall (designated as late canopy).

Potential evapotranspiration (pet) was estimated using the overall temperature average for each month by site (Rock Sound and Madiera Road) and using the Thornthwaite potential evapotranspiration (http://onlinehydro.sdsu.edu/onlinethornthwaite.php), which is a temperature-only method. Temperature-only methods are not as accurate as radiation-based methods (Lu et al. 2005) or methods that incorporate other meteorological parameters (Bautista et al. 2009); however, the temperature-based estimates provide a useful index for monthly comparisons.

We included a categorical predictor variable (slope) to categorize plants found on ridge tops, midslope, or in low areas. We expected plants on ridge tops to experience drier conditions than plants in low areas with a more developed soil layer.

Appendix 4. Phenology models for the response variables "unripe fruit" and "ripe fruit" for three shrub species. Fixed-effect predictor variables are listed for each model, and random effects (site and plant ID) were included in all models.[a] Predictor variables are defined in the text and in Appendix 3.

Model	Predictor variables
Global	wi + mo + sm mean + rain + rain prev + temp hi + late canopy + height + width + stem diam + stem no + pet + slope + (rain*sm mean) + (stem diam*stem no) + (height*wi) + (wi*mo) + (wi*rain) + (wi*temp hi)
Climate subglobal	rain + rain prev + sm mean + late canopy + temp hi + pet + slope + (rain*sm mean)
Winter rain	rain + rain prev + sm mean + (rain*sm mean)
Evaporation	temp hi + pet
Sunlight	late canopy
Likely combo	rain + sm mean + late canopy + (rain*sm mean)
Plant subglobal	height + width + stem diam + stem no + (height*width) + (stem diam* stem no)
Crown	height + width + (height*width)
Stem	stem diam + stem no + (stem diam*stem no)
Temporal	wi + mo + (wi*mo)

[a] Site was treated as a fixed effect for *Erithalis fruticosa* unripe-fruit models and included in the climate subglobal and sunlight models.

Appendix 5. Model-fit results for the global model for each set of models using the likelihood ratio test statistic (LRT χ^2) for unripe and ripe fruit monitored over three winters (October–May, 2006–2009) on marked individuals of *Chiococca alba*, *Erithalis fruticosa*, and *Lantana involucrata* on southern Eleuthera, The Bahamas.

Species	LRT χ^2	df	*P*
C. alba, unripe	979.7	41	0.005
C. alba, ripe	638.7	41	0.005
E. fruticosa, unripe	624.4	43	0.005
E. fruticosa, ripe	613.7	39	0.005
L. involucrata, unripe	557.3	38	0.005
L. involucrata, ripe	456.5	38	0.005

Appendix 6. Temporal model parameter estimates (± SE) for unripe and ripe *Chiococca alba*, *Erithalis fruticosa*, and *Lantana involucrata* fruits monitored on marked plants (Fig. 3) monthly (October–May, corresponding to months 1–8) over three winters, 2006–2007 (W1), 2007–2008 (W2), and 2008–2009 (W3), on southern Eleuthera, The Bahamas.

