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Trends in reproductive success of Hawaiian seabirds: is guild membership a good criterion for choosing indicator species?

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Abstract

Because it is rarely possible to monitor all species that occur in sensitive or threatened ecosystems, much theoretical consideration has been given to the process of choosing indicator species. We evaluated whether foraging guild classification or nest site might be an adequate means to select indicator species for monitoring the reproductive success of a suite of Hawaiian seabird species. We examined the reproductive success of six species representing three foraging guilds and two types of nest sites over an 18-year period. For two of the three foraging guilds, there was a strong correlation between the reproductive success of birds from the same guild, and there was a weaker correlation for the third guild. In contrast, there were no significant reproductive success correlations for pairs of species from different foraging guilds but with the same nest sites. Thus, the within-guild correlations are likely to be driven by guild-specific food availability rather than by similarity in nest site. Because of the weak nature of one of the within-guild correlations, and because there is little detailed information on the causes of nest failure in this system, we recommend continuing to monitor multiple indicator species per foraging guild. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Monitoring populations of long-lived species for conservation can be difficult and expensive. For such species, the detection of moderate population declines requires many years of monitoring (Bart and Robson, 1995; Gerber et al., 1999), and, because these species typically have low annual reproductive output (Stearns, 1992), population recoveries are likely slow even after management actions correct the factor(s) causing declines. An alternative approach to attempting to monitor population trends is to monitor reproductive success. Because reproductive success can exhibit rapid changes in response to biotic and abiotic factors (Rotenberry and Wiens, 1991), such a monitoring approach can enable researchers to detect environmental problems prior to the onset of severe population declines.

For areas in which entire ecosystems are considered sensitive or threatened, it is often not logistically or financially possible to monitor all species that may be of conservation concern. As a consequence, a great deal of theoretical work has focused on the process of choosing indicator species (Landres et al., 1988; Noss, 1990; Hilty and Merenlender, 2000). For a monitoring program designed to measure reproductive success, indicator species should be selected on the likelihood that reproductive success is determined by the same external factors as that of species of concern that are not being monitored. In many species of birds, food availability is a primary determinant of reproductive output (Martin, 1987). For this reason, classical ecology has emphasized the role of food in avian life history by organizing communities into guilds of species with similar food requirements or foraging methods (Root, 1967; Holmes et al., 1979; Faaborg, 1985). If there is conservation concern about a suite of long-lived bird species, it may be effective to build a monitoring program using indicator species that are selected based upon their foraging guilds. A second possible criterion upon which to base

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the choice of avian indicator species is nest site. Nest site may directly affect reproductive success if either nest predation or weather-mediated nest failure is related to nest location.

Seabirds are the subject of increasing conservation concern, in part because their limited breeding habitat is so crucial to population viability (Harrison et al., 1984) and in part because seabirds are thought to be suffering from increasingly pronounced impacts of commercial fisheries (Croxall et al., 1984; Croxall, 1987; Melvin et al., 1999). As most seabird species are long-lived, monitoring programs that are based on reproductive success may be preferable to those based on population trends. Experimental studies of seabirds have shown that adult body condition, which is dependent upon food availability, can govern reproductive effort and/or reproductive success (Erickstad et al., 1997; Tverra et al., 1997; Dearborn, 2001). Other studies have used between-year variation in food availability (Anderson et al., 1982; Duffy, 1983; Safina et al., 1988; Murphy et al., 1991) and within-year geographic variation in food availability (Monaghan et al., 1989) to demonstrate a link between food availability and seabird reproductive success. Because seabird species specialize on particular prey items or foraging areas, there exists the potential for seabird reproductive success to be heavily impacted by changes in the availability of a narrow class of prey items. For example, Monaghan et al. (1989) found that an episode of low reproductive success at an arctic tern, *Sterna paradisaea*, colony coincided with reduced availability of 4–8 cm sandeels, *Ammodytes marinus*, a prey type that normally comprised a large part of the food fed to arctic tern chicks.

