BREEDING BIOLOGY OF TRISTRAM'S STORM-PETREL *OCEANODROMA TRISTRAMI* AT FRENCH FRIGATE SHOALS AND LAYSAN ISLAND, NORTHWEST HAWAIIAN ISLANDS

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SUMMARY

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We investigated Tristram's Storm-Petrel *Oceanodroma tristrami* on Laysan Island and French Frigate Shoals, Northwest Hawaiian Islands, in the first detailed study of this species' breeding biology. Breeding extended through the boreal winter from mid-October to mid-June. The mean hatching success on Laysan Island was 0.35 in 2004 and 0.46 in 2005; on Tern Island, it was 0.53 in 2005 and 0.61 in 2006. Fledging success was 0.45, and breeding success 0.16 at Laysan in 2004. At Tern Island, mean fledging success during 2005–2008 was 0.48 (range: 0.47 to 0.51) and overall breeding success in 2005 and 2006 was 0.27 and 0.28 respectively. Egg abandonment was common at both locations, but no relationship was evident between abandonment and frequency of visits by researchers. In addition to abandonment, weather and competition with larger burrowing seabirds for nest sites affected breeding success. Tristram's Storm-Petrel appears to have a low reproductive rate compared with other storm-petrels, but whether the population is declining as a consequence is unknown. More research into demography and basic biology, including foraging niche, is recommended.

Key words: Tristram's Storm-Petrel, *Oceanodroma tristrami,* breeding biology, nesting success, population estimates, Hawaiian Islands

INTRODUCTION

Tristram's Storm-Petrel *Oceanodroma tristrami* is a large hydrobatid [up to 112 g (Marks & Leasure 1992)] that breeds only in the Northwest Hawaiian Islands and the Ogasawara archipelago of Japan. Likely never one of the more abundant seabirds in the Hawaiian Leeward Islands, the species was extirpated from Midway (Fisher & Baldwin 1946, Harrison 1990) and Kure (Rauzon *et al.* 1985) atolls by invasive rats (Black Rat *Rattus rattus* and Polynesian Rat *R. exulans* respectively). It has yet to re-establish colonies since rat removal in the late 1990s (B. Flint & C. Vanderlip pers. comm.), although one recent breeding attempt was recorded at Midway (Baker *et al.* 1997). Tristram's Storm-Petrel was also extirpated from several islands at French Frigate Shoals by human activity (Amerson 1971), but those islands have since been recolonized. In Japan, invasive mammals [Black Rat, Siberian Weasel *Mustela sibirica,* and domestic Cat *Felis catus* (Stattersfield *et al.* 1998)] now limit breeding to small predator-free islets in the Ogasawara archipelago, including Tadanaejima and Onbasejima off Kozushima (Slotterback 2002), Kojine off Hachijo of the Izu Islands (F. Sato pers. obs.), Kitanoshima of the Ogasawara (Bonin) Islands (F. Sato pers. obs.), and Nishinoshima (Kawakami *et al.* 2005) and Kitaiwojima of the Volcano Islands (Ornithological Society of Japan 2000). Black Rats reduced a formerly large colony to approximately 150 pairs on Torishima (F. Sato unpubl. data), where a rat eradication program is currently in progress.

Despite its status as near-threatened (BirdLife International 2008) and associated conservation concern (USFWS 2002a), Tristram's Storm-Petrel remains one of the least studied seabirds in the Hawaiian archipelago, if not in the northern hemisphere. Basic information concerning its breeding biology and population status is lacking. Breeding biology was previously studied at a single colony, where small samples and nest abandonment were problematic (Marks & Leasure 1992). With the exception of work at Pearl and Hermes Reef (Wegman & Kropidlowski 2002), all population estimates of Tristram's Storm-Petrel in Hawaii are based on brief visits to islands more than 20 years ago (Rauzon *et al.* 1985). The current study was undertaken to augment the meagre information available on the population biology of this species, with emphasis on breeding success and causes of failure at two breeding sites.

