Self-pollination in island and mainland populations of the introduced hummingbird-pollinated plant, *Nicotiana glauca* (Solanaceae)[1]

Sheila K. Schueller[2]

Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan 48109-1048 USA

Traits associated with self-pollination are common in island plants. This pattern could simply reflect the vestige of selection during colonization. Alternatively (or in addition), the ability to self-pollinate may provide a reproductive assurance benefit in established island plant populations due to inferior island pollinator service. To test these alternatives I studied an introduced plant (*Nicotiana glauca*; Solanaceae) on the California mainland and on two Channel Islands colonized at different times (approximately 30 and 100 yr ago). I compared these populations in terms of (1) capacity for self-pollination (self-compatibility, autogamy, stigma–anther distance, and incidence of a crumpled floral morph) and (2) current selection for the ability to self-pollinate (pollinator service by hummingbirds and the effect of emasculation on reproductive success). In general, island plants exhibited a higher capacity for self-pollination than mainland plants, especially on the most recently colonized island. However, island plants were not visited less frequently or more variably, nor did I detect current selection for selfing on islands. This supports the hypothesis that selfing traits in island plants are the product of a filter to successful establishment during colonization and not of selection for selfing in established island populations.

Key words: California Channel Islands; evolution of plant breeding systems; hummingbird pollination; invasive plant; island biology; *Nicotiana glauca*; self-pollination; Solanaceae; stigma–anther distance.

The ability to self-pollinate is a common feature of island plants (Carlquist, 1974; Ehrendorfer, 1979; Barrett, 1996). The floras of New Zealand (Webb and Kelly, 1993), Hawaii (references in Carr and Powell, 1986), the Galapagos (Rick, 1966; McMullen, 1987), and the Jaun Fernandez Islands (Anderson et al., 2001; Bernardello et al., 2001) have a higher proportion of self-compatible species than comparable mainland floras. Comparisons of the mating system of species or species complexes occurring across mainland and island sites also indicate that traits allowing for self-pollination are more common on islands (Strid, 1969; Ehrendorfer, 1979; Barrett and Shore, 1987; Barrett et al., 1989; Inoue, 1990; Belaoussoff and Shore, 1995; Barrett, 1996).

Self-pollination provides reproductive assurance when outcross pollination is limited, which occurs when mates and/or visits by pollinators are scarce (Darwin, 1876; Müller, 1883; Jain, 1976; Lloyd, 1992). Mates and pollinator scarcity may occur at different times and for different reasons during island colonization and establishment. Mates are likely to be scarce when a plant first arrives on an island. The ability to self-pollinate would allow even a single colonizing individual to reproduce on islands (Baker, 1955, 1967; Stebbins, 1957). Selection for self-pollination due to a lack of mates is less likely after establishment, when plant populations are larger.

Pollinator scarcity may occur on islands for two reasons.

First, islands often lack specialized pollinators or entire taxa of pollinators (Carlquist, 1974; Woodell, 1979; Lloyd, 1985; Howarth and Mull, 1992; McMullen, 1993). Thus, plants with floral morphologies requiring certain pollinator types or species would have difficulty becoming established in their absence (Compton et al., 1994), unless they were able to self-pollinate (Baker, 1967; Ehrendorfer, 1979; Inoue, 1990; Barrett, 1996). Once the plant is established, the colonization of preferred pollinators may follow (Gardner and Early, 1996), or the plant may evolve adaptations to increase pollination effectiveness by available island pollinators (Inoue and Amano, 1986). Second, pollinator scarcity may be experienced not only for plants that are not "pre-adapted" to the available pollinators upon arrival, but also by established populations of even generalized plants. That is, the altered composition and generalist behavior of island pollinators (MacArthur and Wilson, 1967; Carlquist, 1974; Colwell and Fuentes, 1975) is thought to result in overall reduced or inferior pollinator service to island populations compared to the mainland (Feinsinger and Swarm, 1982; Feinsinger et al., 1982).

The few studies comparing visitation to established island and mainland populations find that island plants tend be visited less frequently (Feinsinger et al., 1982; Spears, 1983; Roubik et al., 1985; Inoue et al., 1996) and more variably (Feinsinger et al., 1982; Spears, 1983). The amount and/or quality of pollen dispersed among plants also tends to be lower on islands (Linhart and Feinsinger, 1980; Feinsinger et al., 1982; Spears, 1987). However, it remains unclear how often reduced pollinator service actually limits plant reproductive success and selects for the capacity to self-pollinate. Furthermore, because it is often difficult to view island plants both during the colonization and subsequent establishment phases (but see Shanahan et al., 2001; Thornton et al., 2001), a largely unresolved issue is whether extant island plant traits were present in original colonists or evolved in situ (Sakai et al., 1995; Barrett, 1996). Exceptions to the pattern of higher selfing ability on

islands (Carlquist, 1966; Spears, 1983; Carr and Powell, 1986; Larson and Barrett, 1998) indicate that the strength, mechanism, and timing of selection for selfing is likely to depend on the initial breeding system of colonists and on the nature of island pollinators. Addressing these unknowns requires studying mainland populations with both established and recently colonized island populations, which for most plants is not feasible.

Introduced species provide an opportunity to directly examine the mechanisms of selection for selfing in established and recently colonized island populations because they are widespread and have known and recent colonization dates. *Nicotiana glauca* Graham (tree tobacco, Solanaceae) is a cosmopolitan bird-pollinated plant native to Argentina (Goodspeed, 1954; Hernandez, 1981). It was first recorded in southern California in 1879 (Sauer, 1988) and has since colonized two of the Channel Islands: Santa Catalina Island in the early 1900s (Millspaugh and Nuttall, 1923) and, more recently, Santa Cruz Island in 1971 (Junak et al., 1995). This plant exhibits significant differences across its range in the distance between the stigma and anthers, or herkogamy (Schueller, 2002), a trait which can influence a plant's capacity and tendency to self-pollinate (Karron et al., 1997; Eckert and Schaefer, 1998; Motten and Stone, 2000; Takebayashi and Delph, 2000). *Nicotiana glauca* is hummingbird-pollinated (Woods, 1927; Stiles, 1973; Russell, 1996; Mitchell, 2000), and hummingbirds were present on the Channel Islands well before the initial colonization of *N. glauca* (Johnson, 1972). Thus, pollinator scarcity due to an absence of required pollinators is not a factor in this species. Furthermore, *N. glauca* is currently locally abundant and in large numbers on the islands, and thus mate scarcity is also not an issue. This means that if current pollinator service is measurably lower on islands, it is due to the nature of island pollinator service, the presumed mechanism for selection for reproductive assurance even in established island populations.

In this study I directly examine whether island *N. glauca* plants are currently under selection for increased selfing ability due to reduced pollinator service relative to the mainland or whether current patterns in *N. glauca* selfing may instead reflect selection for selfing in the recent past, during colonization. Specifically, I tested the following predictions: compared to California mainland plants, Channel Island *N. glauca* plants will currently (1) have a higher capacity for self-pollination (including greater autogamy and smaller stigma–anther distances) and (2) be under current selection for the ability to self-pollinate. Measures of current selection for self-pollination include the frequency and variability of hummingbird visitation, the amount of pollen transfer by hummingbirds, pollen limitation to reproductive success, and the effect of emasculation (preventing within-flower pollination) on reproductive success. If current selfing traits are a product of selection for selfing during colonization and not in established populations, then the second prediction will not be met. The pollinator service and colonization hypotheses are not mutually exclusive, but an absence of current island-mainland differences in pollinator service and selection pressures would indicate that features of island pollinators do not in themselves select for selfing on islands.

MATERIALS AND METHODS

Study sites—I studied populations of *N. glauca* on two Channel Islands and adjacent mainland sites. The Channel Islands are a set of eight continental islands located off the coast of southern California, USA. Established populations of *N. glauca* are limited to Santa Catalina Island and Santa Cruz Island (hereafter referred to as CAT and CRU), which are approximately 100 km from each other and are similar in size and distance from the mainland. Santa Catalina Island is a Southern Channel Island and is 194 km² and 32 km from the mainland (Los Angeles County). Santa Cruz Island is a Northern Channel Island and is 249 km² and 30 km from the mainland (Santa Barbara County). The two mainland sites are about 20 km inland, at approximately the same latitude as the islands and are adjacent to large national forests. Starr Ranch (hereafter STA) is a 16.4 km² Audubon Society sanctuary located in southern Orange County, approximately 100 km south of Los Angeles in the foothills of the Santa Anna Mountains. Sedgwick (hereafter SED) is a 24 km² University of California Reserve located in the Santa Ynez Valley, 45 km northwest of Santa Barbara.

