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Grasshopper outbreak challenges conservation status of a small Hawaiian Island

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Abstract A tiny (63.1 ha) and uninhabited Nihoa Island within the Hawaiian Archipelago is situated 250 km NW of Kauai. It is a part of Papahānaumokuākea National Marine Monument established in 2006 and jointly administered by NOAA, USFWS, and the State of Hawaii (Department of Land and Natural Resources). The island's known terrestrial biota include 26 vascular plant species, 27 bird species, and 243 arthropod species. Approximately half of the species are endemic to Nihoa or indigenous to Hawaii. Four plant species and two resident bird species are federally listed as threatened or endangered species. Gray bird grasshopper *Schistocerca nitens* has occurred on the main Hawaiian Islands since 1964 and was first reported from Nihoa in 1977. In 2002–2004, there was an outbreak of this grasshopper that aggravated the drought and denuded most of the island's vegetation. Since then, grasshopper numbers crashed, most probably due to insufficient soil moisture for embryonic development. With subsequent rains, the island's vegetation recovered. During the USFWS expedition to Nihoa in October 2006, grasshopper population assessments were undertaken. Based on 18, 300 × 2 m transect counts, the Nihoa grasshopper population was estimated at 19,430 ± 10,360 individuals. Laboratory rearing of *S. nitens* revealed that its development occurs without diapause. Potentially, the grasshopper can produce as many as four annual generations on Nihoa, although it is likely that only two generations occur. This article reviews the implications of fluctuations in *S. nitens* population dynamics for island flora and entomo- and avifauna, in particular, for the endangered endemics, the insectivorous Millerbirds. Potential threats to the island's biota and challenges for conservation are discussed.

Keywords Nihoa · *Schistocerca nitens* · Alien species · Oceanic Island · Endangered species

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Introduction

Northwestern Hawaiian Islands and their biota

Extending 2,400 km across the north-central Pacific Ocean, the Hawaiian Islands are the most isolated group of high islands on earth and are summits of giant submarine volcanoes. The chain is progressively older in a NW direction and began over 70 million years ago (Howarth and Mull 1992). Besides the better-known main Islands (Niihau, Kauai, Oahu, Molokai, Lanai, Maui, Kahoolawe, and Hawaii), the Hawaiian Archipelago includes several small Northwestern Hawaiian Islands (NWHI) (Fig. 1). These remote Pacific islands contain the largest coral reef system in the U.S. and some of the most pristine underwater habitats in Hawaii. Because they are a protected wildlife sanctuary, marine life in waters surrounding the NWHI exhibits some of the highest biodiversity levels per unit area in Hawaii (Evenhuis and Eldredge 2004). Terrestrial biota on these islands includes numerous endemic plants and animals, particularly arthropods (Gagné and Conant 1983; Conant et al. 1983). Vegetation assemblages in the less disturbed NWHI represent the best remaining examples of their kind in Hawaii, allowing us to imagine how the vegetation cover of the main islands may have looked like before these habitats were devastated by anthropogenic influences, introduced herbivores and invasive weeds.

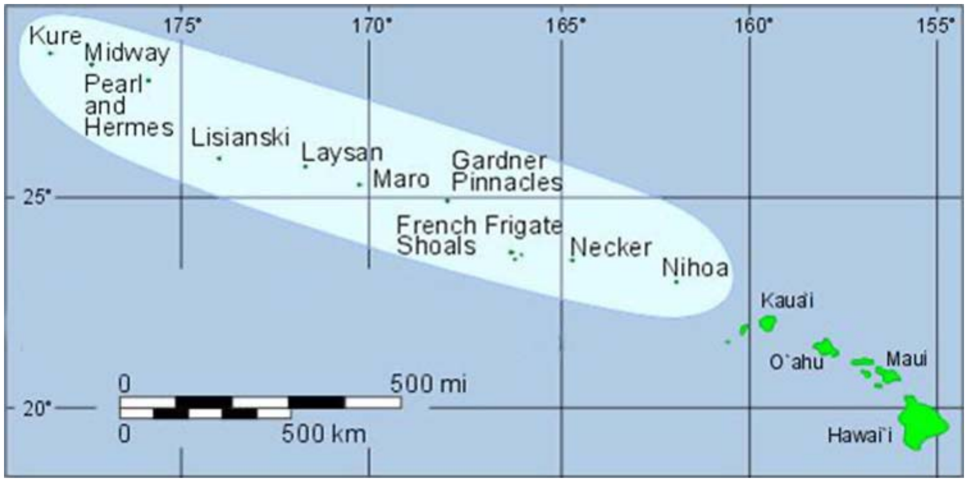

Fig. 1 Northwestern Hawaiian Islands

Nihoa's terrestrial biota: a unique assemblage

Nihoa is the southernmost NWHI island (Fig. 2). It is situated 250 km NW of Kauai. Nihoa is a remnant of an ancient volcanic crater with an emerged land area of 63.1 ha (1.35 by 0.45 km). Geologically, it is the youngest island among the NWHI, with an age calculated at 7.3 million years (Clague 1996). Populated by myriads of birds, it was once known as "Bird Island" (Clapp et al 1977). Unlike most of other NWHI, Nihoa was spared from guano mining and bird feather hunting in the 19th century, and its sparse human settlements were abandoned before the late 1700s (Emory 1928). This contributed to preserving a unique island biota, which is possibly the most intact and the most diverse within the NWHI (Conant et al. 1983). Although Nihoa's area (63.1 ha) amounts to only 0.0038% of the Hawaiian Islands total land area, it contains a remarkably large proportion of biodiversity among the islands. Nihoa's 184 insect and 27 nesting bird species represent respectively 2.2 and 14.8% of the total number of species of these classes in Hawaii (Table 1). More than half of Nihoa's insects are either endemic to the island or indigenous to the Hawaiian Archipelago (Nishida 2001, 2002; Evenhuis and Eldredge 2004). The island's flora includes 26 vascular plants species of which 17 are indigenous and 3 endemic (Christophersen and Caum 1931; Conant 1985). Four of Nihoa's plant species are listed as endangered (Evenhuis and Eldredge 2004). An

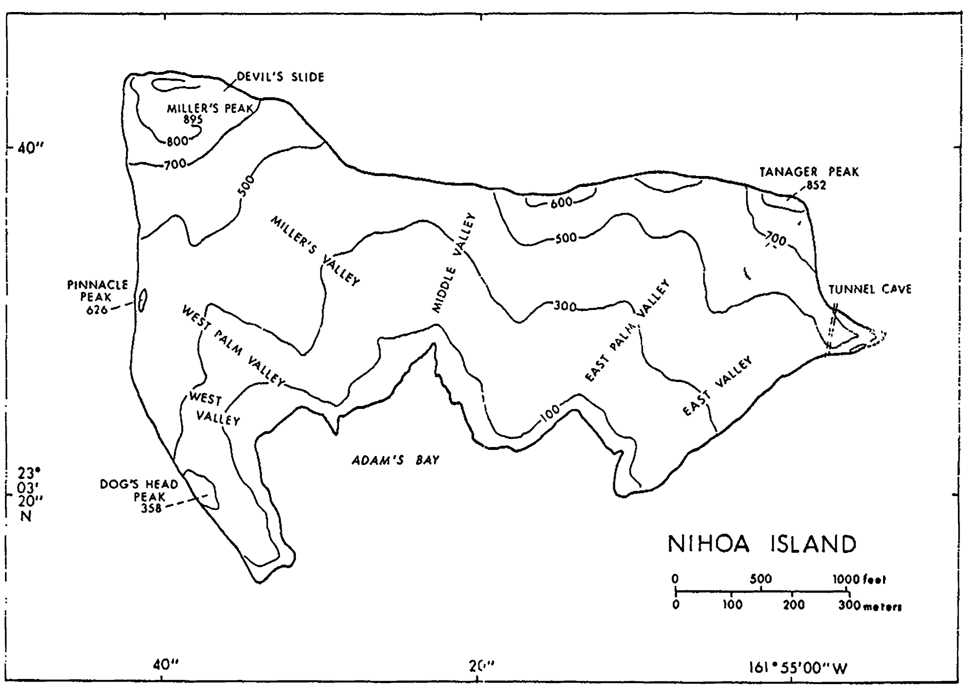

Fig. 2 Nihoa Island (from Clapp et al. 1977)

Table 1 Number and proportion of species from Nihoa compared to all of Hawaii (updated from Eldredge and Evenhuis 2003; Evenhuis and Eldredge 2004)

Taxonomic group	Nihoa	Hawaii total	% of total
Flowering plants	26	2,142	1.2
	END 3 (12%) NIS 6 (23%)	END 896 (42%) NIS 1,139 (53%)	
Insects	184	8,155	2.2
	END 20 (11%) NIS 89 (48%)	END 5,233 (64%) NIS 2,782 (34%)	
Other arthropods	59	1,060	5.6
	END 7 (12%) NIS 15 (25%)	END 295 (28%) NIS 573 (54%)	
Nesting birds	27	183	14.8
	END 2 (7%) NIS 8[a] (30%)	END 63 (34%) NIS 55 (30%)	
Area (ha)	63.1	1,663,600	0.0038

[a] Visitors/migrants; END—species endemic to Nihoa only; NIS—nonindigenous species that do not naturally occur in the Hawaiian Islands and have arrived either accidentally or intentionally through biological control efforts, agricultural imports, etc

additional indigenous plant species, *Solanum nelsonii*, is currently a candidate for listing as endangered or threatened (USFWS 2007).