MATERIALS AND METHODS

Study sites

Observations were conducted at Laysan Island (25°46′N, 171°03′W) and French Frigate Shoals (Tern and East islands, 23°45′N, 166°10′W) in the Hawaiian Islands National Wildlife Refuge. Located 1495 km northwest of Honolulu, Laysan is a 397-ha coral-sand island with a 70-ha hypersaline lake at its center. On Laysan, Tristram's Storm-Petrel is limited to small, scattered subcolonies in a 50- to 250-m band of vegetation around the perimeter of the lake, with the largest subcolony currently in the southwest corner (Ely & Clapp 1973, Marks & Leasure 1992). Vegetation within the subcolonies differs greatly, ranging from open areas with sparse Bunchgrass *Eragrostis variabilis,* to dense vines *Ipomea pes-capae* and *Sicyos pachycarpus.*

French Frigate Shoals is a crescent-shaped coral atoll located 540 km southeast of Laysan Island and 955 km northwest of Honolulu. Of the 12 to 16 coral-sand islets present at any given time, only Tern and East islands currently support vegetation and appreciable numbers of burrowing seabirds. On Tern Island [13.8 ha (USFWS 2002b)] and East Island [4.5 ha (Amerson 1971)] suitable breeding habitat for Tristram's Storm-Petrels appears to be limited to 0.1 ha and 0.8 ha respectively. Tristram's Storm-Petrels began recolonising Tern Island in 1993 (USFWS unpubl. data) and East Island no later than 1985 (Rauzon *et al.* 1985).

Nest-site characteristics and monitoring

Breeding activity was quantified on Laysan Island from November 2003 to June 2004 and from October 2004 to April 2005. At French Frigate Shoals, observations were made December–June in 2005–2008. All breeding sites were located and monitored in daytime using a 2.5-cm diameter infrared video probe (Peep-a-roo: Sandpiper Technologies, Manteca, CA, USA). Presence of an egg was inferred from the presence of an adult in incubating posture for three consecutive nest checks. Breeding sites were visited at four-day intervals in 2004. We reduced the frequency to once every seven days during incubation on Laysan in 2005 and on Tern Island in 2005–2008. Sites at East Island were checked approximately every 21 days (2005 only). Nest-site characteristics were recorded only on Laysan Island, where we noted structure (earthen burrow, inside dense vegetation or rock crevice), maximum width and height of entrance, and burrow length.

Breeding biology

Dates referring to breeding phenology are calculated based on nest checks, from the median of the earliest and latest dates possible. Eggs partially incubated when first recorded were excluded from calculations of the incubation period. Because Tristram's Storm-Petrels likely do not brood their chicks for more than two to three days after hatching (Marks & Leasure 1992), hatching was assumed to have occurred at least two days before first observation of an unattended chick. Chicks were assumed to have fledged if they were fully feathered and at least 70 days old upon discovery of an empty nest.

Hatching success was calculated as the proportion of eggs hatched of those laid. Fledging success was the number of chicks fledged among eggs hatched (Tern Island). Where our sample size was notably small (Laysan in 2004), chicks estimated from mass and development to be fewer than 14 days old when found are included in fledging success, but excluded from calculations of hatching success and fledging period. Breeding success was calculated as the product of hatching success and fledging success.

Interspecific competition

Nest failure because of interspecific competition for breeding sites, specifically with Bonin Petrels *Pterodroma hypoleuca* and Wedge-tailed Shearwaters *Puffinus pacificus,* consisted of annexation of a confirmed Tristram's Storm-Petrel nest site by ejection of the occupying adult or the killing or ejection of the occupying chick. An annexation during the incubation phase involved the substitution of a Tristram's Storm-Petrel egg with another species (adult or egg) or abandonment coincident with enlargement of the burrow and occupation by another species within two nest checks. Annexation during the chick phase included a live chick observed outside the burrow entrance or a missing chick coincident with another species occupying the nest site. Mortalities included chicks found dead at the entrances to burrows dug out by competing species. We recorded "indirect" competition when the loss of a Tristram's Storm-Petrel nest site was caused by the digging activity of another species nearby that resulted in burrow collapse or entombment.

Chick measurements

Chick body mass [±1 g using a 300-g Pesola (Baar, Switzerland) spring balance] and wing chord (±1 mm using a stopped ruler) were taken on Tern Island in 2006. We calculated the growth constant for a logistic model fitted to each chick's mass measurements (hatching to peak mass) (Ricklefs 1967), for chicks of known age that survived to fledge.