All of the sites share the mediterranean climate typical of much of California, with peak flowering of native plants following the rainy months, November to April (Major, 1977; Philbrick and Haller, 1977). All sites have coastal sage scrub, grassland, and chaparral habitats; the islands also have coastal bluff and coastal strand communities (Schoenherr, 1999). Species composition overlaps considerably among islands and between the islands and the mainland, but each island also has a unique set of mainland species as well as endemic species and subspecies, including endemic hummingbird-pollinated plants (Philbrick, 1980; Power, 1980; Junak et al., 1995; Schoenherr, 1999).

Compared to the adjacent mainland, which has as many as five hummingbird species (Garrett and Dunn, 1981), only two hummingbird species are regularly found on the islands (Jones and Collins, in press): Anna's hummingbird (*Calypte anna*; Trochilidae) and the island Allen's hummingbird (*Selasphorus sasin sedentarius*; Trochilidae), which is a sedentary subspecies of the migrating mainland Allen's (*Selasphorus sasin sasin*; Trochilidae; Mitchell, 2000).

Study species—*Nicotiana glauca* Graham (Solanaceae, tree tobacco) is a shrub to small tree native to riverbanks, gullies, and rocky cliffs in northwest Argentina (Goodspeed, 1954). Accidental as well as intentional introductions have made it a cosmopolitan weed (Hernandez, 1981; Schueller, 2002). In California it is common in actively disturbed areas (roadsides, dry streambeds, gullies, and loose slopes), urban settings, as well as grasslands and coastal scrub. It may be found blooming all year in California, but especially from March to October. The flowers have long (~30 mm) yellow to greenish-yellow tubular corollas with the stigma and anthers inserted just within the mouth of the corolla. Anthesis occurs throughout the day, and flowers are receptive about 4 d. Flowers are slightly protogynous, stigmas becoming receptive 1–2 h before anthers dehisce (Hernandez, 1981, personal observation). Fruits are two-valved capsules that dry as they mature and release hundreds of tiny seeds.

Flowers produce large amounts (ca. 20 µL) of dilute nectar (ca. 20% sucrose) and in California are visited by hummingbirds (Woods, 1927; Stiles, 1973; Mitchell, 2000). On the Channel Islands, *N. glauca* is visited predominantly by the island Allen's hummingbird (*Selasphorus sasin sedentarius*) and by Anna's hummingbird (*Calypte anna*) and on the mainland by Anna's and black-chinned (*Archilocus alexandri*) hummingbirds (Schueller, 2002). These hummingbirds are all relatively similar in size and bill morphology (Pyle, 1997).

Capacity for self-pollination—Island–mainland differences in the ability to self-pollinate were measured in terms of self-compatibility, autogamy, stigma–anther distances, and the incidence of a crumpled floral morph. For the pollination experiments described below at least five flowers per plant were allotted to each treatment. I discuss only fruit and not seed set from treatments, because too many fruits were collected after capsules had opened, making seed counts inaccurate. Although fruit set may not reveal late-acting self-incompatibility (Husband and Schemske, 1996), this was not thought to be a major concern in this species given its long history of self-compatibility and geitnogamy (Goodspeed, 1954).

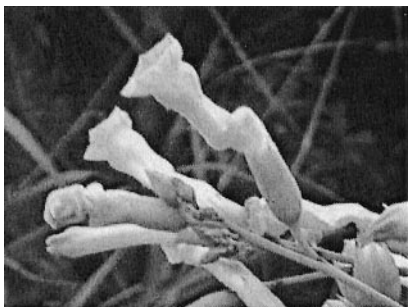To assess self-compatibility I compared fruit set within a plant of hand-

Fig. 1.   *Nicotiana glauca* crumpled flower morph.

self-pollinated (pollen from the same flower or plant) vs. hand-outcross-pollinated (pollen from a plant 5–50 m from the target plant) flowers. Flowers were bagged in fine-mesh (tulle) pollinator-exclusion bags as buds and after treatment. Treatments were completed in the spring and summer of 1999 for at least 10 plants per site at CRU, CAT, SED, and STA. Because of road maintenance, treatments at SED were reduced to only four plants. However, mean fruit set values at SED were consistent with other sites and removal of these data did not change the results of the analysis, so they were included.

To assess whether island plants were more capable of self-pollination (autogamy) than mainland plants, I compared autonomous fruit set with hand-self-pollinated fruit set. Pollinators were excluded in both treatments by bagging flowers as buds and throughout the floral lifetime. Half of the flowers were left unmanipulated, while the other half were hand-self-pollinated by sweeping anthers from the same flower over the stigma until it was saturated with pollen. Treatments were performed in 1998 from early March to late April on 18 plants at CAT, 11 at SED, and 12 at STA and in 1999 for nine plants at STA in March and nine plants at CRU in August. Results from the two years at STA were not found to differ significantly and so were pooled for analysis of site and treatment effects (see *Analysis of fruit set* below). For a subset of the plants from this study, I tested for a significant correlation between the selfing ability of a plant and the mean stigma–anther distance of five untreated flowers on that plant (to avoid disturbing treatment flowers).

Nicotiana glauca flowers have five anthers that sit just below the stigma, but at different heights. I measured minimum herkogamy as the distance from the top of the highest anther to the top of the stigma (to ±0.01 mm) for an average of 10 flowers per 15–30 plants per population (CAT 30, CRU and SED 20 each, and STA 15). Flowers were measured across all populations in 1998 and again at CRU and STA in the late summer to fall of 1999. Data from different seasons were combined for analysis, as season was not found to affect herkogamy (Schueller, 2002). Data were analyzed using nested analyses of variance (ANOVAs) with insularity (island vs. mainland) and population (CAT, CRU; SED, STA) treated as fixed effects and plant as random. I also assessed whether populations differed in among-plant variance in herkogamy using a likelihood ratio test (to account for the hierarchical structure of the data). A significant difference between a model that estimates pooled variance with one that estimates variance separately for each population indicates a difference in variance among populations. Significance was determined using a chi-square test on the likelihood ratio statistic derived from comparing the two models (Little et al., 1996).

Nicotiana glauca plants have a varying proportion of crumpled flowers, a distinct morph which has all the parts of normal flowers, produces nectar, and is visited by hummingbirds (Hernandez, 1981; Schueller, 2002) but has bent to severely crumpled corollas (Fig. 1). Based on breeding system studies of plants in Mexico, Hernandez (1981) concluded that these flowers may contribute significantly to self-pollination, because of their higher fruit set (54%) than uncrumpled flowers (0%) in the absence of pollinators. To determine whether the crumpled morph is more common on islands, I counted the total number of crumpled and normal flowers on at least 10 plants per site per season in the spring, summer and fall of 1998, and spring and summer of 1999. I tested whether proportion of crumpled flowers was associated with the total flowers or age of the plant, estimated as the basal diameter of the

stem. Associations were tested using Spearman's correlations and site effects were tested in a one-way ANOVA on arcsine-transformed proportions.

Pollinator service—To assess whether island plants were visited less frequently or more variably than mainland plants, I observed *N. glauca* plants over three seasons for a total of approximately 163 h across sites in 1998 and 115 h in 1999. Spring observations were made from 2 March to 29 April, in summer from 2 July to 9 September, and in fall from 1 to 18 November. Within a given season I observed at least one island and one mainland site and at least three, and up to 12, different patches of plants within a site. Patches were chosen to represent a range of floral densities (one to more than 20 trees, mostly between 100 and 500 flowers) and habitat types at that site. The same patch was observed for at least 1 h at a time, 1–4 times (over 1–6 d) within a season. A probe of any flower in the patch was counted as one visit. Nonparametric statistics were used to analyze the effects of year, season, and site on patch visitation rate (visits per flower per hour). Over all observations (including additional evening observations) insects visited *N. glauca* flowers on only seven occasions (three bumblebees, three Diptera, and one halictid bee) and so are not discussed further.

Both spatial and temporal variation in visitation rate were estimated to test the prediction that visitation to island plants is more variable than to mainland plants. Temporal variation was quantified as the coefficient of variation for each patch that had been observed for more than one season at a site. The mean of these values within a site estimates both within-year and among-year variation in visitation. Spatial variability was measured as among-patch variation in visitation rate to all patches within a site and season.