Invasive organisms: a threat to island ecosystem

Ocean islands are fragile ecosystems that can be easily and often irrevocably damaged by introducing alien organisms. Due to the restricted land area, Nihoa's resident bird, vascular plant, and terrestrial invertebrate populations are small and at constant risk of extinction (Gagné 1988). A purposeful or inadvertent introduction of an alien organism could devastate native vegetation and trigger a chain reaction decimating associated bird and arthropod populations. Observations over the past few decades showed a steady increase in non-native species (Evenhuis and Eldredge 2004). Among them, a recent (2002–2004) outbreak of the Gray bird, or Vagrant grasshopper *Schistocerca nitens* (Thunberg 1815) (Orthoptera: Acrididae) (Fig. 3), was a particular concern because of its potentially devastating impact on Nihoa's biodiversity, especially plants, birds and insects (Gilmartin 2005). Island visits during 2002–2004, revealed that grasshopper damage to vegetation was extremely high. Most plants constituting the island's vegetative cover (*Sida fallax*, *Chenopodium oahuense*, *Solanum nelsonii*, *Portulaca villosa* etc.), together with the endangered species *Sesbania tomentosa* and *Schiedea verticillata*, appeared completely devoid of foliage; even the leaves of the relict and endangered Nihoa fan palm (*Pritchardia remota*) were noticeably chewed (Wegmann et al. 2002; Culliney 2004; Liittschwager and Middleton 2005) (Fig. 4).

Grasshopper infestation could also impact Nihoa's avifauna (Gilmartin 2005). While the majority of the island's nesting birds are marine or shore birds, there are two endemic resident song birds, Nihoa Millerbird (*Acrocephalus familiaris kingi*) (Fig. 5) and Nihoa Finch (*Telespiza ultima*). Because of their small population, both were added to the U.S. Endangered Species List in 1967. The insectivorous Nihoa Millerbird (the common name reflects its preferred food, "miller moths"—noctuids from genera *Agrotis*, *Helicoverpa*, etc.) appeared to be threatened most by the alien grasshoppers. In the past, a similar bird from Laysan Island (*A. f. familiaris*) became extinct between 1916 and 1923 when introduced rabbits destroyed the island's vegetation and, consequently, decimated the island's insect fauna (Ely and Clapp 1973; Morin et al. 1997; Rauzon 2001).

Endemic insect species, such as the Nihoa conehead katydid (*Banza nihoa*) (Orthoptera: Tettigoniidae), Conant's giant Nihoa tree cricket (*Thaumatogryllus conantae*) (Orthoptera: Gryllidae), Nihoa Rhyncogonus weevil (*Rhyncogonus exsul*) (Coleoptera: Curculionidae; Fig. 6) and others, might also be threatened by *S. nitens* outbreaks (Gilmartin 2005). Numerous endemic insects (particularly, the orthopterans), and thousands of nesting birds, as non-targets, make any actions aimed at reducing the population of *S. nitens* on Nihoa problematic.

Nihoa conservation status

Until recently, Nihoa Island was managed by the U.S. Fish and Wildlife Service (USFWS) as part of the NWHI wildlife preserve. In June 2006, all NWHI were declared the Papahānaumokuākea National Marine Monument, which became the largest single area dedicated to conservation in U.S. history and the world's largest protected marine area. The new monument is managed in a three-way partnership by USFWS, National Oceanic and Atmospheric Administration (NOAA), and the State of

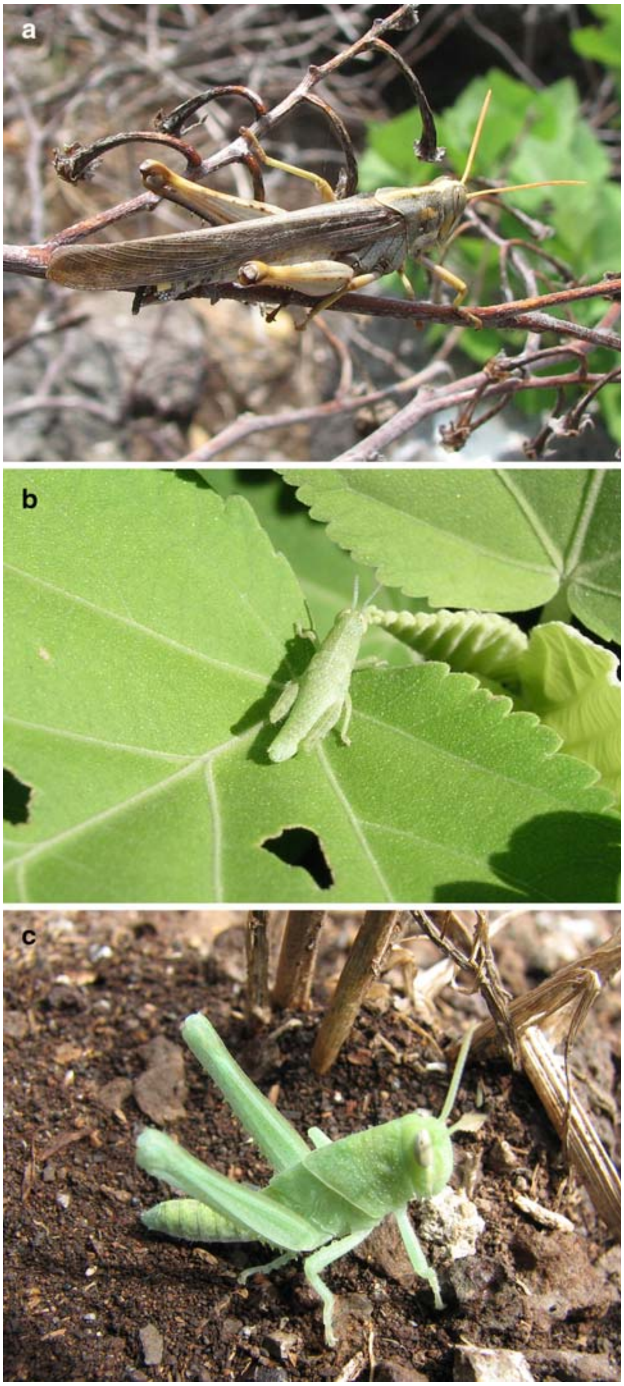

Fig. 3 Grasshoppers *S. nitens* from Nihoa (photos A. Latchininsky) (**a**) adult female (**b**) second instar nymph on *Sida fallax* leaves (**c**) fourth instar nymph

Hawaii (Department of Land and Natural Resources). In 2007, it was included in the U.S. World Heritage Tentative List (US NPS 2007). Nihoa visits are restricted to scientific expeditions by special permit only. Because of the extremely treacherous landing, such visits are usually limited to only one or two per year by a team of four or fewer scientists. I participated in one such expedition in October

Fig. 4 Damage to Nihoa fan palm *Pritchardia remota* by grasshoppers *S. nitens* in 2004 (photo Benton Pang)

Fig. 5 Nihoa Millerbird *Acrocephalus familiaris kingi* (photo A. Latchininsky)

Fig. 6 Nihoa endemic weevil *Rhyncogonus exsul* (photo A. Latchininsky)

2006, with a primary purpose of assessing the grasshopper situation and monitoring the arthropod fauna on the island.

Objectives of this study were: (1) to quantitatively assess the population of *S. nitens* on Nihoa; (2) to examine the parameters of its life cycle under laboratory conditions; (3) to identify critical ecological factors affecting its population dynamics on the island; (4) to estimate its actual or potential impact on Nihoa's vegetation, birds and arthropods; and (5) to consider, if necessary, *S. nitens* population management options that would not adversely affect other arthropods on the island.