	Chiococca alba		*Erithalis fruticosa*		*Lantana involucrata*	
Parameter	Ripe	Unripe	Ripe	Unripe	Ripe	Unripe
Intercept	5.48 ± 0.33	7.88 ± 0.38	2.86 ± 0.33	6.37 ± 0.37	3.72 ± 0.38	4.29 ± 0.40
Winter 1	–0.74 ± 0.38	–1.09 ± 0.32	[a] 0.23 ± 0.27	1.42 ± 0.38	0.41 ± 0.40	2.28 ± 0.40
Winter 2	–3.83 ± 0.38	–2.19 ± 0.32	–1.72 ± 0.27	–2.49 ± 0.38	–1.13 ± 0.40	–1.05 ± 0.40
Winter 3	0	0	0	0	0	0
Month 1	–4.28 ± 0.38	0.45 ± 0.32	1.63 ± 0.27	1.82 ± 0.38	–1.01 ± 0.40	–0.94 ± 0.40
Month 2	–1.63 ± 0.38	0. 40 ± 0.32	0.49 ± 0.27	1.19 ± 0.38	–0.75 ± 0.40	0.30 ± 0.40 [a]
Month 3	0	0	0	0	0	0
Month 4	0.81 ± 0.38	–0.63 ± 0.32	–0.82 ± 0.27	–1.42 ± 0.38	–0.53 ± 0.40	–2.28 ± 0.40
Month 5	–0.29 ± 0.38 [a]	–1.88 ± 0.32	–1.58 ± 0.27	–2.26 ± 0.38	–3.19 ± 0.40	–3.86 ± 0.41
Month 6	–2.81 ± 0.38	–2.90 ± 0.32	–1.90 ± 0.27	–2.82 ± 0.38	–3.40 ± 0.40	–3.36 ± 0.40
Month 7	–4.75 ± 0.38	–5.13 ± 0.32	–2.25 ± 0.27	–3.76 ± 0.38	–3.20 ± 0.40	–3.77 ± 0.40
Month 8	–4.68 ± 0.54	–5.16 ± 0.45	–2.17 ± 0.38	–2.29 ± 0.54	–1.37 ± 0.56	–2.62 ± 0.57
Winter 1*month 1	3.51 ± 0.54	–0.95 ± 0.45	–2.94 ± 0.38	–3.94 ± 0.54	–0.22 ± 0.56 [a]	–4.13 ± 0.57
Winter 1*month 2	–0.58 ± 0.54	–1.05 ± 0.45	–2.66 ± 0.38	–4.45 ± 0.54	–2.71 ± 0.56	–3.54 ± 0.57
Winter 1*month 4	–3.30 ± 0.54	–1.12 ± 0.45	–1.64 ± 0.38	–2.77 ± 0.54	0.26 ± 0.56 [a]	–1.76 ± 0.57
Winter 1*month 5	–3.12 ± 0.54	–1.31 ± 0.45	–0.62 ± 0.38	–2.10 ± 0.54	–0.45 ± 0.56 [a]	–2.48 ± 0.57
Winter 1*month 6	–1.29 ± 0.54	–1.16 ± 0.45	–0.42 ± 0.38	–1.52 ± 0.54	–0.69 ± 0.56	–3.01 ± 0.57
Winter 1*month 7	0	0	0	0	0	0
Winter 1*month 8	0	0	0	0	0	0
Winter 2*month 1	5.87 ± 0.54	0.32 ± 0.45 [a]	–1.54 ± 0.38	0.22 ± 0.54 [a]	–0.29 ± 0.56 [a]	0.96 ± 0.57
Winter 2*month 2	2.11 ± 0.54	–0.06 ± 0.45 [a]	–0.69 ± 0.38	–0.01 ± 0.54 [a]	0.75 ± 0.55	0.63 ± 0.57
Winter 2*month 3	0	0	0	0	0	0
Winter 2*month 4	–1.36 ± 0.54	–0.79 ± 0.45	0.43 ± 0.38	0.91 ± 0.54	0.64 ± 0.55	2.65 ± 0.57
Winter 2*month 5	–0.86 ± 0.54	–0.69 ± 0.45	1.12 ± 0.38	1.87 ± 0.54	1.93 ± 0.56	2.02 ± 0.57
Winter 2*month 6	1.33 ± 0.54	–0.68 ± 0.45	1.68 ± 0.38	2.73 ± 0.54	1.65 ± 0.56	1.62 ± 0.57
Winter 2*month 7	3.26 ± 0.54	0.73 ± 0.45	2.48 ± 0.38	4.89 ± 0.54	1.94 ± 0.56	2.99 ± 0.57
Winter 3*all months	0	0	0	0	0	0

[a] Upper and lower confidence limits include zero.

Appendix 7. Candidate models for overwinter site persistence in Kirtland's Warblers on southern Eleuthera, The Bahamas. Two separate analyses were conducted using Akaike's information criterion: the first included biomass of fruit and arthropods (winters 2003–2004 through 2005–2006) and involved 28 candidate models, and the second included biomass of fruit without arthropods (winters 2003–2004 through 2008–2009) and involved 20 candidate models. See text for details.

Candidate Models for Fruit and Arthropods Set	Candidate Models for Fruit Set
Null model	Null model
Age	Age
Sex	Sex
Age + sex	Age + sex
Live fruit + ripe fruit + foliage arthropods + ground arthropods	Age + sex + age*sex
Live fruit + ripe fruit	Live fruit + ripe fruit
Foliage arthropods + ground arthropods	Live fruit
Live fruit + ground arthropods	Ripe fruit
Live fruit + foliage arthropods	Habitat PC2
Habitat PC2	Rain 30-day
Rain 30-day	Rain 60-day
Rain 60-day	Age + sex + live fruit
Age + sex + live fruit	Age + sex + habitat PC2
Age + sex + ground arthropods	Age + sex + habitat PC2 + age*habitat PC2 + sex*habitat PC2
Age + sex + fol inv	Age + sex + rain 30-day
Age + sex + habitat PC2	Live fruit + habitat PC2
Age + sex + rain 30-day	Live fruit + rain 30-day
Live fruit + habitat PC2	Age + sex + live fruit + habitat PC2
Ground arthropods + habitat PC2	Age + sex + live fruit + rain 30-day
Foliage arthropods + habitat PC2	Global model
Live fruit + rain 30-day	
Ground arthropods + rain 30-day	
Foliage arthropods + rain 30-day	
Age + sex + live fruit + habitat PC2	
Age + sex + live fruit + rain 30-day	
Age + sex + ground arthropods + rain 30-day	
Age + sex + foliage arthropods + rain 30-day	
Global model	

Appendix 8. Summary of captures and observations of color-banded Kirtland's Warblers during 55 visits from 9 February through 1 May 2004 in Ocean Hole (OH), a 1.7-ha study site on southern Eleuthera, The Bahamas. Shown are the color-band combinations for each individual as well as its age (A = adult, J = juvenile), sex (M = male, F = female), original capture date, last date of recapture in 2004, date first observed at OH, date last observed at OH, period (in days) observed present at OH, percentage of days found in the period at OH, mean detections per observation period, and mean detections per observer hour. The latter measure corrects for observer effort by number of warbler detections in the observation period by observer hours (number of observers × hours of observation).

