LONG-TERM STUDY OF APPARENT SURVIVAL IN PACIFIC GOLDEN-PLOVERS AT A WINTERING GROUND ON OAHU, HAWAIIAN ISLANDS

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ABSTRACT.—We monitored the apparent survival of territorial and nonterritorial Pacific Golden-Plovers (*Pluvialis fulva*) for 20 consecutive nonbreeding seasons at a wintering ground within Bellows Air Force Station (BAFS) on the eastern shore of Oahu, Hawaii. Territorial birds were especially site-faithful from season to season, and each surviving individual reoccupied the same territory held in previous seasons. On average, territorial birds were resighted for about twice as many postbanding seasons (4.2) as nonterritorial birds (1.8). Open-population modeling indicated that apparent survival varied by age and territorial status. Our most parsimonious model estimated apparent annual survival rates in territorial plovers as 0.90 for young birds (age determined from retained juvenal primaries) from their first through their second wintering season, and 0.80 for adults over numerous seasons. For nonterritorial plovers, the corresponding values were 0.82 and 0.67, respectively. Despite lower apparent survival in nonterritorial plovers, it remains uncertain whether nonterritoriality actually results in shorter life spans. Some surviving nonterritorial birds may have gone undetected (detection probability of 0.70) because of permanent emigration from the study area. Given strong site-fidelity of territorial birds and the relative certainty of detecting them (probability = 1.0), we regarded the disappearance of a plover from its territory as an indicator of mortality. From last-recorded sightings, we concluded that territorial birds died with about equal frequency during the nonbreeding and breeding seasons. Because the latter is of much shorter duration, time-relative hazards were greatest while birds were away from the wintering grounds. Winter mortality was caused by accidents (collisions with overhead wires and other obstructions), and probable predation by owls. We estimated mean additional life expectancy among territorial plovers at 5.1 years for first-year birds, and 4.5 years for unknown-age adults. The oldest known-age individual was a male that lived 13 years 10 months; in adults of uncertain ages, one male survived to a minimum age of 18 years 10 months, and two females to at least 17 years 10 months. Pacific Golden-Plovers wintering at BAFS, especially territorial birds, demonstrated relatively high rates of apparent survival combined with adaptability for coexistence with humans in an urban environment. *Received 18 February 2000, accepted 11 October 2000.*

THE PACIFIC GOLDEN-PLOVER (*Pluvialis fulva*) is among the world's foremost transoceanic migrants. It breeds on tundras in Siberia and western Alaska, and winters from coastal California (where it is relatively rare) across a vast region including most of the insular Pacific, coastal Australia, and southeastern Asia. The Hawaiian Islands are located at the northern end of the main winter range, and large numbers of plovers (most, if not all, appear to be of Alaskan provenance) winter there. Migrations to and from Hawaii involve nonstop flights of at least 4,000 km (Johnson and Connors 1996, Johnson et al. 1997a).

Wintering behavior of golden-plovers on Oahu (Johnson et al. 1981, 1989; Johnson and Connors 1996) takes two forms: many birds defend feeding territories, whereas others are nonterritorial and feed in flocks of varying densities. Territories typically are on lawns and range in area from approximately 0.05 to 0.4 ha. Birds occupy those spaces for the entire wintering season and, unless disturbed by such factors as human activities, dogs, or high winds, remain on them throughout each day. At dusk, most plovers retreat to communal roosting sites and then return to their territories before dawn; a few remain on territories for all or part of the night, or return from roosts during the night. Like the Black-bellied Plover

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(*P. squatarola*; Townshend 1985), individual Pacific Golden-Plovers appear to select either the territorial or nonterritorial mode of behavior during their first wintering season and then retain that behavior for life (Johnson and Connors 1996). A high degree of interyear site fidelity is characteristic of both groups, especially territorial birds. Each territorial plover reoccupies its territory from previous seasons, and nonterritorial individuals tend to reappear on the same feeding sites. Those behavioral traits make it relatively easy to monitor annual survival.