Materials and methods

Site description

Detailed descriptions of Nihoa can be found in Clapp et al. (1977), Conant (1985), Rauzon (2001) and Evenhuis and Eldredge (2004). In brief, the island is located at roughly 23°3.6′ N and 161°55.4′ W. It is characterized by steep slopes, rocky outcroppings, six well developed valleys, and precipitous cliffs. Its two highest points are situated in the NW corner (Miller's Peak, 269 m) and in the NE corner (Tanager Peak, 256 m) (Fig. 2), making it the tallest among NWHI. The northern, eastern and western sides of the island are sheer sea cliffs, 10–265 m high. The southern side features a wave-cut terrace which provides a landing site. One small sandy beach is at the SW end of the island, and is frequented by groups of the endangered endemic Hawaiian monk seal (*Monachus schauinslandi*). Nihoa's climate is dry subtropical, probably close to that of French Frigate Shoals, with average yearly temperatures around 24°C and annual rainfall of about 750 mm (Morin et al. 1997; USGS 2006). There are no fresh water sources on the island, although rains create 5–7 temporary seepages in the valleys and depressions.

Nihoa's vegetation is dominated by dry, scrub-type low shrubs of *Sida fallax*, *Chenopodium oahuense*, *Solanum nelsonii*, and *Sesbania tomentosa* (Christophersen and Caum 1931). In two valleys, there are Nihoa fan palm (*Pritchardia remota*) groves with trees reaching 6 m in height. At higher elevations, rocks are covered by clumps of a native grass, *Eragrostis variabilis* (Conant 1985).

Grasshopper population assessments

During my stay on the island, between 11 and 22 October 2006, several grasshopper population assessment methods were attempted (Onsager and Henry 1977; Thompson 1987), but none of them appeared to be satisfactory for Nihoa's conditions. Taking into account the complicated relief, dense vegetation cover, and relatively low abundance of *S. nitens* in October 2006, the following method was selected. I calibrated my walking speed at approximately 300 m/h and counted all adult grasshoppers flushed out of the vegetation in the 2 m wide visual field, advancing along a more or less straight line for one hour. Each transect covered a 600 m^2 area. In total, 18 transect counts were accomplished between October 12 and 21, 2006. In two of the 18 transects, I counted both adults and nymphs. The transects sampled the entire island except its western extremity known as Dog's Face where, according to different observers, the grasshoppers were less abundant than elsewhere on the island (Wegmann et al. 2002). Approximate transect locations are shown in Fig. 7.

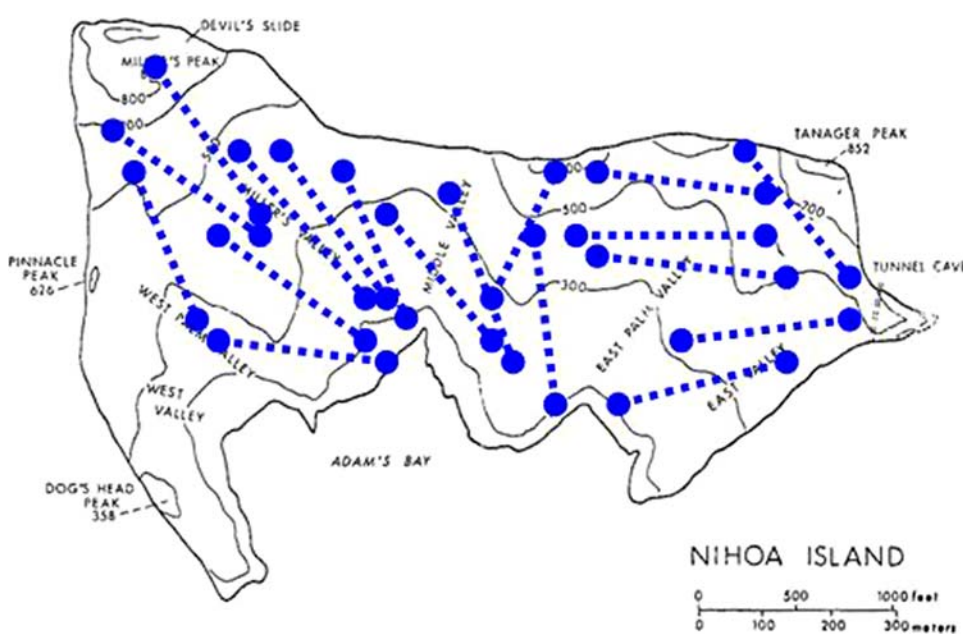

Fig. 7 Location of 18 transects used for *S. nitens* counts in October 2006

Results of the counts were expressed in terms of descriptive statistics (Southwood 1987) and then extrapolated for the entire area of the island (63.1 ha).

S. nitens life history under laboratory conditions

S. nitens life cycle parameters were studied in the University of Wyoming (Laramie, WY, USA) entomology laboratory. Fourteen mid- to late instar nymphs of both sexes were brought alive from Nihoa. Constrained by technical difficulties until September 2007, the grasshoppers were kept in 25 × 25 × 25 cm wooden cages with plastic front sliding panels and mesh sides at a constant temperature of 30 ± 1°C and a 24-h light. Grasshoppers bred successfully under these conditions; however, such regime was not realistic for Nihoa. Beginning in September 2007, the grasshoppers were transferred to larger (50 × 50 × 50 cm) aluminum cages with mesh sides and plastic front panels with sleeves. Cages were kept in controlled climate cabinets (Percival Scientific, Model E-36X) at a temperature of 28 ± 0.5°C at daytime (12 h) and 22 ± 0.5°C at night (12 h), which approximated the weather conditions on the island (Conant and Morin 2001). Plastic cups with moist soil were offered for oviposition. Fresh food was replaced daily; food plants included a variety of foliage species such as lettuce, cotoneaster, hibiscus, dandelion, sweet clover, red clover, crab apple, avocado, various thistles and others.

Results and discussion

How did *S. nitens* reach Nihoa?

S. nitens is thought to be a recent introduction to Nihoa. Its distribution area extends from northern South America through Mexico and the southwestern United States (Capinera et al. 2004). The grasshopper was first captured on the main Hawaiian Islands in 1964 (Anonymous 1965a) and identified initially as *Schistocerca vaga* (Scudder 1899) by J. W. Beardsley (Anonymous 1965b). It was first reported from Nihoa under the name of *S. nitens* in 1977 (Beardsley 1980). In 2000, the grasshoppers became numerous enough to warrant concern expressed by Nishida (2001). In 2002 and 2004, scientists visiting the island were confronted by numerous grasshoppers that denuded 90% of the island's vegetation (Wegmann et al. 2002; Culliney 2004). In 2003 and 2005, however, the grasshopper numbers seemed to decrease, and the island's plants showed signs of recovery (Gilmartin 2005; Wegmann 2005). In April and October 2006, Nihoa's vegetation appeared lush and green, and the grasshopper population was relatively low. Observations in March 2007 revealed abundant island vegetative cover and low grasshopper numbers (Rowland et al. 2007). In August 2007, the grasshopper numbers remained low but the vegetation dried out significantly (Marc MacDonald pers. comm. 2008).

S. nitens appeared to reach Nihoa from the main Hawaiian Islands following trade winds without human influence. Grasshopper and locust species from the genus *Schistocerca* Stål are large, strong flyers with a notorious migratory potential. In 1988, swarms of Desert locust (*S. gregaria*) crossed the Atlantic Ocean covering 5,000 km from West Africa to the Caribbean Islands in 10 days (Kevan 1989; Ritchie and Pedgley 1989). For its part, *S. nitens* was found on Socorro Island situated about 500 km off Baja California, which suggests the ability to colonize from the mainland (Song et al. 2006). Nihoa is located only 250 km NW from the island of Kauai and with favorable trade winds, the grasshoppers could cover the distance in a day or two. On the mainland, an adult female of *S. nitens* (identification confirmed by Dr. Hojun Song, BYU) was captured in August 2007 near Cheyenne (WY), about 1,000 km north off the limit of the known distribution area for the species.

S. nitens is found on other NWHI such as Necker and French Frigate Shoals (Beardsley 1980; Nishida 2001). More recently, the progression to the NW resulted in *S. nitens* findings on two even more remote locations of NWHI—Laysan (John Schmerfeld pers. comm., 2006) and Lisianski (Jon Sprague pers. comm., 2007 via Beth Flint), which are located 1,500 km NW from Nihoa. Should they be considered alien? Or is this a natural process in the expansion of their distribution area?