Reproductive success of seabirds may also be affected by general nest location. Some seabird species nest in trees and shrubs, others nest on the ground, and others nest underground in burrows or talus piles. Some members of a foraging guild have common nest sites, and general nest site location may contribute to reproductive success in a manner that prevents guild membership per se from being a useful predictor of reproductive success. For example, in the western Aleutian Islands, common ravens, *Corvus corax*, prey upon eggs of common murres, *Uria aalge*, and thick-billed murres, *Uria lomvia*, which nest on exposed cliff ledges, but not upon eggs of horned puffins, *Fratercula corniculata*, or tufted puffins, *Fratercula cirrhata*, which nest in rock crevices and burrows (V. Byrd, US Fish and Wildlife Service, unpublished data). In the absence of nest predators, weather can create interspecific patterns in nest success by causing nest failure at one type of nest site but not another. For example, strong winds may cause the failure of nests in shrubs without affecting ground nests or burrow nests, and high surf or heavy rain may flood ground nests without affecting shrub nests.

In this paper, we explore the appropriateness of using indicator species to monitor the reproductive success of a suite of long-lived seabird species. By examining the correlation between the reproductive success of within-guild species pairs, we will test whether one member of a foraging guild might serve as an indicator species for the reproductive success of other members of its guild. To test whether nest location, rather than food availability, is a main determinant of reproductive success, we also examine the correlation between reproductive success of birds with same nest sites. Lastly, we test whether there has been an overall decline in reproductive success for this suite of Hawaiian seabird species over the years that they have been monitored.

2. Methods

2.1. Study area and seabird community

We examined the reproductive success of seabirds on Tern Island, in the Hawaiian Islands National Wildlife Refuge (NWR), from 1980 to 1998. The Hawaiian Islands NWR encompasses a chain of small islands extending 1400 km northwest from the main Hawaiian Islands. The small land area of these islands is dominated by the breeding activity of 18 species of seabirds. Tern Island (23° 50′ N, 166° 10′ W) is a 14-ha island located in French Frigate Shoals, roughly in the midpoint of the Hawaiian Archipelago. Seabird monitoring on Tern Island began in 1979, when the island was returned to US Fish and Wildlife Service control following its use by the US Navy and the US Coast Guard. Currently, Tern Island is roughly 1 km by 200 m, with the middle third maintained as a sand and crushed-coral runway. The majority of the island is dominated by a mix of shrubs (primarily *Tournefortia argentea*), small vascular plants (including *Chenopodium oahuense*, *Portulaca* spp., *Ipomea pes-caprae*, *Lepturus repens*, and *Boerhavia repens*), and open sandy areas. Approximately 200,000 individuals of 16 seabird species breed on Tern Island. See Amerson (1971) and Harrison et al. (1984) for more details.

The seabirds of Tern Island are long-lived: the range of maximum recorded lifespan is 10 years for Christmas shearwater, *Puffinus nativitatis*, to 42 years for Laysan albatross, *Diomedea immutabilis* (US Fish and Wildlife Service, unpublished data). As a consequence, moderate declines in population size would take many years of monitoring to detect. Furthermore, accurate estimates of population size can be made difficult by daily and seasonal variation in colony attendance (e.g. Weidinger, 1996). For these reasons, monitoring efforts have focused primarily on measures of reproductive success.

The choice of species for monitoring on the Hawaiian Islands NWR was based in part on foraging guilds (US Fish and Wildlife Service, 1983, 1985). The seabird community in this refuge is composed of five foraging guilds, as determined by a comprehensive study of foraging observations and identification of prey from stomach samples (Harrison et al., 1983): (1) the albatrosses, consisting of the Laysan albatross and black-footed albatross, *D. nigripes*; (2) the Pelecaniformes, consisting of the red-footed booby, *Sula sula*, masked booby, *S. dactylatra*, brown booby, *S. leucogaster*, red-tailed tropicbird, *Phaethon rubricauda*, and great frigatebird, *Fregata minor*; (3) the tuna birds, consisting of the sooty tern, *Sterna fuscata*, brown noddy, *Anous stolidus*, black noddy, *A. minutus*, white tern, *Gygis alba*, wedge-tailed shearwater, *Puffinus pacificus*, and Christmas shearwater; (4) the nocturnal petrels, consisting of the Bonin petrel, *Pterodroma hypoleuca*, Bulwer's petrel, *Bulweria bulwerii*, and Tristram's storm-petrel, *Oceanodroma tristrami*; and (5) the neuston-feeding terns, consisting of the blue-gray noddy, *Procelsterna cerulea*, and the gray-backed tern, *Sterna lunata*.