To determine whether island pollinators were transferring less pollen among island plants than mainland plants, I measured the amount of pollen deposited on the stigma and removed from the anthers of flowers that had been open to natural pollination for 3 d. Approximate measures of pollen deposited and removed were made in the field as the percentage of stigma covered with pollen (0–100%) and number of empty anthers (0–5), respectively. Pollen on the stigma is visible as a white film, and touched anthers lose their pollen (it adheres to the surface of the bill) and appear dark or ''empty'' relative to undisturbed anthers, which remain white and rounded with pollen. Although approximate estimates of pollen transfer, these measures are directly associated with pollinator visitation (Schueller, 2002) and provide a conservative test of differences among sites in the quantity of pollen transfer. I measured pollen transfer on five flowers per plant for at least six plants per site from CRU and STA in November 1999 and CRU, CAT, STA, and MON in June 2000.

To determine if plant reproductive success is limited by pollen on the islands more than on the mainland, I compared the fruit set of open-pollinated and supplemental-hand-cross-pollinated flowers. If reproductive success is pollen-limited, fruit set of open-pollinated flowers will be significantly lower than fruit set of hand-pollinated flowers. I performed these treatments in 1998 for 24 plants at CAT, 11 at SED, and 12 at STA; and in 1999 for 10 plants at CRU, 17 at CAT, and 13 at STA. Because seasons within a year (spring/summer) did not differ detectably or interact with treatment effects on fruit set, data were pooled by year for analyses of site effects (see *Analysis of fruit set* below).

Selection for reproductive assurance—To test whether within-flower selfing currently provides a greater reproductive assurance benefit to island than to mainland plants, I compared the fruit set of open-pollinated intact flowers with open-pollinated emasculated flowers across sites. Flowers were emasculated by removing all anthers with fine forceps before they dehisced. Paired treatments were done for at least 10 plants in the spring of 1998 at CAT, SED, and STA; summer 1998 at STA; and summer of 1999 at CRU. If the ability to self-pollinate on islands is a product of current selection due to inadequate island pollinator service, then emasculated flowers will produce significantly fewer fruits than intact flowers on islands but not on the mainland.

Analysis of fruit set—Site and treatment effects on fruit set were analyzed using a generalized linear model with a binomial (each flower succeeds or fails at producing a fruit) error distribution in PROC GENMOD in SAS (Al-

TABLE 1. Self-compatibility of *Nicotiana glauca* plants from two Channel Island and two California mainland sites based on fruit set of self- and cross-pollinated flowers. Values are mean percent fruit set ±95% confidence intervals (number of flowers). N = number of plants.

| Site | N | Treatment | |
		Self	Outcross
Santa Cruz Island	10	83 ± 9 (47)	74 ± 13 (64)
Santa Catalina Island	16	80 ± 10 (69)	86 ± 9 (60)
Sedgwick	4	50 ± 57 (6)	67 ± 54 (6)
Starr	9	60 ± 13 (37)	59 ± 17 (55)

lison, 1999; SAS Institute, 1999). I used plant as a repeated subject to account for clustering of flowers within plants (Diggle et al., 1994). Because this analysis did not pair treatments by plant, an additional analysis was performed for the autogamy experiment, where the magnitude of difference between treatments within a plant was of interest. I calculated the ratio of autonomous to hand-self-pollinated fruit set separately for each plant and then used nonparametric tests to determine the effect of site on this within-plant measure of treatment differences.

RESULTS

Capacity for self-pollination—*Self-compatibility*—Fruit set did not differ between self- and outcross-pollinated flowers (Table 1; treatment effect: $\chi^2 = 0.24$, df = 1, $P = 0.62$) nor did sites differ in treatment effects (treatment-site interaction: $\chi^2 = 2.49$, df = 3, $P = 0.48$), indicating that both mainland and island populations of *N. glauca* are self-compatible.

Autogamy—There was both a significant effect of treatment ($\chi^2 = 31.45$, df = 1, $P < 0.0001$) and site ($\chi^2 = 14.00$, df = 3, $P = 0.003$) on fruit set. Island sites had significantly higher autogamous fruit set than SED and a trend towards higher autogamous fruit set than STA (Fig. 2). However, islands also had higher hand-self-pollinated fruit set, indicating that autogamous fruit set might be higher on islands at least in part because island plants have more resources to allocate to fruits. Sites did not differ in the relationship between the two treatments (treatment by site interaction: $\chi^2 = 0.27$, df = 3, $P =$

Fig. 3. Selfing ability of *Nicotiana glauca* plants across Channel Island (CRU = Santa Cruz, CAT = Santa Catalina) and California mainland sites (SED = Sedgwick, STA = Starr). Different letters indicate significant differences (based on Bonferroni-corrected results of Mann-Whitney U tests).

0.97). Site differences in selfing ability were, however, apparent in the analysis of individual plant ratios of autonomous self- to hand-self-pollinated fruit set: CRU plants had a significantly greater selfing ability than STA plants, but CAT and SED did not differ significantly from each other or other sites (Fig. 3).

Herkogamy—Stigma–anther distances varied significantly between island and mainland ($F_{1,2} = 63.58$, $P = 0.0001$) and among sites ($F_{2,78} = 7.63$, $P = 0.001$). Anthers of island plants are up to 0.5 mm closer to the stigma than those of mainland plants and are closest (Fig. 4) and least variable (Table 2) on the most recently colonized island, CRU.

Relationship between selfing ability and herkogamy—Selfing ability (the ratio of autogamous to hand-self-pollinated fruit set) increased significantly with decreasing stigma–anther distance: $r (23) = -0.58$, $P = 0.005$.

Incidence of crumpled morph—Island plants had a significantly larger proportion of crumpled flowers than mainland plants (site effect: $F_{3,77} = 65.76$, $P < 0.001$). The CRU plants had a significantly higher percentage of crumpled flowers than
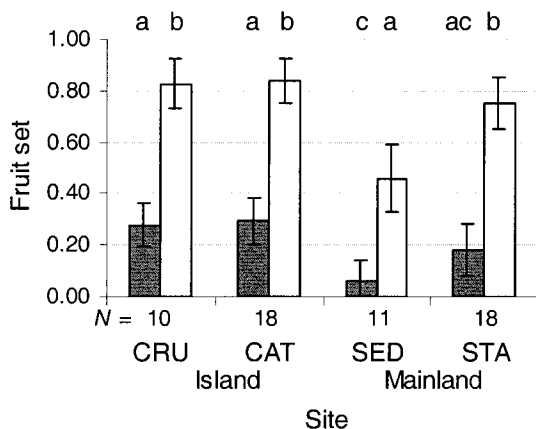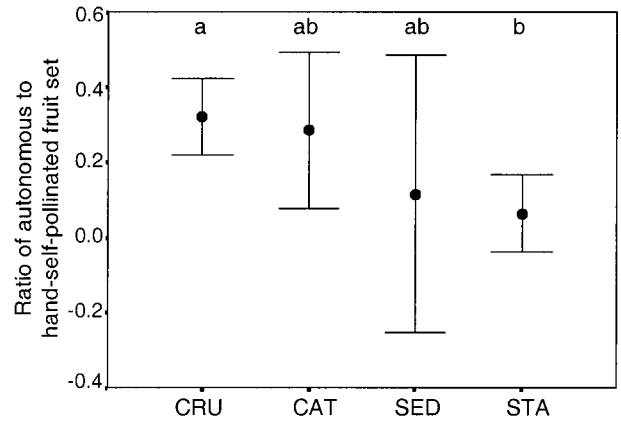
Fig. 2. Fruit set of autonomous self-pollinated (shaded bars) vs. hand-self-pollinated flowers (open bars) of *Nicotiana glauca* plants across Channel Island (CRU = Santa Cruz, CAT = Santa Catalina) and California mainland sites (SED = Sedgwick, STA = Starr). Means with different letters are significantly different from each other ($P < 0.05$, differences of least squares means). Error bars are 95% confidence intervals for the mean.
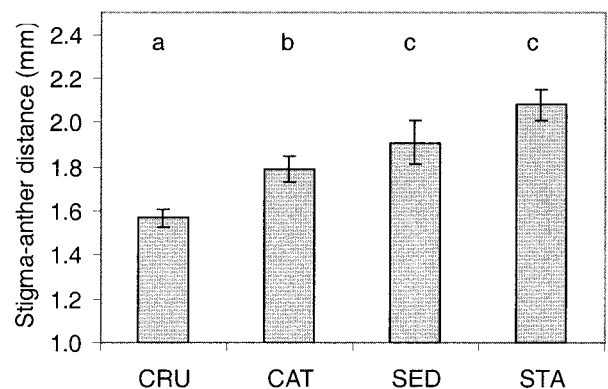
Fig. 4. Stigma–anther distances of Channel Island (CRU and CAT) and California mainland (SED and STA) populations of *Nicotiana glauca*. Significant differences among populations are indicated by different letters within a graph (Tukey's post hoc multiple comparisons, $P < 0.01$).