Howarth and Mull (1992) consider "alien" the insect species that were inadvertently or purposefully brought to the Hawaiian Islands by humans. Most specialists believe that the initial arrival of *S. nitens* on the main Hawaiian Islands was a human-aided migration (Nishida 2001; Evenhuis and Eldredge 2004). This opinion was based on the fact that the first specimen of *S. nitens*, a gravid female, was captured on Coast Guard base at Sand Island, Oahu (Anonymous 1965a). However, published accounts of the first collections of *S. nitens* from Oahu are not unequivocal. Several days after the initial specimen capture, numerous adult males and females were captured within the same area and "many additional grasshoppers were seen" (Anonymous 1965b). Rather than an accidental introduction, which is typically restricted to a limited number of specimens, the picture of numerous adult grasshoppers flying together in the same area appears more consistent with swarm's arrival. Interestingly, all attempts to find the grasshoppers near the docks or at the airport—traditional sites of new species' introductions on Oahu—failed (Anonymous 1965b). Although the possibility of ship hitch-hiking cannot be completely ruled out in the initial arrival of *S. nitens* to the main Hawaiian Islands, wind-assisted migration seems an equally plausible hypothesis. Reaching Nihoa from the main islands unassisted is also likely.

Examples of two well-known insect migrants may give some weight to this point of view. In October 2006, I caught a Painted Lady butterfly (*Vanessa cardui*) on Nihoa, which was the first ever record of this species from the island. Also, on several occasions, I observed a dragonfly (possibly a green darner *Anax junius*). On one of these occasions the dragonfly was laying eggs in a seepage pond. The dragonfly observation appears particularly interesting because although fresh water supplies are meager and intermittent on Nihoa, several species of chironomids and other aquatic dipterans have been recorded on the island (Evenhuis and Eldredge 2004). Therefore, the possibility for a dragonfly to establish a resident colony on the island cannot be ruled out entirely. In 2004, a dragonfly was seen on Nihoa also (Culliney 2004).

Historical records of *S. nitens* on Nihoa and other NWHI are summarized in Table 2. Since its initial appearance on Oahu, the grasshopper made an impressive progression in the NW direction.

Quantitative assessments: how many grasshoppers are there on Nihoa?

The total number of adult *S. nitens* observed during the 18 transect counts was 133 (Table 3). Extrapolated to the area of Nihoa (63.1 ha), the estimated total adult population of *S. nitens* on the island consisted of 7,772 ± 4,144 individuals (95% confidence interval). Unlike adults, visual estimates of nymphal populations were more difficult because of their smaller size, cryptic coloration, and tendency to remain in the dense foliage even when disturbed. Two attempts to count all developmental stages of grasshoppers along the 300 m transects on October 17 and 19 yielded 21 adults and 32 nymphs, and 11 adults and 16 nymphs, respectively. Thus, the number of nymphs was approximated as being 1.5 times higher than the number of adults. Hence, the estimated nymph total on the island was 11,658 ± 6,216 individuals, and the total nymphs plus adults was 19,430 ± 10,360.

It is interesting to compare these findings with the only previous quantitative estimate of *S. nitens* population (Wegmann et al. 2002). Wegmann did his counts on September 8, 2002, when the grasshoppers appeared to be numerous, and "nine-tenths of Nihoa's vegetative cover was nude, stripped of all leaves, buds, flowers and seeds" by the grasshoppers (*l.c.*). The author made six, 50 m long transect surveys sweeping the tops of the vegetation with an insect net (50 cm diameter opening) every 2 s. The collections yielded 4, 8, 5, 1, 1, and 1 grasshopper respectively (developmental stages not indicated). Assuming that, (1) he conducted his sweeping 0.5 m to the right and 0.5 m to the left from the center line of the transect, and (2) he collected *all* available grasshoppers, this would mean each transect covered 50 m^2, and the mean count for the transect would be 3.333 ± 2.875 individuals, which corresponds to 42,062 ± 36,282 grasshoppers on the entire island. These numbers are approximately two times higher than my calculations in October 2006 (19,430 ± 10,360). The grasshoppers must have been especially active between 9:55 and 10:45AM when Wegmann did his survey, and most probably, he was only able to catch a fraction of the grasshopper population, while many of them, especially adults, escaped capture. If this was the case, the actual grasshopper population on Nihoa in September 2002 was much (maybe, several times) higher.

Grasshopper *S. nitens* life history on Nihoa: how many annual generations are possible?

During my first days on the island (October 12–14), grasshoppers were represented by two distinct age cohorts: early (first and second, rarely third) instar nymphs and adults. During my last days (October 18–22), the grasshopper population was represented mostly by mid- to late instar (third to fifth) nymphs and senescent adults. Among the adults, males outnumbered females by approximately 5:1, which may indicate the end of the adult life span (see e.g. Latchininsky and Launois-Luong 1997). Other aging signs such as missing hind legs, dull coloration and worn out wing tips were also common. Several captured adults soon died in the vials. The presence of young nymphs together with senescent adults indicates that *S. nitens* on Nihoa exhibit continuous development, without quiescence or diapause. Senescent adults seen in October probably hatched about 3 months earlier, i.e. in mid- to late July. Subsequent generations should have hatched in early January, 2007 and another in late March or April. This prediction was confirmed by Rowland et al. (2007) who observed adults and hatchlings in late March 2007. In theory, the grasshopper may produce up to four annual generations on the island. In reality, this number may go down if winter temperatures are significantly lower and the soil is dry delaying grasshopper embryonic development.

Laboratory rearing of *S. nitens*: what are the life-cycle parameters?

Between November 2006 and January 2007, the *S. nitens* colony produced five successive generations under

Table 2 Historical records on *S. nitens* on Nihoa and other NWHI (compiled from different sources)

Year	Month, date	*Schistocerca nitens* population	Vegetation state	Observer or Reporter; Reference
1964	August 3, 1964	Specimen found on Sand Island, Oahu	NA	Anonymous (1965a)
	August 10, 1964	Confirmation of establishment (second specimen collected from Sand Island)		Anonymous (1965b)
1977	?	Specimen(s) found on Nihoa	NA	Collector George Balazs; Beardsley (1980)
1977	August 14	Specimen collected from Necker	NA	Collector George Balazs; Beardsley (1980)
1983	?	Specimen(s) found on Nihoa	NA	Wayne Gagné (1983) (G. Nishida pers. comm.)
1997	? (few hours on the island)	Numerous grasshoppers observed	NA	Beth Flint (in Gilmartin 2005)
2000	September 9–21	Numerous specimens observed and collected by G. Nishida	Very dry conditions. Some shrubs left leafless by *S. nitens*; concern about vegetation damage expressed by G. Nishida	Nishida (2001); Beth Flint (in Gilmartin 2005)
2000	September 24–27	Reported from Necker and French Frigate Shoals	NA	Nishida (2001); Evenhuis and Elderidge (2004)
2001	September 1	Low numbers	NA	Alexander Wegmann (in Wegmann et al. 2002)
2002	September 2–9	Extremely high. A total estimate for the island (recalculated by A. Latchininsky based on A. Wegmann's 6 transect counts): 42,062 ± 36,282	9/10 of island's vegetation denuded. Three patches of *Schiedea* grazed to root level. Fans, stems, seed cases and bark of *Pritchardia* chewed	Alexander Wegmann (in Wegmann et al. 2002)
2003	?	Numbers are lower than in 2002	Verdant plant community	Gilmartin (2005)
2003	August (?)	High *S. nitens* numbers	Many damaged plants	Liittschwager and Middleton (2005)
2004	August 29–September 1	Extremely high. 70+ grasshoppers accumulated on orange peel in 20 min. Grasshoppers seem to converge on patches of remaining green vegetation	*Sesbania*, *Sida*, *Pritchardia* and other plant species are severely damaged. Twigs are often girdled. *Eragrostis variabilis* is generally less attacked although some leaf blades are 50% chewed. Some *Sesbania* shrubs are surprisingly healthy amid completely defoliated plant community	John Culliney (Culliney 2004)
2004	August 13 and September 4 (?)	Very high grasshopper numbers	Island's vegetation is devastated	Liittschwager and Middleton (2005)
2004	September 4	Two nymphs found on Necker	Healthy, green vegetation	John Culliney (Culliney 2004)
2005	Late June (2 h on the island)	No grasshoppers seen	Verdant plant community	Alexander Wegmann (Wegmann 2005)
2005	August 13–20	Low grasshopper numbers. Two adult females, 7 adult males, 2 moderate size nymphs, and 2 small nymphs were collected. The nymphs were found in Devil's Slide	Very lush vegetation despite August being a "dry season"	Pete Oboyski (Oboyski 2005)
2006	April 1–9	Low grasshopper numbers: a total of 9 individuals seen by four observers over 9 days	Vegetation is green, only a few old *S. nitens* chew observed	Natalia Tangalin and Stefan Kropidlowski (in Kropidlowski 2006)
2006	October 11–22	Moderate to low grasshopper densities observed. Age: mostly 1–3 instar nymphs and adults. Population estimate: 7,772 ± 3,954 adults (based on 18 transect counts) and 11,658 ± 5,931 nymphs. Total adults plus nymphs: 19,430 ± 9,885	Lush, green vegetation all over the island. No signs of fresh *S. nitens* chew on *Pritchardia*. Some insignificant damage (shot-holes) to leaves of *Sida*, *Solanum* and *Sesbania*	Alexandre Latchininsky (Latchininsky 2006)