Within foraging guilds, species have been chosen for monitoring on Tern Island based upon ease of monitoring and upon width of breeding range, with species ranging throughout the Hawaiian Islands NWR being of high monitoring priority. Six species within three foraging guilds have been the subject of long-term reproductive success monitoring on Tern Island: the Laysan albatross and black-footed albatross within the albatross guild; the red-footed booby and red-tailed tropicbird in the Pelecaniformes guild; and the black noddy and white tern within the tuna bird guild. These species nest either on the ground (tropicbird and the albatrosses) or in shrubs (black noddy, white tern, and red-footed booby) on Tern Island (Table 1).

2.2. Monitoring and analyzing reproductive success

Reproductive success in this study is defined as the probability that an egg survives through the fledging of the chick (i.e. chicks fledged per egg laid); because these six species have one-egg clutches, this measure is also equivalent to chicks fledged per breeding attempt. The methods and history of monitoring vary by species. For both albatross species, individuals lay a single egg per year, and egg-laying is quite synchronous. When a nest fails, the pair does not make a second breeding attempt. Thus, the number of albatross nesting attempts on Tern Island can be estimated by making a single island-wide count of eggs after the peak of egg-laying. The number of chicks that fledge was determined by banding all chicks and then subtracting the number of banded chicks subsequently found dead. Dead banded chicks are inevitably found for three reasons: (1) chick carcasses are easy to see because chicks are very large at banding age; (2) there are no predators of these chicks, so dead chicks do not disappear; and (3) the island is small, and researchers actively look for dead banded birds in the course of conducting all fieldwork. Furthermore, banding is conducted just prior to fledging, and most chick mortality occurs when chicks are young.

For the remaining four species, egg-laying is less synchronous and individuals are capable of multiple breeding attempts per year, necessitating a different approach to monitoring reproductive success. For these species, nests were monitored in study plots that encompassed a subset of all of the nests on the island. In these plots, new nests were flagged and then checked on a regular basis to determine the number of nests that failed prior to fledging. Chicks were banded as they approached fledging, and all dead chicks found anywhere on the island were recorded; this insured that any movements of old chicks into or out of the study plots prior to fledging would not affect measures of reproductive success. In most years, plots were checked every 2 days, but in some years, nest checks were made every day or every 3 days.

Prior to 1995, all study plots were chosen subjectively, and locations of plots were changed several times. In 1995, new permanent study plots were randomly established for black noddies, red-footed boobies, and red-tailed tropicbirds (Dearborn and Anders, 1996). The plots currently in use for white terns were subjectively chosen, but the same plots have been used since 1992. These plots encompass a large block of natural shrub habitat and several buildings where terns nest on divots chiseled in the window ledges. All white tern nests on buildings were excluded from the analyses in this paper.

Egg-laying occurs primarily in spring for red-footed boobies and red-tailed tropicbirds and from winter through spring for white terns. In contrast, black noddy

Table 1
Reproductive success was measured annually for six species from three foraging guilds and two nest sites

Species	Guild	Nest site	Years of data	Nests monitored per year[a]
Laysan albatross	Albatross	Ground (bare)	1980–1998	1204 (505–1987)
Black-footed albatross	Albatross	Ground (bare)	1981–1998	637 (96–1519)
Red-tailed tropicbird	Pelecaniform	Ground (sheltered)	1980–1982, 1984–1998	242 (60–480)
Red-footed booby	Pelecaniform	Shrub (nest)	1981–1998	320 (49–757)
White tern	Tuna birds	Shrub (branch)	1980–1982, 1989–1998	76 (36–111)
Black noddy	Tuna birds	Shrub (nest)	1980–1998	690 (595–797)

[a] Number of nests monitored per year are given as mean (range).

breeding is relatively continuous in some years; thus, 'yearly' measures of reproductive success for black noddies are frequently determined by calendar year cutoffs.

In years for which data are available, study plots have typically included 25–40% of all nesting attempts on the entire island (range 20–100%). The randomly-chosen permanent study plots that were delineated in 1995 for black noddies, red-footed boobies, and red-tailed tropicbirds encompass approximately 20–30% of all nests of those species on the island.

We used Pearson correlation analyses to test for positive relationships among the within-year reproductive success of birds that were from the same foraging guild or that had similar nest sites. To provide a clear test of which factor(s) influenced reproductive success, we computed six different types of pairwise correlations: species in the same foraging guild (regardless of nest site), species with the same nest sites (regardless of foraging guild), species that shared both foraging guild and nest site, species in the same foraging guild but with different nest sites, species with the same nest sites but different foraging guilds, and species that share neither foraging guild nor nest site. For each of these six groups, we calculated the Pearson correlation coefficient for each pair of species. We then averaged the correlation coefficients for all pairs within the group. Comparison of the average correlation for each group provides separate tests of the effects of foraging guild and nest site on reproductive success and provides a null model by examining the correlations between species that share neither factor.