TABLE 2. Variability in *Nicotiana glauca* stigma–anther distance for two Channel Island (CAT = Santa Catalina and CRU = Santa Cruz) and two mainland California (SED = Sedgwick and STA = Starr) sites. Estimate of among-plant variance within a site (covariance parameter) and coefficients of variation (CV; to account for differences in means) are shown. Results of likelihood ratio tests for equal variance among populations: $\chi^2 = 11.4$, df = 3, $P = 0.01$.

| | Site | | | |
Measure of variation	CAT	CRU	SED	STA
N	27	19	20	15
Among-plant variance	0.02	0.0001	0.12	0.03
CV (%)	15.94	10.12	22.45	13.23

TABLE 3. Relationship between the proportion of crumpled-morph flowers on a *Nicotiana glauca* tree and the total number of flowers or tree size (diameter at base). Number of plants sampled is in parentheses. None of the correlations are significant at the $\alpha = 0.05$ level. An insufficient number of plants were sized for analysis at Santa Cruz Island.

| | Spearman's rho with proportion crumpled | |
Site	Total number of flowers	Tree size
Santa Cruz Island	0.26 (10)	—
Santa Catalina Island	−0.16 (34)	0.43 (10)
Starr Ranch	0.02 (22)	0.40 (6)
Sedgwick Reserve	−0.08 (32)	0.09 (10)

any site (mean ± 1 SD: 86 ± 12%, N = 10; Tukey's post hoc multiple comparisons, $P < 0.05$), followed by CAT (25 ± 24%, N = 34), while the two mainland sites had significantly lower and equivalent proportions of crumpled flowers (SED: 4 ± 4%, N = 15; STA: 8 ± 9%, N = 22). The proportion of flowers on a plant that were crumpled was not correlated with either the total number of flowers on a plant or with plant size (diameter at the base) at any site (Table 3).

Pollinator service—*Visitation frequency and variability*— Island plants were not visited less frequently than mainland plants (Fig. 5). On average, a flower at any site received less than one visit per hour, and there was no trend towards a lower island visitation rate, nor a statistically detectable difference among sites for any season in either 1998 or 1999 or both years combined (Kruskal Wallis *P*-values all greater than 0.30). Neither temporal nor spatial variability in visitation rates were significantly higher on islands (Table 4; temporal: $t = -1.10$, df = 29, one-tailed $P = 0.14$; spatial $t = -0.70$, df = 15, one-tailed $P = 0.25$).

Pollen transfer—Contrary to predictions, pollen transfer was not lower on islands than on the mainland (Fig. 6). The amount of pollen removed from flowers tended to be greater at CRU than STA in November 1999 (Mann-Whitney $U = 1723.5$, $P = 0.052$) and was significantly greater on both islands than both mainland sites in June 2000 (site effect: $\chi^2 = 27.1$, df = 3, $P < 0.0001$). Similarly, significantly more pollen was deposited on the stigmas of CRU island plants than STA plants in November 1999 (Mann-Whitney $U = 1098.5$, $P < 0.001$), and in June 2000 pollen deposition was significantly greater on CRU island than both mainland sites (site effect: $\chi^2 = 24.6$, df = 3, $P < 0.0001$).

Pollen limitation to success—Fruit set of island plants was not pollen limited in either 1998 or 1999 (Fig. 7). In 1998 fruit set exhibited a significant increase with hand-pollination at both mainland sites, but not CAT island. There was a significant effect of treatment ($\chi^2 = 15.01$, df = 1, $P = 0.0001$) and site ($\chi^2 = 14.95$, df = 2, $P = 0.0006$) on fruit set and a significant difference among sites in treatment effect ($\chi^2 = 9.76$, df = 2, $P = 0.007$). In 1999 plants were not pollen limited at any site (nonsignificant treatment effect: $\chi^2 = 1.88$, df = 1, $P = 0.17$, and treatment by site interaction: $\chi^2 = 0.54$, df = 2, $P = 0.76$). The lower mean fruit set at CRU (site effect: $\chi^2 = 13.82$, df = 2, $P = 0.001$) reflects predation on all fruits by birds in that season.

Selection for reproductive assurance—Contrary to predictions, removing a flower's capacity for self-pollination tended to affect mainland, but not island plants. Fruit set of emasculated flowers was significantly lower than intact flowers at STA in one season and also tended to be lower at SED but
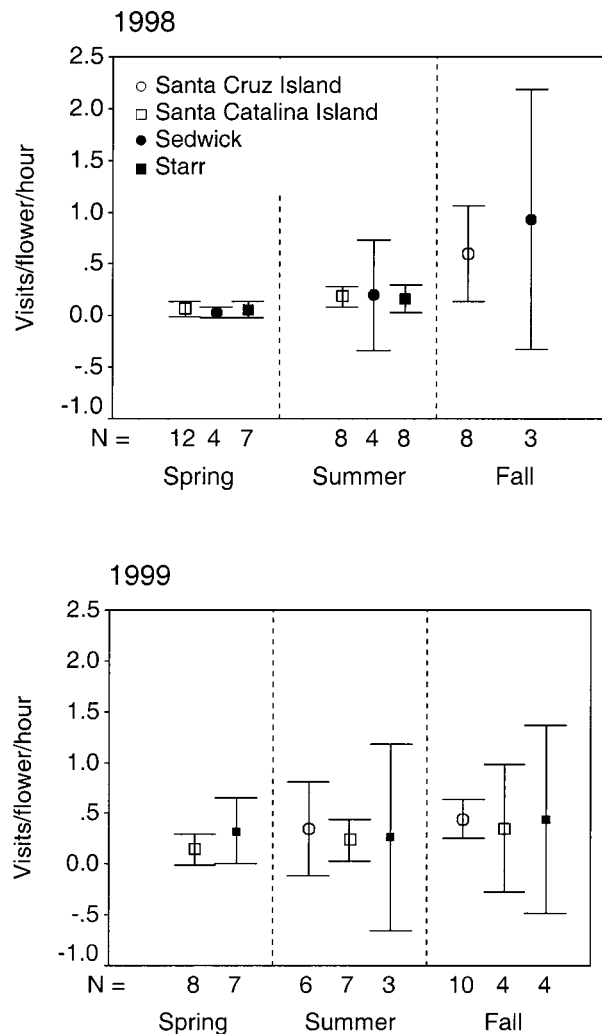

Fig. 5. Frequency of visits to *Nicotiana glauca* flowers by hummingbirds across Channel Island (open symbols) and mainland sites (filled symbols) in 1998 and 1999. Error bars are 95% confidence intervals for the mean. Sample sizes are number of patches of plants, each observed a mean of 1.5 h per season.

TABLE 4.   Coefficients of variation reflecting temporal and spatial variability in visitation rate to Channel Island and California mainland plants of *Nicotiana glauca* by hummingbirds. Values are mean ± 1 SD with sample size in parentheses.