Table 2 continued

Year	Month, date	*Schistocerca nitens* population	Vegetation state	Observer or Reporter; Reference
2006	October 11–22	Reported from Laysan	NA	John Schmerfeld observed a Laysan finch catching an adult *S. nitens* (pers. comm.)
2007	March 16–25	Low grasshopper numbers. Only 14 individuals were observed along 54 Millerbird and finch transects. Adults and nymphs are observed, including hatchlings on 3/21. Higher densities in the SE part of the island	Lush, green vegetation with little or no insect damage. However, plants of *Sesbania* showed noticeable damage, especially in the eastern part of the island, presumably by grasshoppers	Ian Jones (in Rowland et al. 2007)
2007	June (22?)	An adult captured and photographed on Lisianski	NA	Jon Sprague (pers. comm. 2007 via Beth Flint)
2007	Mid-July to mid-September	Low grasshopper numbers: one adult flushed out of vegetation every 15 min. Sometimes localized concentrations of 3–4 adults within few m. Increased grasshopper numbers in mid-September	Very dry vegetation. *Sida* and *Sesbania* almost entirely absent. Green pockets of *Solanum nelsonii* and *Chenopodium oahuense* present	Mark Alexander MacDonald (pers. comm. 2008)

Table 3 Transect counts of *S. nitens* on Nihoa in October 2006

Date	Transect # and Adult count
October 12	#1–1
October 13	#2–8, #3–6, #4–10
October 15	#5–3, #6–2
October 16	#7–4
October 17	#8–9, #9–12
October 19	#10–12, #11–15, #12–5, #13–6
October 20	#14–8, #15–13
October 21	#16–7, #17–8, #18–4
Total	18 transects, 133 adults

laboratory conditions. Nymphal development included five instars. At 28 ± 0.5°C (12 h D) and 22 ± 0.5°C (12 h N), the time from hatching to adult emergence ranged from 32 to 40 days, with males completing their nymphal development 3–5 days earlier than females. Mating started 8–12 days after fledging and females began laying eggs 7–10 days after mating. Females laid egg-pods every 10–15 days during their life span, which in some individuals extended more 150 days. Each egg-pod contained on average 66.25 ± 20.36 eggs with a minimum of 32 and a maximum of 97 eggs (Table 4). Egg-pod structure was typical for the genus *Schistocerca*: it consisted basically of eggs with some white foam secretion without any protection (hard walls) from adverse conditions. Egg viability and duration of the embryonic development largely depended on soil moisture. In the cages kept under the constant air temperature of 30 ± 1°C, when the soil was moistened every other day, eggs started to hatch in about 14 days. If the soil was moistened only once a week, hatching occurred about one month after oviposition. If the soil was maintained dry, the eggs succumbed from desiccation and no hatching occurred. Further research is needed to estimate how long the eggs would remain viable in dry soil.

Table 4 Number of eggs in *S. nitens* egg-pods from grasshoppers reared under laboratory conditions at constant temperature 30 ± 1°C

N	Number of eggs in egg-pod
1	32
2	97
3	68
4	74
5	55
6	86
7	52
8	66
Average	66.25 ± 20.36

Which ecological factors are critical for *S. nitens* population dynamics?

Grasshopper population on Nihoa in October 2006 consisted of relatively low numbers but appeared healthy and exhibited a high reproductive potential. After a population explosion in 2004, grasshopper numbers crashed, most likely due to extreme drought and lack of food, but the numbers seen in October 2006 may reflect an early "bouncing back" situation. The "boom and bust" population fluctuations are typical for other *Schistocerca* species, and, confined to a limited area, such oscillations may even be more pronounced on Nihoa. In the recent past, grasshopper numbers appeared high in 2002 and 2004, but relatively low in 2003, 2005, April and October 2006, as well as in March and August 2007 (Table 2). A fragile equilibrium between vegetation and the primary herbivores (grasshoppers) may be shattered if rainfall continues to be scarce for a prolonged period (several weeks). In such a case, quick vegetation drying combined with rapid grasshopper population growth may result in considerable damage to the island's ecosystem. However, based on what was observed in 2002–2007, this process appears to be reversible and the island's natural, self-regulatory mechanisms have thus far managed to overcome the grasshopper population explosions.

At this point, data are insufficient regarding the potential role of natural enemies in population regulation of *S. nitens*. Egg predation by an alien beetle, *Trox suberosus*, should not be excluded as a species from the same genus (*T. procerus*) is well known for its detrimental impacts on grasshopper eggs in Africa (Greathead et al. 1994). Predators or parasitoids of nymphs and adult grasshoppers appear to be scarce, being limited to arachnids and Millerbirds.

It is likely that grasshopper numbers crashed after the 2004 peak due to egg desiccation in the soil. Recent visits to Nihoa suggest that its climate exhibits seasonality, with higher temperatures and long dry periods from mid-spring to mid-autumn while the other half of the year appears to be cooler with increased precipitation. Laboratory observations confirmed that *S. nitens* does not exhibit embryonic diapause, an adaptation that allows more temperate grasshopper species to survive long periods of unfavorable weather conditions. While dry and hot weather is beneficial for nymphs and adults, the *S. nitens* eggs laid in the soil require moisture for successful development. Without moisture, the eggs of another species from the same genus, *S. gregaria*, cannot survive more than 60 days (Duranton and Lecoq 1990). Apparently, *S. nitens* has similar constraints in its life cycle. This duality in ecological requirements appears to produce a "built-in" auto-regulating mechanism in the grasshopper population dynamics. Prolonged hot and dry weather would contribute to a build-up of grasshopper numbers with a 100-fold increase possible in just one generation, although more likely there would only be a 20- to 30-fold increase. Furthermore, drought would cause grasshoppers to concentrate on the few remaining green patches, increasing plant damage. After a certain period, excessive drought would cause massive egg losses, and the grasshopper population will collapse. Unfortunately, all these considerations remain largely speculative because regular weather monitoring was absent on Nihoa until the first six Hobo weather stations were deployed in April 2006.

On Laysan Island, 12 years of meteorological observations revealed significant fluctuations in rainfall among years (400–1,600 mm) and between months (36–120 mm), with the maximum annual precipitation falling in winter and the minimum in summer (Athens et al. 2007). If a similar rainfall pattern is likely for Nihoa, an excessively long dry period from February until August may become critical for the grasshopper population dynamics due to insufficient soil moisture for embryonic development. A drought occurred on Laysan during 2002–2004. Nihoa over the same years also appeared to experience a precipitation deficit (see descriptions of vegetation state in Table 2). While initially the dry and hot weather contributed to faster grasshopper development and a population increase, the continuing drought resulted in the dramatic crash of the grasshopper numbers due to embryonic mortality. In 2005–2006, Nihoa's vegetation recovered from the drought and the grasshopper attack. Surviving *S. nitens* maintained relatively low population densities in 2006 and 2007.

S. nitens feeding preferences: which plants are at risk?

High numbers of *S. nitens* observed in 2002 and 2004 resulted in severe damage to Nihoa's vegetation. Particularly affected were *Sida fallax* (Malvaceae), *Sesbania tomentosa* (Fabaceae), *Solanum nelsonii* (Solanaceae), *Chenopodium oahuense* (Chenopodiaceae), *Schiedea verticillata* (Caryophyllaceae), and *Pritchardia remota* (Arecaceae) (Fig. 4) (Gilmartin 2005). The native grass *Eragrostis variabilis* (Poaceae) was less frequently attacked by the grasshopper (Culliney 2004). Indeed, although *Schistocerca* grasshoppers are polyphagous (for example, the diet of the Desert locust includes over 600 plant species from all major families (Uvarov 1977)), they exhibit a marked predilection towards forbs and reluctantly feed on grasses. This apparently is also true for *S. nitens* and while on the island it refused to feed on *E. variabilis*. Under the laboratory conditions in Wyoming, *S. nitens* fed on plants from Malvaceae, Asteraceae, Fabaceae, Rosaceae, Chenopodiaceae and, less willingly, Salicaceae and

Poaceae; certain Apiaceae plants were rejected. Based on field observations in October 2006, the feeding preferences of *S. nitens* on Nihoa could be ranked as follows, from the most to the least appetizing species: *Sida fallax* > *Sesbania tomentosa* > *Solanum nelsonii* > *Chenopodium oahuense* > *Schiedea verticillata* > *Pritchardia remota*.