Population estimates

Population estimates reflect the number of active breeding sites present. On Laysan, we based our estimate on the average burrow density of the southern subcolony applied to the estimated area of additional subcolonies. Tern Island was small enough to allow a direct count, but such a count was not possible on East Island, where we made only infrequent visits of short duration. Instead, the island was divided into 10-m transects. We made a direct count of burrows in every other transect, and the number of occupied burrows present in the unsurveyed transects was estimated from the mean densities in the two adjacent transects.

Statistical analysis

Statistical analyses were performed using the Minitab software package (release 13: Minitab, State College, PA, USA). We used binomial logistic regression models with a logit link function to analyse relationships between nest success and nest-site characteristics, laying date, frequency of nest checks, and burrow collapse (Hosmer & Lemeshow 1989). The same models were also used to test the relationship between annexation by Bonin Petrels or Wedge-tailed Shearwaters and Tristram's Storm-Petrel nest-site characteristics and location. Statistical results were considered significant when $P \leq 0.05$. Values reported are means ± standard deviation.

RESULTS

Nest-site characteristics

Occupied burrow density at the southern end of the lake on Laysan averaged 0.025 m^{-2} but reached 0.105 m^{-2} in some locations. Mean occupied burrow densities on Tern and East islands were 0.111 m^{-2} and 0.028 m^{-2} respectively.

Nest sites on Laysan included earthen burrows, dense vegetation and rocky crevices (74%, 17%, and 10% respectively; n = 115). Tristram's Storm-Petrel colony sites in French Frigate Shoals lacked rocky crevices and dense vegetation—all nest sites there were earthen burrows. Burrow entrances measured 8.9 ± 2.4 cm in width and 5.5 ± 1.7 cm in height in January 2004 (n = 42), but 10.3 ± 4.8 cm in width and 7.0 ± 2.5 cm in height in January 2005 (n = 48). Burrow length was highly variable (36.6 ± 15.3 cm; range: 15–70 cm; n = 42). No relationship was observed between burrow characteristics and either hatching success (n = 46: $G = 7.987$, $P = 0.24$) or fledging success (n = 36: $G = 2.673$, $P = 0.75$), but our sample size did not allow for a test of the significance of interaction terms.

Breeding phenology

Laying, hatching and fledging dates appeared roughly similar on Laysan and Tern islands (Table 1). Phenology within the islands did not differ significantly between years, and the timing on Laysan closely matched the 1988 and 1990 breeding seasons described by Marks & Leasure (1992). Much overlap of breeding stages was observed on Tern Island in 2005 (Fig. 1).

Incubation period and hatching

Eggs on Laysan measured 39.3 ± 1.1 mm by 28.8 ± 0.3 mm and had a mean mass of 18.2 ± 0.8 g (n = 4). The incubation period (Tern Island 2005) lasted 44.5 ± 5.3 days (range: 39–55 days; n = 21). One egg was incubated for 64 ± 6 days before being abandoned.

TABLE 1
Comparison of phenology of Tristram's Storm-Petrel *Oceanodroma tristrami* between years and islands in the northwest Hawaiian Islands

	Laysan Island		Tern Island			
	2004	2005	2005	2006	2007	2008
First egg	15 Dec	14 Dec	13 Dec	19 Dec		
Last egg	3 Mar		14 Feb	20 Feb		
First hatch	29 Jan	1 Feb	27 Jan	2 Feb		
Last hatch	17 Mar	>21 Mar	10 Mar	5 Mar		
First fledge	20 Apr		17 Apr	30 Apr	27 Apr	15 Apr
Last fledge	15 Jun		10 Jun	9 Jun	15 May	19 May