CV	Santa Cruz Island	Santa Catalina Island	Sedgwick	Starr
Temporal	77 ± 49% (9)	101 ± 57% (11)	90 ± 48% (3)	120 ± 49% (8)
Spatial	94 ± 34% (3)	119 ± 37% (6)	115 ± 59% (3)	128 ± 28% (5)

not CAT or CRU (Table 5). The difference between island and mainland sites in treatment effects was not significant at the $\alpha = 0.05$ level ($\chi^2 = 3.45$, df = 1, $P = 0.063$), in part because of the large variation in fruit set for both treatments (coefficients of variation ranged from 49 to 160%, with a mean of 84%).
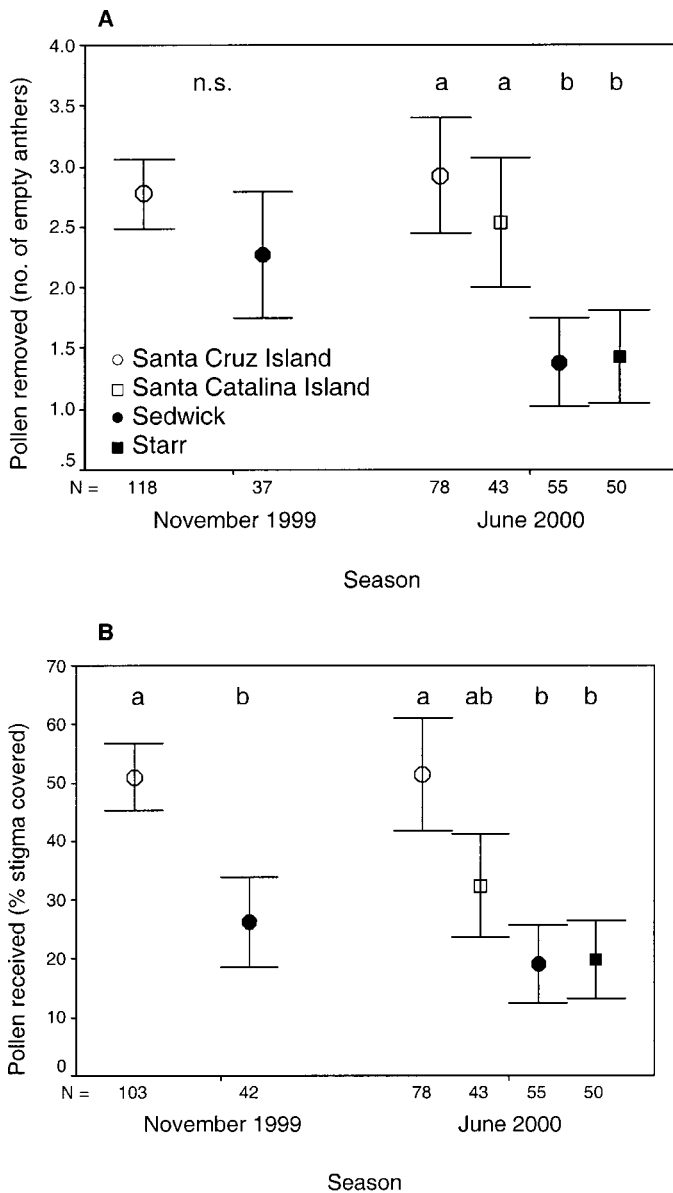

Fig. 6.   Pollen removed (A) and deposited (B) for *Nicotiana glauca* flowers across Channel Island (open symbols) and mainland sites (filled symbols) by season. Error bars are 95% confidence intervals for the mean. Different letters within a chart and season indicate significant differences (Mann-Whitney *U* tests, Bonferroni-corrected for June 2000 comparisons).

DISCUSSION

My results indicate a tendency towards higher selfing ability in island plants, especially on the most recently colonized island (smaller stigma–anther distances, trend towards higher autogamy, and a higher proportion of selfing morph flowers), but a lack of current selection for selfing on islands (island plants experience neither reduced pollinator service nor is there a reproductive advantage of within-flower pollination on islands). These results do not support the hypothesis that selfing is favored in established island populations due to reduced pollinator service. Instead, my results suggest that selfing traits on islands are the product of a filter to successful establishment during colonization.

Capacity for self-pollination—Fruit set of unmanipulated bagged flowers indicates that California *N. glauca* plants have
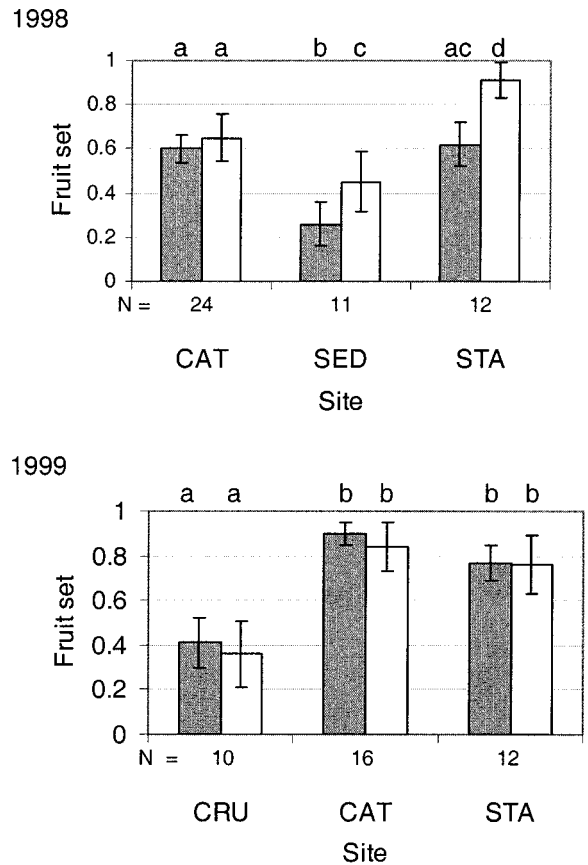
Fig. 7.   Pollen limitation of fruit set based on the difference in fruit set of naturally pollinated (shaded bars) and supplemental hand-pollinated flowers (open bars) of *Nicotiana glauca* on Channel Island (CRU = Santa Cruz, CAT = Santa Catalina) and mainland sites (SED = Sedgwick, STA = Starr) in 1998 and 1999. Means with different letters within a year are significantly different from each other ($P < 0.05$, differences of least squares means). Error bars are 95% confidence intervals for the mean.

TABLE 5. Effect of emasculation (anther removal) on open-pollinated fruit set for plants across Channel Island and California mainland sites. Values are mean percent fruit set ±95% CI (number of flowers). N = number of plants. All tests have one degree of freedom. Percent decrease = $100[(I - E)/I]$, where I = mean intact fruit set and E = mean emasculated fruit set. Asterisk denotes significant treatment difference ($P <$ 0.05).

Season and Site	Treatment		Percent decrease	Significance tests		
	Emasculated	Intact		N	χ^2	P
Spring 1998						
Santa Catalina Island	58 ± 10 (103)	60 ± 7 (220)	3%	24	0.70	0.40
Sedgwick	18 ± 9 (68)	26 ± 10 (77)	31%	11	3.13	0.08
Starr	36 ± 13 (59)	62 ± 10 (91)	72%	12	5.86	0.02*
Summer 1998						
Starr	15 ± 17 (20)	23 ± 19 (22)	35%	6	0.26	0.61
Summer 1999						
Santa Cruz Island	40 ± 20 (25)	41 ± 11 (86)	2%	10	0.04	0.84

at least a limited ability to self-pollinate (contrary to studies of *N. glauca* in Mexico by Hernandez [1981] that found 0% fruit set in the absence of pollinators) and that selfing ability is slightly higher on islands. Island–mainland differences in selfing ability were somewhat diluted by within-site variation in stigma–anther distance (as in Daehler, 1998). Stigma–anther distance is also variable within a plant, but even when measurements were not made on the same flowers there was a significant within-plant relationship between selfing ability and mean herkogamy. This indicates that stigma–anther distance is a plant trait on which selection could act if it is heritable. The apparent maintenance of island–mainland differences in stigma–anther distance in a preliminary sample of greenhouse plants grown from seed suggests that it is heritable (Schueller, 2002).

The pattern of higher selfing potential on islands is also indicated by a higher proportion of crumpled flowers in island plants, especially the most recently colonized site, CRU. This pattern does not appear to be an artifact of abiotic differences among sites. Proportion of crumpled flowers was not related to the size or total number of flowers on a tree (both presumably related to resources). Furthermore, although crumpled flowers were least prevalent across all sites in periods of highest rainfall (Schueller, 2002), the site with the highest proportion of crumpled flowers (CRU) tends to have higher rainfall than other sites (Schueller, 2002).

The value of the crumpled morph flower as a reproductive assurance mechanism remains unclear. Hernandez (1981) found that crumpled flowers self much more readily than normal flowers, which makes sense given that their stigma and anthers are often, though not always, completely overlapping (personal observation). On the other hand, Hernandez (1981) observed that the seeds of these flowers have much lower germination rates than normal seeds. Whether crumpled flowers behave similarly in California plants is not yet known.