Extrapolating from dietary preferences knowledge of other grasshopper species from genus *Schistocerca*, it is possible to hypothesize that most of Nihoa plant species from broad-leaved families should be included in the circle of *S. nitens* food sources. Besides the species mentioned earlier, this list should include *Sicyos pachycarpus* (Cucurbitaceae), *Chamaesyce celastroides* (Euphorbiaceae), *Rumex albescens* (Polygonaceae), *Tribulus cistoides* (Zygophyllaceae), *Portulaca* spp. (Portulacaceae), *Ipomoea* spp. (Convolvulaceae), and the critically endangered (if not extinct) *Amaranthus brownii* (Amaranthaceae), which was last reported from Nihoa in 1983 (Conant 1985; USFWS 2006). In my opinion, among the four endangered plants of Nihoa, it is *A. brownii* that should be considered most vulnerable to grasshopper depredation, followed by *S. verticillata, S. tomentosa* and *P. remota*. I base this ranking on: (1) actual and likely *S. nitens* feeding preferences, and (2) plant species population size on the island. Indirectly, this assumption regarding *A. brownii* can be supported by observations on *S. gregaria* feeding related by Predtechensky (1935). During a severe Desert locust invasion in the former Soviet Union in 1929, at one occasion hatching occurred within a weedy cotton field. The weeds included 11 species from six plant families. Scientists collected a large quantity of *S. gregaria* young nymphs and placed them on cotton plants. However, after some time, all of the nymphs invariably were found feeding on a single weed species, *Amaranthus angustifolium*.

Behavior of *S. nitens* on Nihoa: an adaptation to the island habitat?

Usually, bright green *S. nitens* nymphs were found basking and feeding on leaves of the shrubs *Sida fallax, Sesbania tomentosa*, or *Solanum nelsonii*. Frequently, several young instar nymphs were observed on one plant, sometimes on just one leaf. When disturbed, the nymphs usually jumped off the plant down to the ground and continued jumping until they were a safe distance from the predator, after which they climbed up a shrub again. This tendency to stay in the canopy rather than on the ground is quite typical for many *Schistocerca* species. Adults, however, often exhibited different behavior, basking not only on the plants but on the ground as well. When disturbed, the adults usually made an escape flight and landed either on vegetation or on the ground. Such flights were relatively short, between 3 and 10 m only. This is different from many other *Schistocerca* species, (e.g., *S. americana*) which often fly considerable distances from the source of disturbance (Capinera et al. 2004). Such reduction in escape flight distance may be a useful adaptation to the small-size island habitat preventing the grasshoppers from being blown into the ocean. However, other observers have not noted this tendency (M. MacDonald, pers. comm.))

Grasshoppers and Millerbirds: are the birds at risk?

In 2002–2004, *S. nitens* severely defoliated Nihoa's vegetation, especially the shrubs of *S. tomentosa*, *S. fallax* and *Ch. oahuense*. Millerbirds nest in these plants (Conant et al. 1983; Morin et al. 1997) and thus may have been negatively impacted by the grasshoppers. Indirectly, Millerbirds may suffer from a grasshopper outbreak because plant defoliation may reduce numerous herbivore insect populations that constitute the birds' main food. It is known that the devegetation of Laysan, coupled with the effects of guano mining, resulted in the extinction of the Laysan Millerbird (*Acrocephalus familiaris familiaris*) along with two other endemic birds, the Laysan rail (*Porzana palmeri*) and the Laysan honeycreeper (*Himatione sanguinea freethi*) (Ely and Clapp 1973; Conant et al. 1983; Conant and Morin 2001).

Millerbird counts on Nihoa in 2006 showed that the grasshopper impact, as a food resource, was potentially positive and the birds likely benefited from high grasshopper numbers in previous years. Kropidlowski (2006) estimated 746 Millerbirds on the island in April 2006, and Beth Flint's (pers. comm.) counts in October 2006 (741) came close to this. Both numbers are record highs for Nihoa during 40 years of observations (Fig. 8). Carrying capacity (K) on the island for this species is estimated at 600 birds (USFWS 1984); although, Conant and Morin (2001) consider this number a substantial overestimate and advance a more reasonable $K = 380$. As such, Millerbird numbers in 2006 almost twice exceeded the island's carrying capacity. This is a marked increase from 1994 and 1996, when Millerbird estimates remained well below 200 (Morin et al. 1997). In 2002, when the grasshopper population was high, the Millerbird population was estimated at about 450, while in 2005, when virtually no grasshoppers were found in June, Millerbird estimates dropped below 200. In March 2007, after a relatively "low" grasshopper year 2006, the Millerbird numbers were estimated at 427 (Rowland et al. 2007; Fig. 8). Although more data on the population dynamics of both, the Millerbirds and the grasshoppers are needed to warrant statistically supported inferences, the changes in Millerbird population might reflect the grasshopper fluctuations on the island.

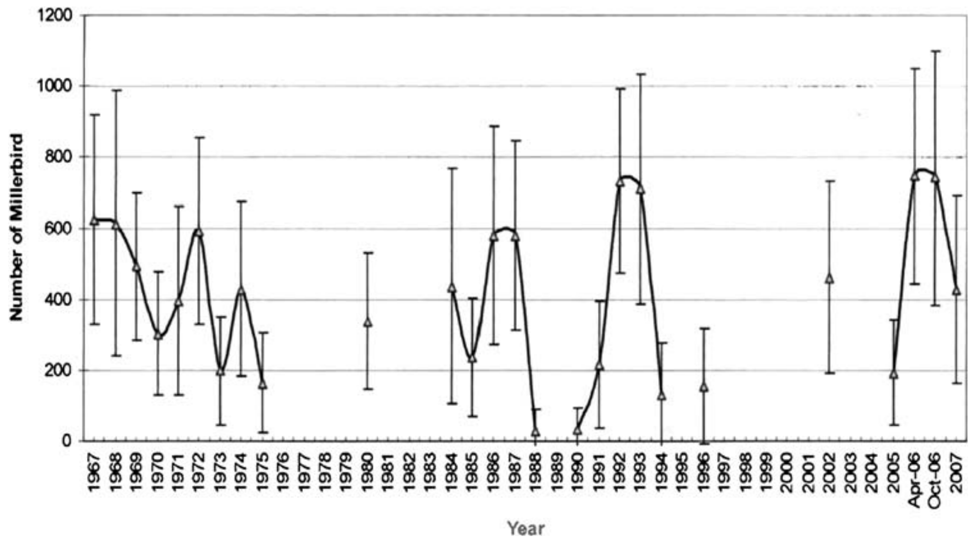

Fig. 8 Nihoa Millerbird population estimates 1967–2007 by USFWS, 95% confidence interval (from Morin et al. 1997) updated by data from Kropidlowski (2006) and Rowland et al. (2007)

My observations on Nihoa Millerbirds in October 2006 did not reveal feeding on grasshoppers, although it was documented in the past (Morin et al. 1997). It may be that grasshopper numbers were too low and did not represent an attractive and easy-to-obtain food source. Judging from bird and the grasshopper sizes, it is reasonable to expect that grasshopper nymphs, especially the young instars, would be manageable prey for the Millerbirds. This is probably true for adult male grasshoppers as well because they are much smaller in size than females: male body length is 24–46 mm and female body length is 40–66 mm (Capinera et al. 2004). Adult females (~3 g) are probably too large for the Millerbirds (~18 g) to consume in one piece. Successful Millerbird feeding on a *S. nitens* nymph was documented by Culliney (2004). At high numbers, grasshoppers (particularly nymphs) provide an abundant and accessible food source for the birds (Wegmann in Liittschwager and Middleton 2005), which may produce more than one clutch per year during its nesting period from January to September (Morin et al. 1997). There is no doubt that the grasshoppers are among the favorite foods for Millerbirds: *S. nitens* body parts were found in 69% of the bird's fecal samples analyzed between 1980 and 1993 (Morin et al. 1997).