We used linear regression to test for long-term declines in reproductive success of each species.

3. Results

Among the three pairs of species that shared a foraging guild, there was a highly significant between-species correlation in reproductive success for the albatross guild ($r = 0.751$, $n = 18$ years, $P < 0.001$) and for the Pelecaniform guild ($r = 0.669$, $n = 17$, $P = 0.003$); there was a weaker correlation in the tuna bird guild ($r = 0.526$, $n = 13$, $P = 0.065$; Fig. 1). In contrast, the average between-species correlation was low for species that shared the same type of nest site (Table 2). In particular, the correlation between species that shared nest sites but not foraging guilds (average $r = 0.0531$) was not substantially greater than the null model (i.e. the correlation between species that shared neither nest sites nor foraging guilds; average $r = 0.0162$).

We detected significant declines in reproductive success over time for the red-footed booby ($B = -0.0139$, $t = -3.36$, $P = 0.004$) and red-tailed tropicbird ($B = -0.0133$, $t = -2.26$, $P = 0.038$), and a probable decline

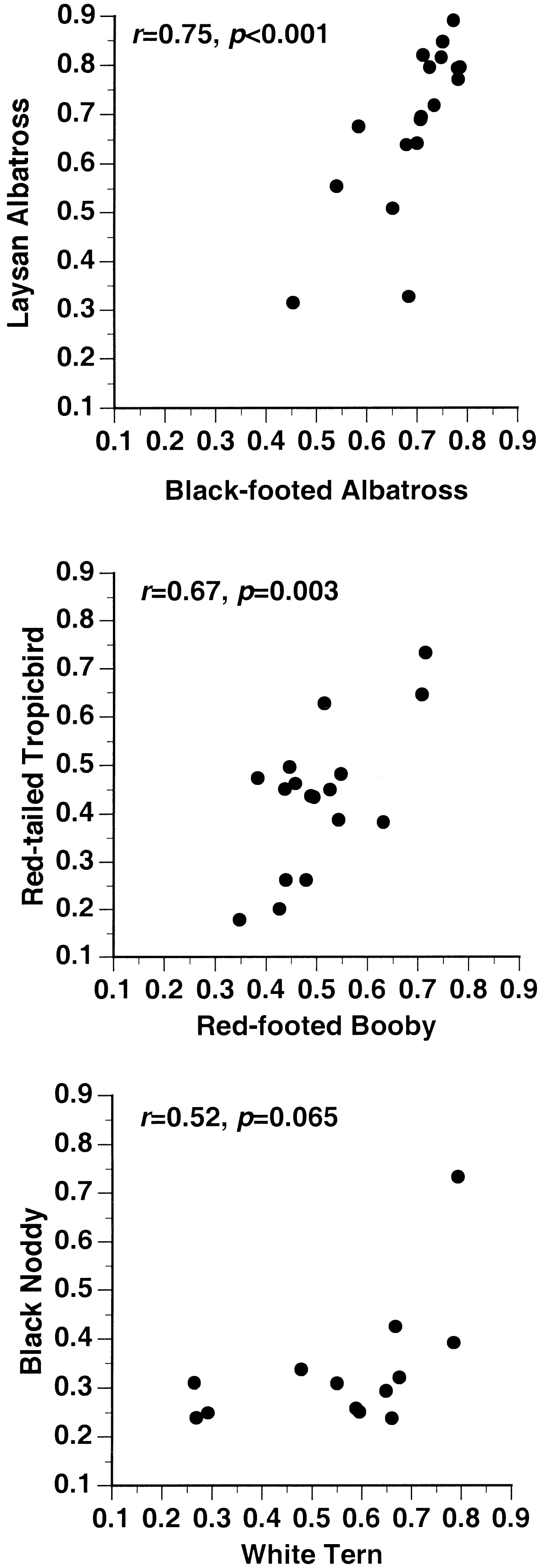

Fig. 1. Reproductive success correlations for species within the same foraging guild: albatrosses, Pelecaniformes, and tuna birds. Each point is a yearly estimate of reproductive success.

for the black noddy ($B = -0.0127$, $t = -2.08$, $P = 0.053$; Fig. 2). The reproductive success of the black-footed albatross showed a slight increase ($B = 0.009$, $t = 2.56$, $P = 0.021$), and there was no change in the reproductive success of the Laysan albatross ($B = 0.003$, $t = 0.45$, $P = 0.660$) or white terns ($B = -0.0045$, $t = -0.70$, $P = 0.499$).