Pollinator service—Contrary to predictions, the frequency and variability of visits to plants were equivalent across sites. The handful of other studies that have compared island and mainland pollinator visitation indicate that although island plants tend be visited less frequently and/or more variably, island-mainland differences are subtle or inconsistent (Linhart and Feinsinger, 1980; Feinsinger et al., 1982; Spears, 1983; Roubik et al., 1985; Inoue et al., 1996). Nonetheless, infrequent or unreliable visitation to island plants is often invoked to explain selection for reproductive assurance mechanisms on

islands (Carlquist, 1974; Ehrendorfer, 1979; Spears, 1987; Barrett, 1996; Anderson et al., 2001). Upon closer consideration, it is not clear why, except for initially small populations or specialized plants, visitation to island plants should be less frequent or more variable. Theory predicts that under reduced diversity, island populations should compensate and increase in density relative to the mainland (MacArthur et al., 1972; Williamson, 1981). This would mean that the abundance of pollinators, and therefore the frequency of visitation, should not be reduced on islands. Feinsinger et al. (1982, p. 494), on the other hand, argue that a less diverse assemblage of pollinators will be unable to use all of the available resources on islands and therefore "by chance some food items may be neglected," leading to less frequent and more variable visitation to island plants.

If a decrease in pollinator diversity is the presumed mechanism leading to reduced visitation frequency on islands, then it is apparent why *N. glauca* does not show this pattern. The diversity of common visitors to *N. glauca* is the same across island and mainland sites (Schueller, 2002). Furthermore, it has large floral displays with copious nectar (flowers produce five times as much nectar as common native hummingbird-pollinated plant species; unpublished data) and so it is not a species that is "apt to be overlooked" (Feinsinger et al., 1982, p. 504) by island pollinators. On the other hand, similar island–mainland differences in pollinator service were observed for a native hummingbird-pollinated plant (Schueller, 2002), suggesting that the lack of reduced island pollinator service on the Channel Islands is not only due to the attractiveness of *N. glauca*.

Although visitation to *N. glauca* was not significantly different among sites, measures of successful pollination were, in the opposite direction than predicted. Very few studies have determined whether island-mainland differences in pollinator service translate into reproductive success differences. Lower island fruit or seed set has been documented for one specialized tropical bird-pollinated plant (Linhart and Feinsinger, 1980) and for both a generalized and a specialized insect-pollinated plant, the latter only in one year (Spears, 1987). Pollen-limitation to reproductive success, which distinguishes between the effect of pollinators and resources on island plant success, was only measured by Spears (1987), who detected it in island plants only in one year and only for a specialized species. Thus, my results and previous studies highlight the need to directly test the assumption that plant reproductive

success is reduced on islands because of inadequate pollinator service.

Selection for self-pollination—Removing anthers within a flower completely eliminates the potential for within-flower self-pollination and thus should have a significant effect on plants that rely on selfing as a reproductive assurance mechanism (Schoen and Lloyd, 1992). My results instead indicate that *N. glauca* is facultatively xenogamous (Cruden and Lyon, 1989) and does not rely heavily on autonomous and facilitated self-pollination, especially on the islands. These results are consistent with phenotypic selection studies in which I failed to detect negative selection on stigma–anther distance on islands (Schueller, 2002).

While a few experimental emasculation experiments have documented benefits of self-pollination in selfing species (Motten, 1982; Piper et al., 1986), the majority have not (Bernhardt, 1976; Cruden and Lyon, 1989; Leclerc-Potvin and Ritland, 1994; Klips and Snow, 1997; Eckert and Schaefer, 1998), even in species with ornate self-pollination mechanisms (Nagy et al., 1999). To my knowledge this is the first study to directly quantify the reproductive assurance benefit of selfing in island populations. Thus, it is especially interesting that not only did I find a lack of the expected benefit of selfing on islands, but the tendency of a benefit on the mainland. This does not reject the idea that selfing provides reproductive assurance for at least some island plants but highlights that established plants in systems without the absence of major pollinators—which may be a common situation, even in isolated islands—may not benefit from selfing.

Patterns related to time since colonization—Selfing traits appear to be most developed where *N. glauca* has most recently colonized. Santa Cruz Island, the most recently colonized island, has the smallest mean and variance in stigma-anther distance, the highest selfing ability, and the highest proportion of crumpled flowers. Santa Catalina Island, which was colonized approximately 70 yr prior to CRU, exhibits fewer selfing traits than CRU, but more than either mainland site, where *N. glauca* has been the longest (though still relatively recently). Even differences on the mainland, where *N. glauca* is thought to have had a south to north expansion (Harris, 1966), correspond with colonization history: though not statistically different, the northern site, SED, tends to have smaller mean stigma–anther distance and higher selfing ability than the southern site, STA.

The mechanism of selfing (''mode,'' sensu Lloyd, 1992; Lloyd and Schoen, 1992) for other island plants also suggests that selfing traits are a vestige of the filter to colonization in established populations. On the Juan Fernandez Islands, for example, endemic plants are largely self-compatible but not capable of autonomous pollination (Anderson et al., 2001). Original colonists may have been self-compatible and autogamous, and while it is implausible to reestablish complex self-incompatibility systems (Baker, 1967; Carlquist, 1974; Ehrendorfer, 1979), autogamy can be decreased by increased separation of the stigma and anthers in space (herkogamy) or time (dichogamy). Carlquist (1965, p. 266) also argues that while self-pollination is ''a successful scheme for initial establishment . . . over long periods of time it would be a poor recipe for survival,'' and thus selection for outcrossing mechanisms is believed to occur after establishment (Ehrendorfer, 1979; Barrett, 1996). Alternatively, traits favoring outcrossing, such

as dichogamy, herkogamy, and heterostyly, are not the product of selection against selfing once established, but mechanisms to reduce pollen discounting (loss) from geitonogamy (Harder and Barrett, 1995), especially in self-compatible plants with large floral displays (Bernardello et al., 2001), such as *N. glauca*. Whatever the cause of loss of selfing traits on islands, it appears that the advantage of selfing may be only, or primarily, associated with the colonization event. After a population becomes established and has enough mates and is attracting island pollinators, as is the case for *N. glauca* on the Channel Islands, self-pollination is not required for successful reproduction.

Alternative explanations for island self-pollination patterns—Selfing may arise and be maintained in island populations simply because of relaxed selection against it. If plants on islands start from a few individuals, then island selfing rates will be high (simply by crossing with closely related individuals or through pollinator-facilitated selfing), resulting in more homogeneous inbred island populations. Thus, the relative fitness of a selfer on islands would not be much lower than its neighbors, and selfers may perpetuate more easily than on the mainland, where it competes with outcrossers. Further investigation of selfing rates and levels of genetic variance and inbreeding depression in island and mainland populations under field conditions (see Barrett, 1996) are necessary to test this hypothesis.

I also cannot exclude the possibility that *N. glauca* selfing patterns are simply a product of drift. The narrow variance in stigma–anther distance on CRU may reflect the genetic bottleneck event of colonization, and the high incidence of crumpled flowers may be a case of random fixation of recessive alleles (as in island patterns of abnormal tepal development in *Eichhornia paniculata*; see Barrett, 1996).

Conclusions—Several studies have inferred (Schemske et al., 1978; Motten, 1982; Rathcke and Real, 1983; Fenster and Ritland, 1994) and fewer have quantified (Fausto et al., 2001) a negative correlation between pollinator service and the capacity for self-pollination among populations. On islands, the relationship between pollinator scarcity and plant selfing is largely inferred, because of the lack of a mainland comparison (Carlquist, 1974; Anderson et al., 2001). Existing island–mainland comparisons of individual plant species breeding systems support the reproductive assurance hypothesis in some cases (Inoue, 1988; Barrett et al., 1989; Barrett and Husband, 1990), but not others (Spears, 1987), or lack explicit data on pollination, necessary to test this hypothesis (Larson and Barrett, 1998).

My results do not support the hypothesis that an increased ability to self-pollinate arises because of inadequate pollinator service to established island populations. Instead, my results suggest that a filter on nonselfers during colonization is likely to be more important, as well as possibly neutral and selective processes unrelated to pollinator conditions on islands.

LITERATURE CITED

ALLISON, P. D. 1999. Logistic regression using the SAS System: theory and application. SAS Institute, Cary, North Carolina, USA.