The second Nihoa endemic and endangered songbird, the Nihoa Finch did not seem to be impacted by the grasshopper outbreak. They are approximately 10 times more numerous than Millerbirds (Conant et al. 1983) and the recent fluctuations in their numbers (see Rowland et al. 2007) did not appear to exhibit any trend. Unlike Millerbirds, the omnivorous, and ecologically adaptable finches survived the devegetation of Laysan in the past.

Are Nihoa's endemic insects threatened by *S. nitens*?

Coupled with drought, the Gray bird grasshopper outbreak in 2002–2004 led to significant defoliation on Nihoa. In turn, this could have produced a severe impact on the arthropods that depend on the island's vegetation. I observed several Nihoa endemic insects in October 2006. Nihoa Rhyncogonus weevil (*Rhyncogonus exsul*) adults feed primarily on the same plants as those preferred by *S. nitens*: *S. tomentosa*, *Ch. oahuense, S. fallax* etc. It was reasonable to expect that the weevil's population would decrease after losing its food sources to the grasshopper. However, adult weevils were common in October 2006 and, according to Rowland et al. (2007), in March 2007. UV light collections in October 2006 yielded two different click beetles (probably, endemic *Itodacnus* spp.) species, several endemic noctuid moths species as well as oecophorid moths from genus *Thyrocopa*. At the same time, despite a significant effort, I was not able to find Nihoa's three orthopteran endemics: Nihoa conehead katydid *Banza nihoa*, Conant's giant Nihoa tree cricket *Thaumatogryllus conantae* or Nihoa giant rock cricket *Caconemobius nihoensis*. The latter inhabits the splash areas, so it is unlikely to be affected by *S. nitens*. *Thaumatogryllus conantae*, however, appears to be confined to a limited habitat, the so-called Devil's Slide in the NW part of the island (Evenhuis and Eldredge 2004). Vegetation there was impacted by the grasshoppers, so it is possible that the cricket's numbers decreased after the grasshopper outbreak. At this point, I do not have data regarding the potential impact of the grasshopper outbreak on the endemic Nihoa katydid *Banza nihoa*, which is the only Nihoa insect included in the IUCN Red List (listed as "vulnerable" meaning it is "facing a high risk of extinction in the wild in the medium-term future") (IUCN 2007). Without further and more detailed observations, it is impossible to provide any insight regarding the impact of *S. nitens* on other endemic Nihoa insects.

Nihoa's ecosystem after the grasshopper invasion: what happened, what to expect and what can be done?

The *S. nitens* outbreak in 2002–2004, which devastated Nihoa's vegetation, was considered a threat to biodiversity and a challenge to conservation (Gilmartin 2005). Impacts on several endemic and endangered plant species appeared to be particularly pronounced. Since then, and through at least March 2007, grasshopper numbers crashed and the island's vegetation, including the endemics, has recovered. Moreover, the available (although admittedly fragmentary) data on the Millerbird population showed that the grasshoppers might have provided a plentiful food source allowing the birds to increase their population. In this respect, the grasshopper invasion may be considered as beneficial to these critically endangered birds. High Millerbird numbers may allow USFWS to consider the plans of translocating some birds to Laysan Island (Conant and Morin 2001; Fleischer et al. 2007), a conservation measure that is only possible during high-population years (Morin et al. 1997).

It is not clear how the grasshoppers affected the population dynamics of other Nihoa herbivores (primarily arthropods). Food source depletion during the grasshopper outbreak might have decreased the numbers of many Lepidoptera, Coleoptera, Hemiptera and other plant feeders. However, observations in October 2006 showed that several noctuid species, as well as the endemic weevil *Rh. exsul* were quite common, despite their apparent competition with *S. nitens* for resources.

Collecting the detailed meteorological data from April 2006 through present, along with future scientific expeditions will help clarify questions regarding the *S. nitens* life cycle on Nihoa as well as biotic and abiotic factors governing its population dynamics. Further laboratory studies on the impact of soil dryness on the grasshopper egg viability may elucidate factors limiting the insect's reproductive potential. The state of Nihoa's vegetation can be monitored using remotely sensed data. High resolution satellite imagery (e.g. SPOT) would be instrumental in early detection of vegetation changes on the island.

If the grasshoppers produce another outbreak in the future, should we take measures to reduce their numbers? Because of the complicated island relief and rich flora and fauna, eradication would not be possible. Traditional grasshopper control options, such as chemical spraying or biological insecticides, are hardly viable on Nihoa given the logistical constraints, potential severe non-target effects and risks of bringing exotic microorganisms (Gilmartin 2005). One possible alternative is to use stations with insecticidal baits strategically placed in areas of grasshopper concentrations. Baiting has reduced non-target impact and provides environmental and logistical advantages over conventional anti-grasshopper spraying (Latchininsky and VanDyke 2006). However, any control method on Nihoa should be applied with maximum diligence, only as a last resort; and its consequences should be closely monitored.

Should *S. nitens* be considered alien, with all the legal consequences of such a status? As it was shown earlier, published accounts of the grasshopper's arrival on Oahu (Anonymous 1965a, b) are not convincing and they leave room for different interpretations. A recent natural expansion in the distribution range (Table 2) of this highly mobile insect impressed even those specialists who did not question its alien status in the past: "given the distances *S. nitens* has managed in the NWHI, and the general track of hurricanes coming up from Mexico, I don't think we could fully discount the possibility that they could manage the distance with the aid of storms" (Gordon Nishida pers. comm., 2008).

Nihoa has survived disasters in the past. In 1885, a landing party accompanying Princess Lili'uokalani accidentally started a fire that consumed virtually all Nihoa fan palms on the island (Clapp et al. 1977). The palms have recovered, and in April 2006 there were 1,042 adult trees and 1,718 seedlings (Kropidlowski 2006). Maybe, the grasshopper outbreaks on Nihoa should be considered not as destructive plagues of alien invaders, but as self-regulating natural processes, similar to forest fires, which might be beneficial for the island's ecosystem in the long run. *S. nitens* populations on Nihoa and other NWHI should be closely monitored to better understand their impact on the islands' biota. Control measures should be avoided unless grasshopper numbers become overwhelming for a prolonged period (several weeks in a row). At lower population densities, grasshoppers are known to increase plant production, accelerate nutrient cycling (Belovsky and Slade 2000), contribute to soil building (Belovsky et al. 2000), and provide food source for numerous animals, primarily birds (McEwen et al. 2000).

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References

Anonymous (1965a) Notes and exhibitions for September 1964. New immigrant acridids. Proc Hawaiian Entomol Soc 19(1):27

Anonymous (1965b) Notes and exhibitions for September 1964. *Schistocerca vaga* (Scudder). Proc Hawaiian Entomol Soc 19(1):28

Athens JS, Ward JV, Blinn DW (2007) Vegetation history of Laysan Island, Northwestern Hawaiian Islands. Pac Sci 61(1):17–37

Beardsley JW (1980) Notes and exhibitions for October 1977. Proc Hawaiian Entomol Soc 23(2):182

Belovsky GE, Slade JB (2000) Insect herbivory accelerates nutrient cycling and increases plant production. Proc Natl Acad Sci 97(26):14412–14417

Belovsky GE, Joern A, Lockwood JA (2000). Grasshoppers—plus and minus: the grasshopper problem on a regional basis and a look at beneficial effects of grasshoppers. Section VII-16 in Cuningham GL and Sampson MW, Grasshopper Integrated Pest Management User Handbook, USDA-APHIS Tech Bull No 1809, Washington, DC, http://www.sidney.ars.usda.gov/grasshopper/Handbook/VII/vii_16.htm

Capinera JL, Scott RD, Walker TJ (2004). Field guide to grasshoppers, Katydids, and crickets of the United States. Cornell University Press, Ithaca and London

Christophersen E, Caum EL (1931) Vascular plants of the Leeward Islands, Hawaii. Bernice P Bishop Museum Bull No 81:1–41

Clague DA (1996) Growth and subsidence of the Hawaiian-Emperor volcanic chain. In: Keast A, Miller SE (eds) The origin and evolution of Pacific Island biotas, New Guinea to Eastern Polynesia: patterns and processes. SPB Academic Publishers, Amsterdam, pp 35–50

Clapp RB, Kridler E, Fleet RR (1977) The natural history of Nihoa Island, Northwestern Hawaiian Islands. Atoll Research Bull No 207, Washington, DC

Conant S (1985) Recent observations on the plants of Nihoa Island, Northwestern Hawaiian Islands. Pac Sci 39(2):135–149