4. Discussion

This study showed that the reproductive success of pairs of Hawaiian seabird species from the same foraging guild was correlated, particularly for the albatross guild and the Pelecaniform guild. This result is consistent with the notion that seabird reproductive success is tied to food availability, a hypothesis that has been supported for a variety of seabird species (Duffy, 1983; Safina et al., 1988; Montevecchi, 1993). The absence of between-guild within-nest-site correlations in this study rejects the alternate explanation that nest site similarity drives the within-guild correlations that we observed: the reproductive success of species with same nest sites but belonging to different foraging guilds exhibited a mean correlation that was roughly equivalent to the null model correlations between species that shared neither a nest site nor a foraging guild. Nest sites do have the potential to contribute to reproductive success in this system, as bouts of nest failure on Tern Island are sometimes caused by high surf washing over ground nests but not affecting shrub nests (personal observation), but the lack of between-guild within-nest-site correlations in our study suggests that such events are not primary determinants of island-wide reproductive success over the course of a breeding season for these seabirds.

The most likely explanation for correlated annual reproductive success within foraging guilds of Hawaiian seabirds is that reproductive success of guild members is similarly affected by annual fluctuations in food availability (Harrison et al., 1983). However, there are two factors other than food availability that could account for within-foraging-guild correlations in reproductive success. First, there is generally higher overlap of breeding phenology within rather than between guilds (US Fish and Wildlife Service, unpublished data). Laysan and black-footed albatross egg-laying on Tern Island occurs within a span of roughly one month. Red-footed booby and red-tailed tropicbird phenologies overlap extensively with one another and with the phenologies of the other species within the Pelecaniformes guild. Black noddies and white terns may breed throughout much of the year. These two species, along with the other species in the tuna bird guild, exhibit the lowest level of within-guild breeding synchrony, and they exhibit the weakest within-guild correlation in reproductive success.

Table 2
Mean Pearson correlation coefficients for reproductive success of pairs of species grouped by similarity in foraging guild and nest site

Ecological similarity between species	No. of species pairs	Mean bivariate correlation (*r*)
Same foraging guild	3	0.6582
Same nest site	6	0.2871
Same foraging guild, same nest site	2	0.6527
Same foraging guild, different nest site	1	0.6691
Same nest site, different foraging guild	4	0.0531
Different foraging guild, different nest site	8	0.0162

Synchronous breeding phenology could produce a similarity in reproductive success in at least two ways. First, there could be discrete weather events (e.g. storms, extreme heat) that cause nest failure. Second, there could be short-term changes in the availability of a wide array of prey items (i.e. changes that would similarly affect the availability of food for all birds breeding at that time, regardless of guild membership); in this case, food availability would be driving the similarity in reproductive success within a guild not due to the direct effect of feeding on the same specific resource, but only because these particular pairs of species were breeding at the same time.

Phylogeny is a final factor that could account for the within-guild correlation in reproductive success. The within-guild species pairs that we studied are more closely related than the between-guild pairs. The extent to which species exhibit correlations in reproductive success could be an effect of some unidentified traits whose similarity is due to common ancestry.

5. Management recommendations

Results of this study indicate that reproductive success is correlated between seabird species within the same foraging guild, and thus that foraging guild may be a good criterion for choosing indicator species in this system. However, because correlations in reproductive success were weak among tuna bird guild members, and because within-guild correlations in reproductive success may be driven partly by similar breeding phenology, we recommend using at least two species within a foraging guild as reproductive success indicators for each guild. Future work should also focus on the causes of nest failure in order to improve our understanding of the mechanism of within-guild correlations.