Little is known about the survival of migrant shorebirds on insular Pacific wintering grounds. The only published findings for the region consist of Marks and Redmond's (1996) investigation of Bristle-thighed Curlews (*Numenius tahitiensis*) and occasional comments about Pacific Golden-Plovers in some of our earlier papers (Johnson et al. 1989, 1993; Johnson and Connors 1996). In this paper, we report annual survival estimates based on seasonal resightings and open-population modeling for territorial and nonterritorial Pacific Golden-Plovers banded from 1979 to 1991 in Hawaii. The data were gathered over 20 consecutive wintering seasons through spring 1999.

METHODS

The study site, Bellows Air Force Station (BAFS), borders the eastern shore of Oahu near the town of Waimanalo. After World War II, the property was set aside as a military recreational facility. In recent years, parts of the station have been used as a training area for U.S. Marine Corps amphibious and ground maneuvers. We concentrated our work at the northeastern end of the station where golden-plover habitats have remained essentially unchanged since the project began. These habitats consist of extensive lawns, open (sparse understory) groves of ironwood trees (*Casuarina equisetifolia*), and unused brushy runways. Based on our counts over the years, that portion of BAFS supports a wintering population of about 100–150 birds.

We captured 163 plovers during 10 of the 12 wintering seasons from 1979–1980 through 1990–1991. Birds were caught in mist nets from about 0400 to 0630 as they returned predawn from nocturnal roosts on nearby offshore islands. We marked each individual with a unique combination of color bands plus a U.S. Geological Survey metal band (all placed on the tibiotarsi), and determined age and sex from distinctive plumage characteristics including retention of the juvenal primaries until the second pre-

basic molt (Johnson and Johnson 1983, Johnson and Connors 1996). In all, we banded 113 adults (classed as ASY for after second year; i.e. older than second calendar year of life) and 50 first-year (<1 year old) birds. Of the latter, 47 were SY individuals (in their second calendar year) and 3 were HY birds (hatching year, within a few weeks of 1 January) when captured. To simplify further discussion, all 50 first-year birds will be referred to as the SY age class. First-year plovers were ~10 months old at spring migration (early in the previous July is a reasonable estimate of hatching time; Johnson and Connors 1996), whereas the only assumption possible with birds captured as adults was an age of at least 1 year 10 months at the first spring migration after banding. Almost all banding was done in the spring (March and April) when dimorphic coloration was advanced sufficiently to indicate sex (Johnson and Johnson 1983, Johnson and Connors 1996). For birds captured earlier in the season when plumages are monomorphic, we were able to determine sex through observations during the ensuing spring or in a subsequent season.

After release, we made repeated observations to determine each bird's status (territorial or nonterritorial) and recorded locations of territories on a map. We monitored the marked plovers at BAFS each nonbreeding season (August to April) from 1979–1980 through 1998–1999. By the end of that time, only a few long-lived survivors remained. Monitoring was especially frequent (every few days) during fall arrival in August and September and for about six weeks ending with spring departure in late April. During the rest of the wintering season, surveys were conducted at irregular intervals. Plover habitats at BAFS are traversed by a network of roads from which the birds were easily seen, and all observations reported here were made using a vehicle as a mobile blind. Plovers tolerated close approach (often <15 m) such that band combinations usually could be read with binoculars or occasionally a spotting scope. Our data suggest that no marked territorial plovers escaped detection. That was not the case for nonterritorial birds (see below). Spring departure from BAFS was indicated by disappearance of birds from their territories, beginning with an occasional individual and progressing to all plovers within a week or less. We used the last recorded sighting of each territorial bird (the fates of nonterritorial plovers were too uncertain) as an indication of when mortality occurred. If a plover was present at spring departure, but failed to return the following fall, we assumed that death occurred during migration or on the breeding grounds. A fall returnee that disappeared before spring migration was considered to have died on the wintering grounds. All of the banding and monitoring field work was conducted by the Johnsons and Bruners.