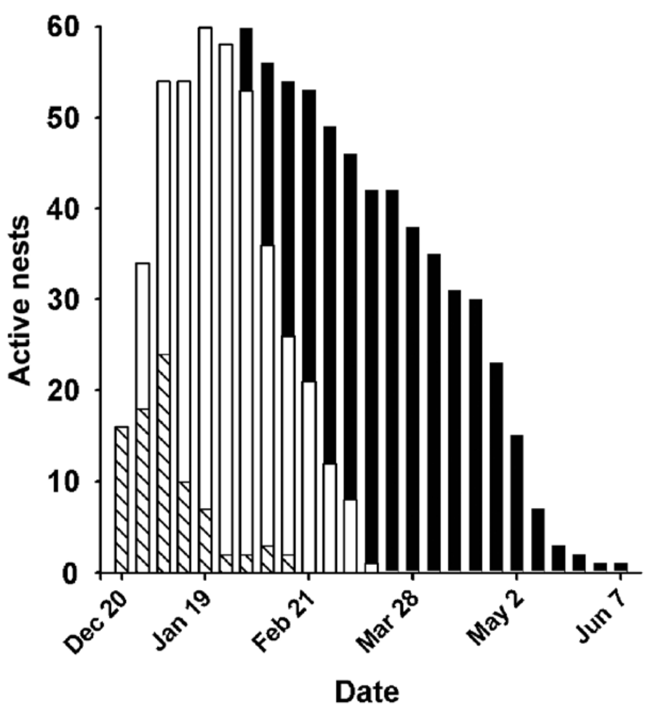

Fig. 1. Nesting phenology of Tristram's Storm-Petrel *Oceanodroma tristrami* on Tern Island in 2005, showing new nest sites (crosshatched), nest sites where incubation continued (open) and nest sites with chicks (solid).

Laysan Finches *Telespiza cantans* were effective egg predators, depredating 90% of unattended eggs within two to four days (n = 21). No egg survived unattended beyond eight days. Despite that vulnerability, egg neglect was observed in 10% of nests on Laysan in 2004 (n = 48). Egg neglect was not recorded on Laysan in 2005 (n = 56) or at French Frigate Shoals in 2005 (n = 114) or 2006 (n = 51).

Hatching success on Laysan Island was 0.35 in 2004 (n = 48) and 0.46 in 2005 (n = 56); on Tern Island, it was 0.53 in 2005 (n = 86) and 0.62 in 2006 (n = 34). Hatching success on East Island in 2005 was 0.54 (n = 28). No detectable relationship between laying date and hatching success was found in any breeding season. Researcher disturbance did not appear to influence hatching success. There were no differences, after controlling for other known sources of failure, among nests checked at intervals of four days (Laysan 2004), seven days (Laysan 2005, Tern 2005 and 2006), or 21 days (East Island 2005; n = 169: $G = 4.40$, $P = 0.11$). Nor did the rate of abandonment differ significantly between years on Laysan (n = 82: $G = 1.714$, $P = 0.19$) or between islands at French Frigate Shoals (n = 87: $G = 0.023$, $P = 0.88$).

Causes of egg mortality were numerous and varied between islands (Table 2). No relationship was found between Bonin Petrel annexation and nest-site characteristics (n = 31: $G = 3.789$, $P = 0.285$). A heavy rain in December accounted for the largest percentage of failed nests on Tern Island in 2005. Laysan and East islands experienced the same weather, but because surveys had not yet begun on those islands, the effect on nesting success is unknown.

TABLE 2
Causes of hatching failure of Tristram's Storm-Petrels *Oceanodroma tristrami* in the northwest Hawaiian Islands

Cause[a]	Percentage of nests affected				
	Laysan Island		East Island	Tern Island	
	2004	2005	2005	2005	2006
Abandoned	35	27	21	17	29
Collapse	6	5	13	5	9
Researcher disturbance[b]	1	2		1	
Rain				21	
Infertile egg	4	1		3	
Damaged egg				1	
Conspecific activity				1	
Bonin Petrel *Pterodroma hypoleuca*	6	6			
Wedge-tailed Shearwater *Puffinus pacificus*			2	3	
Albatross spp.	2	1			
Total	n=48	n=56	n=28	n=87	n=34

[a] Egg predation by Laysan Finches *Telespiza cantans* was an additional, unquantified cause of hatching failure.
[b] Collapse caused by a researcher during monitoring.