Among the six seabird species examined here, we detected declines in reproductive success for red-footed boobies and red-tailed tropicbirds, a possible declining trend for black noddies, and a slight increase in reproductive success for black-footed albatrosses. As expected from the within-guild correlations, the two species

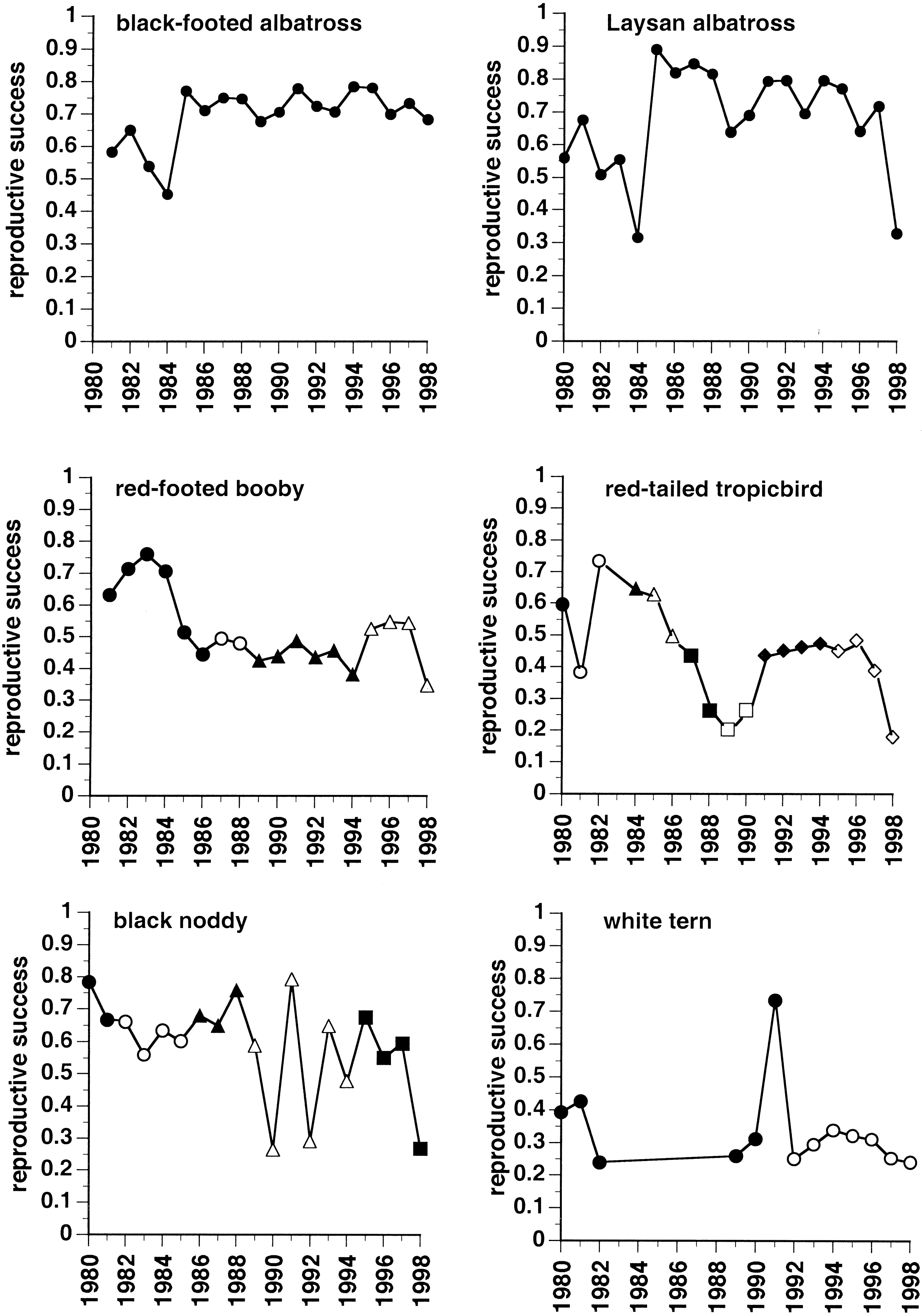

Fig. 2. Temporal trends in reproductive success for six seabird species monitored on Tern Island. Change in symbol indicates a change in either frequency of nest searches or nest checks or a change in location of study plot on the island.

showing pronounced declines were both in the same guild — Pelecaniformes. For both the red-footed booby and the red-tailed tropicbird, the decline was manifested as a fairly abrupt drop during the mid-1980s, rather than as a general long-term decrease (Fig. 2). It is not known whether this reflects a decline from historic levels or, alternately, a return to "normal" from a high level of reproductive success in the early 1980s. Many species experienced low reproductive success in 1998, and future monitoring will indicate whether this decline should be of management concern. Information obtained from continued monitoring will improve our ability to safeguard seabird populations and the marine environment on which they depend.

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