TABLE 1. Evaluation of open-population mark–resight models of apparent survival and detection probability of Pacific Golden-Plovers banded at Bellows Air Force Station, 1979–1999.

Covariates related to apparent survival[a]	Covariates related to detectability[a]	No. of para-meters	Δ QAIC$_c$[b]	QAIC$_c$ weight[c]	Deviance[d]
Age + territory	Territory	5	0.00	0.347	480.68
Age + territory + interaction	Territory	6	1.13	0.197	479.61
Age + sex + territory	Territory	6	1.68	0.150	480.26
Territory	Territory	4	2.69	0.090	486.26
Age	Territory	4	3.54	0.059	487.26
Sex + territory	Territory	5	4.38	0.039	485.85
Age + sex	Territory	5	5.02	0.028	486.60
Age + sex + interaction	Territory	6	5.03	0.028	484.21
Age + sex + territory + interaction	Territory	10	5.62	0.021	475.21
Sex + territory + interaction	Territory	6	6.02	0.017	485.38
No covariates	Territory	3	6.08	0.017	492.65
Sex	Territory	4	7.56	0.008	492.00
No covariates	No covariates	2	64.84	0.000	564.43

[a] Covariates used in models allowed estimated parameters to vary by (1) age—SY birds vs. ASY birds; (2) territory—territorial vs. nonterritorial birds; (3) sex of birds; and (4) interaction (i.e. all possible interactions among covariates in the model).

[b] The difference (Δ QAIC$_c$) between the QAIC$_c$ value for the best model (645.60) and the value for each competing model was used to evaluate the relative plausibility of competing models (see Methods).

[c] Weight of evidence in favor of a given model, calculated according to Burnham and Anderson's procedure (1998). Weights for all models sum to 1 and thus, provide relative weights for each model considered.

[d] Deviance is the difference between $-2 \times$ ln(Likelihood) of the current model and the saturated model.

Estimates of apparent annual survival and detection probabilities were derived (by J. Rotella) using open-population modeling (Pollock et al. 1990, Lebreton et al. 1992, Burnham and Anderson 1998) based on 20 years of mark-resighting data from all cohorts marked in the 10 capture years. *Apparent survival probability* was the probability that a bird alive in spring of year i remained available for resighting until spring of year $i + 1$ (i.e. survived through this interval and did not permanently emigrate from the study area). Detection probability was the probability that a bird alive in year i was observed in year i. We developed a list of candidate models (Table 1), produced estimates, and evaluated competing models of variation in survival and detection probability using Program MARK (G. C. White, Colorado State University). We used open-population models to evaluate relationships among apparent survival rate (ϕ) and three categorical covariates (two classes/covariate): (1) age class (ϕ allowed to differ between the SY and ASY birds), (2) sex, and (3) territorial status (territory holder or not). For models that considered age class, apparent survival was calculated for (1) the first spring to the second spring season of life (first year's data for SY birds), and (2) subsequent spring-to-spring years of life (post-first-year data for SY birds merged with data for ASY birds). Estimates of apparent survival accounted for the fact that some nonterritorial plovers reappeared after one or more seasons of being undetected, and thus were alive in those seasons when undetected. Because our sample of known-age birds (SY when captured) was relatively small, we did not test whether apparent sur-

vival rate varied with increasing age. We evaluated two versions of each model that contained multiple covariates: (1) a model with main effects of covariates only and (2) a model with main effects and all possible interactions among covariates. We also evaluated whether detection probability differed between territorial and nonterritorial birds.