ANDERSON, G. J., G. BERNARDELLO, T. F. STUESSY, AND D. J. CRAWFORD. 2001. Breeding system and pollination of selected plants endemic to Juan Fernandez Islands. *American Journal of Botany* 88: 220–233.

BAKER, H. G. 1955. Self-compatibility and establishment after "long-distance" dispersal. *Evolution* 9: 347–349.

BAKER, H. G. 1967. Support for Baker's law—as a rule. *Evolution* 21: 853–856.

BARRETT, S. C. H. 1996. The reproductive biology and genetics of island plants. *Philosophical Transactions of the Royal Society of London B* 351: 725–733.

BARRETT, S. C. H., AND B. C. HUSBAND. 1990. Variation in outcrossing rate in *Eichhornia paniculata*: the role of demographic and reproductive factors. *Plant Species Biology* 5: 41–56.

BARRETT, S. C. H., M. T. MORGAN, AND B. C. HUSBAND. 1989. The dissolution of a complex genetic polymorphism—the evolution of self-fertilization in tristylous *Eichhornia paniculata* (Pontederiaceae). *Evolution* 43: 1398–1416.

BARRETT, S. C. H., AND J. S. SHORE. 1987. Variation and evolution of breeding systems in the *Turnera ulmifolia* complex (Turneraceae). *Evolution* 41: 340–354.

BELAOUSSOFF, S., AND J. S. SHORE. 1995. Floral correlates and fitness consequences of mating-system variation in *Turnera ulmifolia*. *Evolution* 49: 545–556.

BERNARDELLO, G., G. J. ANDERSON, T. F. STUESSY, AND D. J. CRAWFORD. 2001. A survey of floral traits, breeding systems, floral visitors, and pollination systems of the angiosperms of the Juan Fernandez Islands (Chile). *Botanical Review* 67: 255–308.

BERNHARDT, P. 1976. The pollination ecology of *Hepatica acutiloba* DC (Ranunculaceae). *Bulletin of the Torrey Botanical Club* 103: 155–158.

CARLQUIST, S. 1965. Island life: a natural history of the islands of the world. Natural History Press, New York, New York, USA.

CARLQUIST, S. 1966. The biota of long-distance dispersal. IV. Genetic systems in the floras of oceanic islands. *Evolution* 20: 443–455.

CARLQUIST, S. 1974. Island biology. Columbia University Press, New York, New York, USA.

CARR, G. D., AND E. A. POWELL. 1986. Self-incompatibility in the Hawaiian Madiinae (Compositae): an exception to Baker's Rule. *Evolution* 40: 430–434.

COLWELL, R. K., AND E. R. FUENTES. 1975. Experimental studies of the niche. *Annual Review of Ecology and Systematics* 6: 281–310.

COMPTON, S. G., S. J. ROSS, AND I. W. B. THORNTON. 1994. Pollinator limitation of fig tree reproduction on the island of Anak Krakatua (Indonesia). *Biotropica* 26: 180–186.

CRUDEN, R. W., AND D. L. LYON. 1989. Facultative xenogamy: examination of a mixed mating system. *In* J. H. Bock and Y. B. Linhart [eds.], The evolutionary ecology of plants, 171–208. Westview Press, Boulder, Colorado, USA.

DAEHLER, C. C. 1998. Variation in self-fertility and the reproductive advantage of self-fertility for an invading plant (*Spartina alterniflora*). *Evolutionary Ecology* 12: 553–568.

DARWIN, C. 1876. The effects of cross- and self-fertilization in the vegetable kingdom. John Murray, London, UK.

DIGGLE, P. J., K. Y. LIANG, AND S. ZEGER. 1994. Analysis of longitudinal data. Oxford University Press, New York, New York, USA.

ECKERT, C. G., AND A. SCHAEFER. 1998. Does self-pollination provide reproductive assurance in *Aquilegia canadensis* (Rananculaceae)? *American Journal of Botany* 85: 919–924.

EHRENDORFER, F. 1979. Reproductive biology in island plants. *In* D. Bramwell [ed.], Plants and islands, 293–306. Academic Press, London, UK.

FAUSTO, J. A., V. M. ECKHART, AND M. A. GEBER. 2001. Reproductive assurance and the evolutionary ecology of self-pollination in *Clarkia xantiana* (Onagraceae). *American Journal of Botany* 88: 1794–1800.

FEINSINGER, P., AND L. SWARM. 1982. "Ecological release," seasonal variation in food supply, and the hummingbird *Amazilia tobaci* on Trinidad and Tobago. *Ecology* 63: 1574–1578.

FEINSINGER, P., J. WOLFE, AND L. SWARM. 1982. Island ecology: reduced hummingbird diversity and the pollination biology of plants, Trinidad and Tobago, West Indies. *Ecology* 63: 494–506.

FENSTER, C. B., AND K. RITLAND. 1994. Evidence for natural selection on mating system in *Mimulus* (Scrophulariaceae). *International Journal of Plant Science* 155: 588–596.

GARDNER, R. O., AND J. W. EARLY. 1996. The naturalisation of banyan figs (*Ficus* spp., Moraceae) and their pollinating wasps (Hymenoptera: Agaonidae) in New Zealand. *New Zealand Journal of Botany* 34: 103–110.

GARRETT, K., AND J. DUNN. 1981. Birds of Southern California: status and distribution. Los Angeles Audubon Society, Los Angeles, California, USA.

GOODSPEED, T. H. 1954. The genus *Nicotiana*. Chronica Botanica, Waltham, Massachusetts, USA.

HARDER, L. D., AND S. C. H. BARRETT. 1995. Mating cost of large floral displays in hermaphroditic plants. *Nature* 373: 512–515.

HARRIS, D. R. 1966. Recent plant invasions in the arid and semi-arid southwest of the United States. *Association of American Geographers Annals* 56: 408–422.

HERNANDEZ, H. 1981. Sobre la ecologia reproductiva de *Nicotiana glauca* Grah.: una maleza de distribucion cosmopolita. *Boletin de la Sociedad Botanica de Mexico* 41: 47–73.

HOWARTH, F. G., AND W. P. MULL. 1992. Hawaiian insects and their kin. University of Hawaii Press, Honolulu, Hawaii, USA.

HUSBAND, B. C., AND D. W. SCHEMSKE. 1996. Evolution of the magnitude and timing of inbreeding depression in plants. *Evolution* 50: 54–70.

INOUE, K. 1988. Patterns of breeding-system change in the Izu Islands in *Campanula punctata*: bumblebee-absence hypothesis. *Plant Species Biology* 3: 125–128.

INOUE, K. 1990. Evolution of mating systems in island populations of *Campanula microdentata*: pollinator availability hypothesis. *Plant Species Biology* 5: 57–64.

INOUE, K., AND M. AMANO. 1986. Evolution of *Campanula punctata* Lam. in the Izu Islands: changes of pollinators and evolution of breeding systems. *Plant Species Biology* 1: 89–97.

INOUE, K., M. MAKI, AND M. MASUDA. 1996. Evolution of *Campanula* flowers in relation to insect pollinators on islands. *In* D. Lloyd and S. Barrett [eds.], Floral biology: studies on floral evolution in animal-pollinated plants. Chapman and Hall, New York, New York, USA.

JAIN, S. K. 1976. The evolution of inbreeding in plants. *Annual Review of Ecology and Systematics* 7: 469–469.

JOHNSON, N. K. 1972. Origin and differentiation of the avifauna of the Channel Islands, California. *Condor* 74: 295–315.

JONES, H. L., AND P. W. COLLINS. In press. Birds of California's Channel Islands: their status and abundance. Santa Barbara Museum of Natural History, Santa Barbara, California, USA.

JUNAK, S., T. AYERS, R. SCOTT, D. WILKEN, AND D. YOUNG. 1995. A flora of Santa Cruz Island. Santa Barbara Natural History Museum, Santa Barbara, California, USA.

KARRON, J. D., R. T. JACKSON, N. N. THUMSER, AND S. L. SCHLICHT. 1997. Outcrossing rates of individual *Mimulus ringens* genets are correlated with anther–stigma separation. *Heredity* 79: 365–370.

KLIPS, R. A., AND A. A. SNOW. 1997. Delayed autonomous self-pollination in *Hibiscus laevis* (Malvaceae). *American Journal of Botany* 84: 48–53.

LARSON, B. M. H., AND S. C. H. BARRETT. 1998. Reproductive biology of island and mainland populations of *Primula mistassinca* (Primulaceae) on Lake Huron shorelines. *Canadian Journal of Botany* 76: 1819–1827.