Nestling period and fledging

The mean nestling period was 83.8 ± 2.0 days (n = 5) on Laysan Island in 2004, 83.7 ± 4.7 days (n = 20) on Tern Island in 2005, and 87.1 ± 6.8 days (n = 15) on Tern Island in 2006. Chicks fledged as young as 74 days (Tern Island 2005), and as old as 100 days (Tern Island 2006). Chicks reached a peak mass of 139.7 ± 10.2 g and fledged at 96.9 ± 9.6 g (n = 14; Fig. 2). Using the earliest seasonal value (February) available for adult body mass (Marks & Leasure 1992), chicks peaked at 150% of mean adult mass and fledged within 4%. The logistic growth constant was 0.101 ± 0.008 (n = 12), with chicks requiring an average of 43.5 days to grow from 10% to 90% of asymptotic mass.

Fledging success and overall breeding success were 0.45 (n = 56) and 0.16 (n = 50) respectively on Laysan in 2004. On Tern Island, fledging success was 0.51 in 2005 (n = 45), 0.47 in 2006 (n = 19), 0.47 in 2007 (n = 45), and 0.47 in 2008 (n = 19). Overall breeding successes on Tern Island was 0.27 in 2005 (n = 85) and 0.28 in 2006 (n = 32). Sporadic monitoring of East Island in 2005 did not allow for an accurate assessment of fledging success, but success could not have been more than 0.40 (n = 15), for an overall breeding success below 0.22 (n = 28).

Causes of chick mortality were similar between islands, but the importance of a particular source varied greatly (Table 3). Direct competition from Wedge-tailed Shearwaters on Tern Island was rare in 2005 and 2006; no chicks were killed and only one eviction was recorded in each breeding season. In addition, Wedge-tailed Shearwaters shared burrows with Tristram's Storm-Petrel chicks (20% in 2005, 33% in 2006) for periods of several days, the cohabitation in one instance spanning five consecutive nest checks over a 24-day period. The fledging success of chicks that shared burrows with Wedge-tailed Shearwaters did not differ significantly from those not sharing. In contrast, in 2007 and 2008, Wedge-tailed Shearwaters were responsible for 33% (n = 8) and 40% (n = 4) of Tristram's Storm-Petrel chick mortalities. In 2007, only 4% of observations were of a Tristram's Storm-Petrel chick (n = 2) sharing a burrow with a Wedge-tailed Shearwater. All interactions with Wedge-tailed Shearwaters were fatal in 2008. No relationships were found between annexation of burrows by Wedge-tailed Shearwaters and either nest-site characteristics or location.

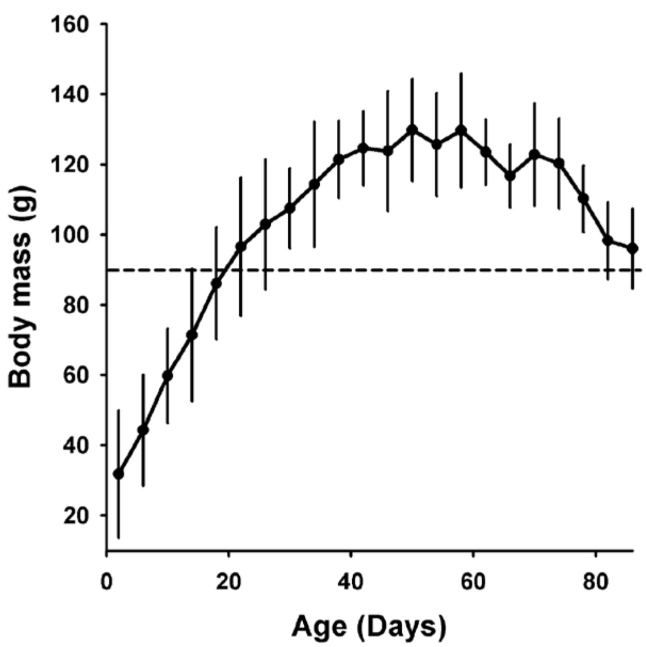

Fig. 2. Mean body mass (± standard deviation) of Tristram's Storm-Petrel *Oceanodroma tristrami* nestlings that survived to fledge on Tern Island in 2006 (n = 12). Dashed line is mean adult mass.