We selected the best approximating model from the candidate list of models using Akaike's Information Criterion (AIC), adjusted for overdispersion and sample size (QAIC$_c$; Burnham and Anderson 1998). We obtained values of QAIC$_c$ for each model from Program MARK and considered the model with the lowest QAIC$_c$ value to be the best. The difference (Δ QAIC$_c$) between the QAIC$_c$ value for the best model and the value for every other model was used to evaluate the relative plausibility of each model. For a model with Δ QAIC$_c$ < 2, 2 to 4, 4 to 7, and 7 to 10, there is strong evidence, definite evidence, weak evidence, and no evidence, respectively, that the model is the best model (Burnham and Anderson 1998). We calculated the QAIC$_c$ weight for each model, and weight of evidence in favor of a given model, according to Burnham and Anderson's (1998) procedure. The weights for all models sum to 1 and thus provide relative weights for each model considered.

We evaluated goodness-of-fit of our most general model using the parametric bootstrap routine provided in Program MARK. Parameter estimates produced by the model being evaluated for goodness-of-fit were used to generate data in parametric bootstrap samples. To assess goodness-of-fit, we con-

ducted 1,000 simulations, ranked the 1,000 estimates of deviance, and calculated the percentage of simulations with a larger deviance value than that observed for the actual data. We also used simulation results to estimate the overdispersion parameter (c) for the data set using two approaches: (1) deviance estimate for the actual data divided by the average deviance for the simulated data sets, and (2) estimate of c for the actual data divided by the average estimate of c for the simulated data sets. Means of simulated values represent the expected values when the model in question provides a perfect fit to the data. We used whichever estimate of c was larger as our estimate of overdispersion.

Initially, we analyzed a subsample of data from 144 birds for which all covariates were known. Of 83 males, 64 were territorial (43 adults and 21 first-year), and 19 were nonterritorial (14 adults and 5 first-year); of 61 females, 40 were territorial (27 adults and 13 first-year), and 21 were nonterritorial (16 adults and 5 first-year). The effective sample size for that analysis was 654. In the most parsimonious model, survival was a function of age class and territorial status (no interaction between the covariates) and detection probability was a function of territorial status (Table 1). Because sex was not a covariate in the best model, we used the entire data set ($n = 163$, effective sample size = 687) to obtain final estimates for survival and detection rates from the best model. We only report estimates from the best model because our 20-year data set with modest samples and three covariates did not allow us to produce parameter estimates averaged across all models. Thus, our estimates do not incorporate model-selection uncertainty (Burnham and Anderson 1998).

To estimate life expectancy, we used estimates of apparent annual survival rate and methods of Seber (1982) and Brownie et al. (1985). Those calculations assume a negative exponential distribution of survival times to estimate expected additional lifetime and the probabilities of birds living for additional numbers of years.

RESULTS

Of the 163 golden-plovers banded, 112 were territorial and 51 nonterritorial. This proportion (69:31) was not a reliable indicator of the relative size of each group in the overall population. Most netting efforts were directed at territorial individuals, and the behavior of nonterritorial birds made it difficult to obtain accurate counts of them. Numerous estimates over the years suggested a territorial–nonterritorial ratio of about 60:40 on the study area. Thirty percent (34 of 112) of territorial plovers were assigned to the SY age class. Sex was

known for 144 birds (83 males and 61 females) and unknown in 19 cases where individuals disappeared before attaining alternate plumage. Capturing more males than females reflected the sex ratio of the Bellows population. Mid-April counts (done in most years) consistently indicated a preponderance of males, ranging from 60 to 67%. Territoriality did not differ significantly ($\chi^2 = 2.33$, df = 1, $P = 0.13$) between males (64 of 83, 77%) and females (40 of 61, 66%).

Spring exodus at BAFS was remarkably constant from year to year. At least 90% of the population usually departed in the period from 23 to 27 April, with lingering birds gone by 1 May. Young plovers typically did not oversummer and made their first northward migration in spring of their second calendar year. First sightings of marked returnees occurred almost entirely in August with arrivals throughout the month, a few birds were first recorded in early September. The first juveniles generally appeared in late September followed by continued arrivals through October.