Conant S, Morin MP (2001) Why isn't the Nihoa Millerbird extinct? In: Scott JM, Conant S, van Riper C III (eds) Evolution, ecology, conservation, and management of Hawaiian birds: a vanishing Avifauna. Studies in Avian Biology, No. 22, pp 338–346

Conant S, Christensen CC, Conant P, Gagné WC, Goff ML (1983) The unique terrestrial biota of the Northwestern Hawaiian Islands. In: Proceedings of the Second Symposium on Resource Investigations in the Northwestern Hawaiian Islands, 25–27 May 1983. University of Hawaii Sea Grant College Report (UNIHI-Sea Grant-MR-84-01), Honolulu, HI, pp 77–94

Culliney J (2004) Nihoa and Necker Islands Expedition, August 27–September 6. An edited transcript of a log of the expedition recorded by John Culliney, Hawaii Pacific University. Personal Observations. Summary of preliminary findings: natural-history, ecology, and taxonomy (unpublished report)

Duranton J-F, Lecoq M (1990) Le Criquet pèlerin au Sahel. CIRAD-PRIFAS, Montpellier and DFPV-AGRHYMET, Niamey

Eldredge LG, Evenhuis NL (2003) Hawaii's biodiversity: a detailed assessment of the numbers of species in the Hawaiian Islands. Bishop Museum Occasional Paper No 76, Bishop Museum Press, Honolulu, HI, 28 pp, http://www.hbs.bishopmuseum.org/pdf/op76.pdf

Ely CA, Clapp RB (1973) The natural history of Laysan Island, Northwestern Hawaiian Islands. Atoll Res Bull No 171, Washington, DC

Emory KP (1928) Archaeology on Nihoa and Necker Islands. Bernice P Bishop Museum Bull No 53, Honolulu, HI

Evenhuis NL, Eldredge LG (2004) Natural history of Nihoa and Necker Islands. Bishop Museum Press, Honolulu, HI

Fleischer RC, Slikas B, Beadell J, Atkins C, McIntosh CE, Conant S (2007) Genetic variability and taxonomic status of the Nihoa and Laysan Millerbirds. Condor 109:954–962

Gagné WC (1988) Conservation priorities in Hawaiian natural systems. Bioscience 38(4):264–271

Gagné WC, Conant S (1983) Nihoa: biological gem of the Northwest Hawaiian Islands. Bishop Museum News 10(7):3–5

Gilmartin WG (2005) Workshop to identify research and mitigation measures to address *Schistocerca Nitens* Crisis on Nihoa Island, Northwestern Hawaiian Islands. Honolulu, HI. Hawaii Wildlife Fund, Volcano, HI, April 25–26

Greathead DJ, Kooyman C, Launois-Luong M-H, Popov GB (1994) Les ennemis naturels des criquets du Sahel. CIRAD-PRIFAS, Montpellier, France—CILSS/AGRHYMET/DFPV, Niamey, Niger

Howarth FG, Mull WP (1992) Hawaiian insects and their kin. University of Hawaii Press, Honolulu, HI

IUCN (2007) Orthopteroid Specialist Group 1996. *Banza nihoa*. In: 2007 IUCN Red List of Threatened Species, http://www.iucnredlist.org

Kevan DKM (1989) Transatlantic travelers. Antenna 13:12–15

Kropidlowski S (2006) Nihoa biological monitoring expedition, April 1–9, 2006. Nihoa Island, Northwest Hawaiian Islands, USFWS-Hawaiian Islands National Wildlife Refuge, Honolulu, HI (unpublished report)

Latchininsky AV (2006) Report of the expedition to Nihoa Island with particular attention to grasshopper *Schistocerca nitens*. October 11–22, 2006. Report to US Fish & Wildlife Service. Laramie, WY (unpublished report)

Latchininsky AV, Launois-Luong M-H (1997) Le Criquet pèlerin, *Schistocerca gregaria* (Forskal, 1775), dans la partie nord-orientale de son aire d'invasio—CIRAD-GERDAT-PRIFAS. Montpellier, France/VIZR, St Petersburg, Russia

Latchininsky AV, VanDyke KA (2006) Grasshopper and locust control with poisoned baits: a renaissance of the old strategy? Outlooks Pest Manag 17(3):105–111

Liittschwager D, Middleton S (2005) The Archipelago: portraits of life in the world's most remote Island Sanctuary. National Geographic Books, Washington, DC

McEwen LC, Petersen BE, Althouse CM (2000) Birds and wildlife as grasshopper predators (Section I-10). In Cuningham GL, Sampson MW (eds) Grasshopper integrated pest management user handbook, USDA-APHIS Tech Bull No 1809, Washington, DC, http://www.sidney.ars.usda.gov/grasshopper/Handbook/I/i_10.htm

Morin MP, Conant S, Conant P (1997) Laysan and Nihoa Millerbirds (*Acrocephalus familiaris familiaris* and *A. f. kingi*). No. 302. In: Poole A, Gill F (eds) The birds of North America. The Academy of Natural Sciences, Philadelphia; The American Ornithologists' Union, Washington, DC

Nishida GM (2001) NOWRAMP 2000 Terrestrial Arthropod Report for the U.S. Fish & Wildlife Service, 30 December 2001, http://www.hbs.bishopmuseum.org/pdf/nowramp2000.pdf

Nishida GM (2002) Hawaiian terrestrial arthropod checklist, 4th edn. Bishop Museum Technical Report No. 24, Honolulu, HI

Oboyski P (2005) A preliminary report from the August 13–20, 2005 Nihoa expedition (unpublished report to USFWS)

Onsager JA, Henry JE (1977) Comparison of five methods for estimating density of rangeland grasshoppers. J Econ Entomol 70:187–190

Predtechensky SA (1935) Studies on the desert locust (*Schistocerca gregaria* Forsk.) in Central Asia and Transcaucasus in 1929–1930. Bull of Plant Protection, Series I: Entomology, No. 11. VIZR, Leningrad (in Russian with English summary)

Rauzon MJ (2001) The Isles of Refuge. Wildlife and history of the Northwestern Hawaiian Islands. The University of Hawaii Press, Honolulu, HI

Ritchie M, Pedgley DE (1989) Desert locusts cross the Atlantic. Antenna 13:10–12

Rowland C, Jones IL, Swenson C (2007) Nihoa biological monitoring expedition. Nihoa Island, Northwestern Hawaiian Islands, Hawaiian Islands National Wildlife Refuge. USFWS, Honolulu, Hawaii, March 16–25, http://www.mun.ca/serg/Nihoa_tripreport2007.pdf

Song H Weissman DB, Barrientos-Lozano L, Cano-Santana Z (2006) The locust Island. Am Entomol 52(3):168–181

Southwood TRE (1987) Ecological methods, with particular reference to the study of insect populations. Springer, London

Thompson DC (1987) Sampling rangeland grasshoppers. In: Capinera JL (ed) Integrated pest management on rangeland: a shortgrass prairie perspective. Westview Press, Boulder, CO, pp 219–233

USFWS (1984) Recovery plan for the Northwestern Hawaiian Islands passerines. USFWS, Portland, OR

USFWS (2006) *Amaranthus brownii.* 5-Year review summary and evaluation. USFWS, Pacific Islands Fish and Wildlife Office, Honolulu, HI, http://www.fws.gov/Pacific/ecoservices/endangered/recovery/documents/signedAmaranthusbrownii.pdf

USFWS (2007) Endangered and threatened wildlife and plants; Review of native species that are candidates for listing as endangered or threatened; Annual notice of findings on resubmitted petitions; Annual description of progress on listing actions. Federal Register 72(234), December 6, 2007, 69034–69106, http://www.fws.gov/Midwest/endangered/candidate/2007cnorFR.html

USGS (2006) Translocation Feasibility of the Laysan Teal (*Anas laysanensis*): executive summary, USGS Pacific Island Ecosystems Research Center, http://www.biology.usgs.gov/pierc/

US NPS (2007) The U.S. World Heritage Tentative list (August 2007 Draft). U.S. National Park Service Staff Report, http://www.nps.gov/oia/TLEssayFinal.pdf

Uvarov BP (1977) Grasshoppers and locusts. Vol. 2. COPR. University Press, Cambridge

Wegmann AS (2005) Preliminary report of the trip to Nihoa in June 2005. USFWS-HINWR, Honolulu, HI (unpublished report)

Wegmann AS, David R, Costa M (2002) Biological Monitoring Expedition: Nihoa Island, September 2–9, 2002. USFWS-HINWR, Honolulu, HI (unpublished report)