A small percentage of chicks on Laysan were lost to insects (Table 3; McClelland & Jones in press). Harassment by more than 200 invasive ants *Monomorium pharaonis* caused one chick to leave its burrow permanently. A second mortality involved an unknown species of fly (order Diptera) that laid eggs on the back of a storm-petrel chick. Although still alive at the end of the field season, the chick was in poor condition, covered in larvae, and likely did not survive.

Population estimates

The population of Tristram's Storm-Petrel on Laysan was estimated to be 700 breeding pairs. Applying the average density of the largest colony to the estimated amount of suitable habitat, we believe the population could not have exceeded 2250 breeding pairs. The Tern Island population was at least 112 breeding pairs and likely did not exceed 120 pairs. We placed the East Island population at 160 pairs, a conservative estimate that does not account for nests that may have failed before the survey.

DISCUSSION

Our study provides new data on the breeding biology of Tristram's Storm-Petrel and adds to the existing information from Hawaii and elsewhere. Anecdotal evidence (Rauzon *et al.* 1985) suggested that there may be geographic variation in Tristram's Storm-Petrel phenology, with breeding occurring earlier on more eastern islands in the Northwest Hawaiian Islands archipelago, such as Nihoa. That pattern has been documented in other species with highly synchronized colonies such as Sooty Terns *Sterna fuscata* (Fefer *et al.* 1984). Nevertheless, little difference in phenology was found between French Frigate Shoals and Laysan Island in 2005, although the possibility requires further study over a greater geographic area and range of years.

TABLE 3
Known causes of chick mortality of Tristram's Storm-Petrels *Oceanodroma tristrami* breeding on Laysan and Tern Islands, northwest Hawaiian Islands

Cause	Percentage of chicks affected				
	Laysan Island	Tern Island			
	2004	2005	2006	2007	2008
Dead in burrow	26			20	5
Chick missing	15	29	21	11	16
Burrow collapse	5	2	5	4	10
Wedge-tailed Shearwater *Puffinus pacificus*					
Direct	7	2	5	9	21
Indirect	4	11	21	9	
Invasive arthropod	4				
Total	n=15	n=45	n=19	n=45	n=19

Tristram's Storm-Petrels on Laysan were most often found breeding in burrows, but it should be noted that nest sites in vegetation were extremely cryptic and likely more common than is reported here. In some areas of Laysan, Tristram's Storm-Petrels may also establish burrows in areas dominated by thick vines (Marks & Leasure 1992), but such sites were not surveyed in this study to avoid a possible high level of investigator disturbance.

Tristram's Storm-Petrels excavated their burrows over a period of several weeks. As found in other species of storm-petrels (Harris 1974, Stenhouse & Montevecchi 2000), soil type was a primary factor influencing colony location. Tristram's Storm-Petrels were most often found in shallow, less sandy soils that likely offered greater burrow stability and less competition from Bonin Petrels and Wedge-tailed Shearwaters, which prefer deeper soils (Ely & Clapp 1973). The difference in burrow entrance size between years on Laysan was likely a result of heavy rain that occurred before measurements were taken in 2005. Erosion appeared to enlarge burrow entrances over the course of the breeding season and minor entrance collapses are common, in some cases completely blocking egress until excavation by the off-duty member of a pair.

The most frequent cause of hatching failure for all years and islands was abandonment. Abandonment is a common cause of egg loss in the Procellariidae, typically in response to the presence of humans or predators (Warham 1996). Factors contributing to the high rate of abandonment during this study are unclear, because predators were absent on Tern Island, and the frequency of site checks did not appear to affect the rate of abandonment. To assess the latter possibility better, future comparisons among nests on the same island in the same year are desirable.

It is thought that egg neglect in petrels allows adults to maintain body condition and to avoid incubation-induced mortalities (Boersma & Wheelwright 1979). We cannot gauge the true incidence of egg neglect by Tristram's Storm-Petrels on Laysan, as the percentage of eggs considered abandoned that would have been further incubated had they not been depredated is not known. The persistence of egg-neglect behaviour (as on Laysan in 2004) despite egg predation by Laysan Finches suggests that finch predation does not reduce breeding success to a degree that the benefits of egg neglect are lost. The role of foraging conditions in determining the frequency of egg neglect (and abandonment) is not fully understood (Chaurand & Weimerskirch 1994) and requires further research.