Bird	Age	Sex	Original capture date	Latest recapture (2004)	Date first observed (2004)	Date last observed (2004)	Period present (days)	Days found in period (%)	Mean detections/ observation period	Mean detections/ observer hour
RR-XR	A	M	7 Nov 2003*	17 Feb [a]	5 Apr	8 Apr	4	100	3.50	0.29
JO-RX	A	M	9 Feb 2004	14 Apr	26 Mar	28 Apr	19	63.3	4.93	0.22
OX-RI	A	M	10 Feb 2004	14 Apr	20 Mar	21 Apr	28	93.3	2.89	0.31
OX-RR	A	F	10 Feb 2004	31 Mar	19 Mar	28 Apr	34	91.9	4.03	0.57
OY-XO	A	F	10 Feb 2004	–	15 Mar	15 Mar	1	100	1.00	–
II-XR	J	M	19 Mar 2004	14 Apr	20 Mar	28 Apr	30	83.3	4.93	0.62
XY-YY	A	M	21 Mar 2004	–	21 Mar	23 Apr	20	64.5	2.20	0.23
BY-YX	A	M	22 Mar 2004	–	31 Mar	31 Mar	1	11.1	1.00	0.06
WI-RX	J	M	28 Mar 2004	–	29 Mar	20 Apr	19	95.0	5.05	0.57
YX-YI	J	M	28 Mar 2004	–	28 Mar	14 Apr	27	100.0	2.96	0.39
RX-YR	J	M	4 Apr 2004	–	1 Apr	8 Apr	6	75.0	1.83	0.16
XR-RO	J	F	1 Apr 2004	–	1 Apr	8 Apr	6	75.0	1.67	0.14
YY-RX	A	M	1 April 2004	–	1 April	23 April	14	70.0	1.71	0.22
WX-WW	A	M	13 April 2004	15 April	13 April	2 May	16	88.9	1.94	0.35

[a] Male RR-XR was captured and recaptured at Wemyss Bight (WB), located 2.7 km from OH. All other birds were captured only in OH.

Appendix 9. Color-banded Kirtland's Warblers detected at sites other than the site where originally captured on southern Eleuthera, The Bahamas. Table shows the color-band combination for each bird, sex (M = male, F = female), age (A = adult, J = juvenile), distance between locations (km), whether movement occurred between or within a winter, date bird was first detected at site of origin, date bird was first detected at the new site, winter period (early, October–December; middle, January–through February; late, March–April) when detected, and notes on the locations. Study-site acronyms are defined in Table 1. For additional movements of birds between study sites, see Table 12.

Bird	Sex	Age	Distance (km)	Within or between winters	Date original site	Date new site	Winter periods	Locations
OB-XO	M	J	5.9	Between	13 Nov 2003	11 Oct 2004	Early to early	RS to MR
JW-XY	M	A	7.1	Between	17 Mar 2009	19 Apr 2010	Late to late	Cotton Bay to Gibson Estate
JY-IX	F	J	1.3	Between	15 Mar 2007	2 Feb 2008	Late to middle	RS to DD
II-IX	M	A	6.1	Between	15 Apr 2007	16 Apr 2008	Late to late	Cool Springs to Leary's Field
XW-WR	F	A	0.1	Within	3 Nov 2003	11 Dec 2003	Early to early	WB to Green Castle
XI-WW	F	J	1.9	Within	22 Nov 2004	27 Nov 2004	Early to early	WB to Green Castle
XY-RW	M	A	0.7	Within	22 Jan 2005	17 Mar 2005	Middle to late	OH to Hall's Goat Farm
JO-RX	M	A	0.8	Within	16 Mar 2005	3 Apr 2005	Late to late	OH to Hall's Goat Farm
II-IX	M	J	5.6	Within	10 Nov 2006	15 Apr 2007	Ealy to late	MR to Cool Springs
RJ-XJ	M	J	14.8	Within	28 Jan 2007	21 Apr 2007	Mid to late	RS to Nixon Goat Farm
YI-YX	M	A	1.6	Within	28 Nov 2007	20 Feb 2008	Early to middle	Leary's Field to GF
JX-YI	M	J	2.1	Within	23 Jan 2008	21 Apr 2008	Middle to late	MR to GF
XW-WI	F	J	2.2	Within	28 Nov 2008	05 Apr 2009	Early to late	MR to GF
II-IX	M	A	4.7	Within	30 Jan 2006	15 Apr 2006	Middle to late	RS to GF