LECLERC-POTVIN, C., AND K. RITLAND. 1994. Modes of self-fertilization in *Mimulus guttatus* (Scrophulariaceae): a field experiment. *American Journal of Botany* 81: 199–205.

LINHART, Y., AND P. FEINSINGER. 1980. Plant–hummingbird interactions: effects of island size and degree of specialization on pollination. *Journal of Ecology* 68: 745–760.

LITTLE, R. C., G. A. MILLIKEN, W. W. STROUP, AND R. D. WOLFINGER. 1996. SAS system for mixed models. SAS Institute, Cary, North Carolina, USA.

LLOYD, D. G. 1985. Progress in understanding the natural history of New Zealand plants. *New Zealand Journal of Botany* 23: 707–722.

LLOYD, D. G. 1992. Self- and cross-fertilization in plants. II. The selection of self-fertilization. *International Journal of Plant Science* 153: 370–380.

LLOYD, D. G., AND D. J. SCHOEN. 1992. Self- and cross-fertilization in plants. I. Functional dimensions. *International Journal of Plant Science* 153: 358–369.

MACARTHUR, R. H., J. M. DIAMOND, AND J. R. KARR. 1972. Density compensation in island faunas. *Ecology* 53: 330–342.

MACARTHUR, R. H., AND E. O. WILSON. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

MAJOR, J. 1977. California climate in relation to vegetation. *In* M. G. Barbour and J. Major [eds.], Terrestrial vegetation of California, 11–74. Wiley, New York, New York, USA.

MCMULLEN, C. K. 1987. Breeding systems of selected Galapagos Islands angiosperms. *American Journal of Botany* 74: 1694–1705.

McMULLEN, C. K. 1993. Flower-visiting insects of the Galapagos Islands. *Pan-Pacific Entomologist* 69: 95–106.

MILLSPAUGH, C. F., AND L. W. NUTTALL. 1923. Flora of Santa Catalina Island. Field Museum of Natural History Publication No. 212: 1–413.

MITCHELL, D. E. 2000. Allen's Hummingbird (*Selasphorus sasin*). *In* A. Poole and F. Gill [eds.], The birds of North America, No. 501. The Birds of North America, Philadelphia, Pennsylvania, USA.

MOTTEN, A. F. 1982. Autogamy and competition for pollinators in *Hepatica americana* (Ranunculaceae). *American Journal of Botany* 69: 1296–1305.

MOTTEN, A. F., AND J. L. STONE. 2000. Heritability of stigma position and the effect of stigma–anther separation on outcrossing in a predominantly self-fertilizing weed, *Datura stramonium* (Solanaceae). *American Journal of Botany* 87: 339–347.

MÜLLER, H. 1883. The fertilisation of flowers. Macmillan, London, UK.

NAGY, E. S., L. STRONG, AND L. F. GALLOWAY. 1999. Contribution of delayed autonomous selfing to reproductive success in mountain laurel, *Kalmia latifolia* (Ericaceae). *American Midland Naturalist* 142: 39–46.

PHILBRICK, R. N. 1980. Distribution and evolution of endemic plants of the California islands. *In* D. M. Power [ed.], The California islands: proceedings of a multidisciplinary symposium, 173–188. Santa Barbara Museum of Natural History, Santa Barbara, California, USA.

PHILBRICK, R. N., AND J. R. HALLER. 1977. The southern California islands. *In* M. G. Barbour and J. Major [eds.], Terrestrial vegetation of California, 893–906. Wiley, New York, New York, USA.

PIPER, J. G., B. CHARLESWORTH, AND D. CHARLESWORTH. 1986. Breeding system evolution in *Primula vulgaris* and the role of reproductive assurance. *Heredity* 56: 207–217.

POWER, D. M. 1980. The California islands: proceedings of a multidisciplinary symposium. Santa Barbara Museum of Natural History, Santa Barbara, California, USA.

PYLE, P. 1997. Identification guide to North American birds: a compendium of information on identifying, ageing, and sexing "near-passerines" and passerines in the hand. Slate Creek Press, Bolinas, California, USA.

RATHCKE, B., AND L. REAL. 1983. Autogamy and inbreeding depression in mountain laurel, *Kalmia latifolia* (Ericaceae). *American Journal of Botany* 80: 143–146.

RICK, C. M. 1966. Some plant–animal relations on the Galapagos Islands. *In* R. I. Bowman [ed.], The Galapagos. University of California Press, Berkeley, California, USA.

ROUBIK, D. W., N. HOLBROOK, AND G. PARRA. 1985. Roles of nectar robbers in reproduction of the tropical treelet *Quassia amara* (Simaroubaceae). *Oecologia* 66: 161–167.

RUSSELL, S. M. 1996. Anna's Hummingbird (*Calypte anna*). *In* A. Poole and F. Gill [eds.], The birds of North America, No. 226. The Birds of North America, Philadelphia, Pennsylvania, USA.

SAKAI, A., W. L. WAGNER, D. M. FERGUSON, AND D. R. HERBST. 1995. Biogeographical and ecological correlates of dioecy in the Hawaiian flora. *Ecology* 76: 2530–2543.

SAS INSTITUTE. 1999. SAS/STAT user's guide, version 8. SAS Institute, Cary, North Carolina, USA.

SAUER, J. D. 1988. Plant migration: the dynamics of geographic patterning in seed plant species. University of California Press, Los Angeles, California, USA.

SCHEMSKE, D. W., M. F. WILLSON, M. N. MELAMPY, L. J. MILLER, L. VERNER, K. SCHEMSKE, AND L. B. BEST. 1978. Flowering ecology of some spring woodland herbs. *Ecology* 59: 351–366.

SCHOEN, D. J., AND D. G. LLOYD. 1992. Self and cross-fertilization in plants III. Methods for studying modes and functional aspects of self-fertilization. *International Journal of Plant Sciences* 153: 381–393.

SCHOENHERR, A. 1999. Natural history of the islands of California. University of California Press, Berkeley, California, USA.

SCHUELLER, S. K. 2002. Hummingbird pollination and floral evolution of introduced *Nicotiana glauca* and native *Epilobium canum*: California island-mainland comparisons. Ph.D. dissertation, University of Michigan, Ann Arbor, Michigan, USA.

SHANAHAN, M., R. D. HARRISON, R. YAMUNA, W. BOEN, AND I. W. B. THORNTON. 2001. Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. V. Colonization by figs (*Ficus* spp.), their dispersers and pollinators. *Journal of Biogeography* 28: 1365–1377.

SPEARS, E. E. 1983. A direct measure of pollination effectiveness. *Oecologia* 57: 196–199.

SPEARS, E. E. 1987. Island and mainland pollination ecology of *Centrosema virginianum* and *Opuntia stricta*. *Journal of Ecology* 75: 351–362.

STEBBINS, G. L. 1957. Self-fertilization and population variability in the higher plants. *American Naturalist* 91: 337–354.

STILES, F. G. 1973. Food supply and the annual cycle of the Anna Hummingbird. *University of California Publications in Zoology* 97: 1–109.

STRID, A. 1969. Evolutionary trends in breeding system of *Nigella* (Ranunculaceae). *Botaniska Notiser* 122: 380–397.

TAKEBAYASHI, N., AND L. F. DELPH. 2000. An association between a floral trait and inbreeding depression. *Evolution* 54: 840–846.

THORNTON, I. W. B., S. COOK, J. S. EDWARDS, R. D. HARRISON, C. SCHIPPER, M. SHANAHAN, R. SINGADAN, AND R. YAMUNA. 2001. Colonization of an island volcano, Long Island, Papua New Guinea, and an emergent island, Motmot, in its caldera lake. VII. Overview and discussion. *Journal of Biogeography* 28: 1389–1408.

WEBB, C. J., AND D. KELLY. 1993. The reproductive biology of the New Zealand flora. *Trends in Ecology and Evolution* 8: 442–447.

WILLIAMSON, M. H. 1981. Island populations. Oxford University Press, Oxford, UK.

WOODELL, S. R. 1979. The role of unspecialized pollinators in the reproductive success of Aldabran plants. *Philosophical Transactions of the Royal Society of London B* 286: 99–108.

WOODS, R. S. 1927. Hummingbirds of California: comments on their habitats and characteristics. *Auk* 44: 297–318.