Although burrow collapses are a feature on all islands, they were the greatest source of hatching failure on East Island. East Island has noticeably coarser soil than is seen on the other islands, which likely contributed to the high rate of collapse. East Island also has the largest population of breeding Hawaiian Green Sea Turtles *Chelonia mydas agassizii* (Balazs & Chaloupka 2004), but because turtles were not seen to enter the Tristram's Storm-Petrel colony during the birds' breeding season (winter–spring), we do not consider them a factor in storm-petrel breeding success.

On Laysan, the large Bonin Petrel colony was the greatest source of storm-petrel hatching failure, in part because of the temporal overlap between Tristram's Storm-Petrel and Bonin Petrel breeding seasons (Fefer *et al.* 1984). On islands with large populations of Bonin Petrels, such as Laysan, large numbers of both species prospect and compete for burrows during the same period. The effect of Bonin Petrel activity on Tristram's Storm-Petrel nesting success may explain why the latter species has not been recorded breeding on Lisianski Island, whose density of Bonin Petrels is approximately 4.5 times that of Laysan (calculated from Fefer *et al.* 1984). Further support for this idea comes from the relatively large population of Tristram's Storm-Petrels at Pearl and Hermes Reef, which lacks a large Bonin Petrel presence (Fefer *et al.* 1984).

The largest of the burrowing birds in the leeward archipelago, Wedge-tailed Shearwaters readily evict other burrowing species (Whittow 1997). Shearwaters were the most prevalent cause of chick loss on both Laysan and Tern islands, but the nature of the interaction varied between islands. On Laysan and Tern islands, shearwaters were aggressive competitors for burrows, arriving and prospecting in March and often killing or evicting Tristram's Storm-Petrel chicks. On Tern Island in 2007 and 2008, the only storm-petrel chicks to fledge did so early in the season, when Wedge-tailed Shearwater abundance was low (earlier date of last observed fledging in both years compared to 2005 and 2006; Table 1). We speculate that foraging and thus breeding conditions were poor in 2007 and 2008 (some Tristram's Storm-Petrel chicks fledged below 70 g), perhaps increasing the susceptibility of late-hatching Tristram's chicks to Wedge-tailed Shearwater competition. Contrary to Harrison's (1990) supposition, no Tristram's Storm-Petrel chicks were evicted by Bulwer's Petrel *Bulweria bulwerii* on any island, although some burrows on Laysan were used by Bulwer's Petrels after the chick had fledged or the nest had failed.

Negative interactions with another species, the Laysan Albatross *Phoebastria immutabilis,* were documented on Laysan. Albatrosses were seen to cause Tristram's Storm-Petrel burrows to collapse, and albatross chicks were frequently attracted to burrow entrances, which they altered and blocked in an attempt to create a new nest bowl (Rice & Kenyon 1962).

Tristram's Storm-Petrels breeding on sand islands (Laysan, French Frigate Shoals, Pearl and Hermes Reef, Midway and Kure atolls) apparently suffer significant annual nest loss as a result of weather and the fragility of sand burrows. It was not possible to quantify the number of nests lost to flooding on Laysan in 2005, but flooding of the southern lake area is reportedly common during heavy rains (Willet 1919), and substantial nest failure may occur as a result (Ely & Clapp 1973).

In the company of large numbers of Bonin Petrels and Wedge-tailed Shearwaters, it is likely Tristram's Storm-Petrel rarely achieves breeding success comparable to that of other members of its genus. Breeding success in other *Oceanodroma* species is frequently more than 0.4 chicks per pair [e.g. *O. furcata (*Boersma *et al.* 1980), *O. homochroa* (Ainley 1995), *O. leucorhoa* (Huntington *et al.* 1996), *O. melania* (Ainley & Everett 2001)], but Tristram's Storm-Petrels may lose more than 40% of nests to interspecific competition alone. Another member of the genus with low breeding success is the Band-rumped Storm-Petrel *O. castro* [cool season: 0.16; hot season: 0.29 (Ramos *et al.* 1997)], which also competes for burrowing space with larger, aggressive species.