Pooled resighting records are summarized in Table 2. For perspective as to resightings of known-age plovers in subsequent seasons, we show here birds banded in their first year as separate groups from those captured as adults. The mean number of seasons returned after banding was 4.4 ± SE of 0.5 (range 0–13) for known-age (SY) territorial birds, 3.9 ± 0.4 (range 0–17) for unknown-age (ASY) territorial adults, 2.1 ± 0.4 (range 0–8) for nonterritorial adults, and 1.4 ± 0.4 (range 0–6) for nonterritorial first-year birds. Based on territorial plovers only (postbanding histories of nonterritorial birds were often uncertain), and selecting the most complete records ($n = 97$), 51 birds died while on the wintering grounds, and 46 died during periods of migration or breeding. Of the remaining 15 plovers in our sample of territorial birds, 11 records were unclear as to the probable time of mortality, and 4 individuals were still alive in spring 1999. The oldest individuals were a known-age (SY when banded) male last seen at 13 years 10 months, and three unknown-age (ASY when banded) birds of which two were females at least 17 years 10 months and a male at least 18 years 10 months of age (Table 2). Among territorial plovers, 11 survived longer than nine seasons after banding, 9 of 78 adults and 2 of 34 first-year birds

TABLE 2. Summary of returns of marked Pacific Golden-Plovers at Bellows Air Force Station through spring 1999.

Group and number banded	Seasons after banding[a]																
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Territorial plovers banded as unknown-age adults, $n = 78$	67	56	41	29	20	20	18	14	10	9	6	3	3	3	3	3	1
Territorial plovers banded as known-age first-year birds, $n = 34$	31	28	21	17	15	13	7	7	4	2	1	1	1	0			
Nonterritorial plovers banded as unknown-age adults, $n = 35$	26	17	10	9	6	3	1	1	0								
Nonterritorial plovers banded as known-age first-year birds, $n = 16$	11	7	2	1	1	1	0										

[a] Postbanding seasons from the fall of one year through the spring of the next.

(Table 2). That was not a statistically significant difference between the two age classes ($\chi^2 = 0.88$, df = 1, $P = 0.35$).

Our most general open-population model of apparent survival and detectability had a reasonable fit to the data (6.9% of 1,000 simulated data sets had a deviance larger than that observed in the actual data set). Our most parsimonious model indicated that apparent survival was related to age class and territorial status (Table 1). All three models within two QAIC$_c$ units of the most parsimonious model contained age class and territoriality; one model contained sex. The coefficient associated with sex of a bird was imprecisely estimated in that model (percent coefficient of variation = 168%) and the confidence interval did not discern whether males had greater or lower survival than females. The main effects of age class and territorial status were that birds in the SY class had higher survival rates than older birds and that territorial birds had higher survival rates than nonterritorial birds. The most parsimonious model and the full data set produced the following estimates of apparent survival rate: 0.90 (SE = 0.04) for territorial SY plovers, 0.80 (SE = 0.02) for territorial ASY plovers, 0.82 (SE = 0.08) for nonterritorial SY plovers, and 0.67 (SE = 0.04) for nonterritorial ASY plovers. Estimated detection probabilities were 1.0 (SE = 0.00) for territorial and 0.70 (SE = 0.06) for nonterritorial plovers. The difference in detection rates resulted from the fact that once a territorial individual went undetected in a given season, it was never seen in a subsequent season; whereas 12 of 37 nonterritorial birds found in

postbanding seasons went undetected for one or more seasons, but were seen again in later seasons. Return rates of territorial males (0.82) and females (0.82) did not differ (also see Johnson et al. 1993).

Estimated mean additional life expectancies based on apparent survival estimates from the most parsimonious open-population model were: 5.1 years (95% CI = 4.2–6.0) for territorial SY birds, 4.5 years (95% CI = 3.7–5.4) for territorial ASY birds, 2.8 years (95% CI = 1.9–3.8) for nonterritorial SY birds, and 2.5 years (95% CI = 1.8–3.3) for nonterritorial ASY birds. The probabilities of an adult territorial plover surviving 5 and 10 additional years of life were 0.33 and 0.11, respectively. In nonterritorial adults, those probabilities were estimated to be 0.14 and 0.02, respectively.