Tristram's Storm-Petrels experience scant predation pressure on adults and few mortalities at their breeding sites. However, breeding success on Laysan, Tern, and East islands may be insufficient to maintain current populations. Using the formula described by Brooke (2004), and assuming first breeding at four years of age (a chick banded on Tern in 2002 was captured at the mouth of an active burrow in 2006), annual adult mortality of 5% (a conservative assumption), and immature mortality four times the adult rate [as reported for the European Storm-Petrel *Hydrobates pelagicus* (Brooke 2004)], Tristram's Storm-Petrels would need a mean breeding success of 0.24 for simple replacement (compare with mean breeding success of 0.16 on Laysan and 0.27 on Tern Island).

Our population estimate of 700 breeding pairs on Laysan compares with previous estimates of 500–2500 pairs (Rauzon *et al.* 1985) and 2000–3000 pairs (Ely & Clapp 1973). Laysan, the largest island in the Northwest Hawaiian Islands, may never have been a significant population center for Tristram's Storm-Petrel (Ely & Clapp 1973). Based on current habitat availability and interspecific competition, that status is unlikely to change in the future. The combined population of Tristram's Storm-Petrels on Tern and East islands in 2005 was estimated at 252–280 pairs. However, in May 2005, we observed large numbers of Bulwer's Petrel around La Perouse Pinnacle (8 km south of Tern Island), and the presence of Bulwer's Petrel crevices (the appropriate size for Tristram's Storm-Petrel) suggests possible undocumented breeding of storm-petrels at that site.

The interspecific competition we observed at colonies suggested nest sites were limiting. Floating individuals [adult birds capable of breeding, but prevented by lack of a breeding site (Manuwal 1974)] are common among storm-petrels and may be important burrow competitors in some years (Spear & Ainley 2007). Thus, it is possible that the population of breeding-age birds at colonies is larger than burrow surveys alone would indicate.

Before the present study, only Marks & Leasure (1992) had published research on the breeding biology of Tristram's Storm-Petrel. Several insights and hypotheses advanced in the paper by those authors are addressed by the current research. First, the observations by Marks and Leasure (1992) involved digging into the burrows, which led to 63% abandonment after two rounds of nest checks. They hypothesized that frequent nest abandonment was a result of the alterations made to the burrows, as opposed to natural factors. Consequently, Tristram's Storm-Petrel has generally been regarded as highly sensitive to researcher disturbance, with slight burrow alterations being enough to cause abandonment. However, we found no increase in abandonment among burrows that suffered a minor collapse on Tern Island during 2005–2006 (n = 66: $G = 0.059$, $P = 0.809$), the one location where minor collapses were recorded consistently. This finding suggests that the high abandonment noted by Marks & Leasure (1992) resulted from intrusively digging out the burrows.

Second, Marks & Leasure (1992) hypothesized that Tristram's Storm-Petrels breeding on islands with finches acting as egg predators practiced egg neglect less often than did those breeding on islands lacking finches. We found that Tristram's Storm-Petrels on Laysan do practice egg neglect, at a level difficult to assess accurately, but possibly high in some years. Finally, Marks & Leasure (1992) suggested the intentional introduction of Laysan Finches to Pearl and Hermes Reef might have negatively affected the breeding of Tristram's Storm-Petrel. That unintended effect appears very possible based on our observations.

CONCLUSIONS

Our study demonstrates the need for continued research and monitoring of Tristram's Storm-Petrels. This poorly understood species appears to have a reproductive rate that will not sustain the population unless adult mortality is exceptionally low. More research is required to determine if the breeding seasons reported in this study are representative, especially on Laysan, where only one complete year of data is available. Causes of breeding failure also deserve further investigation. Do poor foraging conditions lead to egg neglect and associated egg losses to finches? Was the increased aggression from Wedge-tailed Shearwaters on Tern Island in 2007 and 2008 normal behaviour, as it appeared to be on Laysan? Unique characteristics on each island and interannual variability influenced Tristram's Storm-Petrel breeding, illustrating the danger of applying results from one colony to another. Research on additional islands is needed, especially non-sand islands that provide a variety of breeding habitats. Further study of this unusual, large-bodied storm-petrel may provide new insights on evolution and adaptation in the genus *Oceanodroma.*

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