DISCUSSION

Annual survival exceeding 70% is relatively common in shorebirds (Evans and Pienkowski 1984, Smith et al. 1992, Marks and Redmond 1996, Burton and Evans 1997, Warnock et al. 1997), and the strong returns at BAFS were not unexpected. Unfortunately, no other detailed survival data exist for Pacific Golden-Plovers in Hawaii or elsewhere on the winter range. It is noteworthy that banding and recapture records many years ago in the Philippine Islands hinted at results similar to ours (McClure 1998). The high rates of survival at BAFS, where a great deal of human activity occurs, demonstrate remarkable abilities for wintering Pacific Golden-Plovers to coexist with people.

At BAFS, "urbanized" plovers defend territories in close proximity to humans, for example around buildings, within campgrounds, and along roadways. Such behavior is unique among the *Pluvialis* plovers (Byrkjedal and Thompson 1998) and unusual among shorebirds in general. Furthermore, BAFS is only one example of a pattern common throughout the main Hawaiian Islands where that species has adapted well to the ecological alterations associated with human settlement. Changes favorable to plovers began there centuries ago with deforestation by Polynesians and have continued to the present. The most significant trend for plovers has been the replacement of forest and shrubland with extensive grassy environments such as parks, golf courses, and lawns (Johnson and Connors 1996). Those areas apparently produce an abundance of invertebrate prey and could be the choicest plover wintering grounds in all of the insular Pacific.

Over the years, human-induced habitats in the main Hawaiian Islands probably have attracted ever increasing numbers of wintering golden-plovers, and as Bruner (1993) pointed out, that region may now host a large fraction of mid-Pacific migrants. For birds wintering at that northerly location, spring migrations may be less arduous, leading to increased survival and breeding success (Pienkowski and Evans 1985). The male-biased sex ratio at BAFS suggests a latitudinal cline with males predominating at the northern end of the range. However, there are conflicting data from Hickam Air Force Base (another major wintering ground on Oahu), where females outnumbered males (O. W. Johnson unpubl. data). Additional comparative information exists from only two sites southwest of Hawaii. At Johnston Island (~1,300 km from Oahu), spring counts showed males outnumbering females by 2:1, and at Enewetak Atoll (~4,300 km from Oahu), there were 1.3 males per female in a randomly collected sample of 53 plovers in monomorphic winter plumage (O. W. Johnson unpubl. data).

On the smaller northwestern Hawaiian Islands, wintering habitat is much more restricted. At Tern Island, mortality from starvation has been reported often among juveniles during fall and early winter (Johnson et al. 1989, unpublished U.S. Fish and Wildlife Service records). Young birds apparently are unable to compete with adults for limited resources

there. Similar mortality may occur elsewhere in the northwestern chain, but the full extent of that phenomenon is uncertain. Known losses on Tern Island, along with our observations of aggressive interactions at Bellows and elsewhere on Oahu (Johnson et al. 1981, Johnson and Connors 1996), suggest that young birds reaching the Hawaiian Islands face intense competition from established adults during their first wintering season. It is possible that Pacific Golden-Plovers follow the winter-competition model (Pienkowski and Evans 1985), which predicts that competition at northernmost wintering grounds forces young birds to migrate farther south where their subsequent survival may be lower than birds wintering to the north (see Marks and Redmond, 1996, for additional discussion of that concept).

Mortality during wintering seasons and during periods of migration and breeding was obvious among site-faithful territorial plovers. Comparable losses no doubt occurred in nonterritorial birds but were clouded by emigration (see below). Similar findings elsewhere (mostly northwestern Europe) variously implicated weather, predation, and emigration in survival-rate estimates for wintering shorebirds (Evans and Pienkowski 1984, Smith et al. 1992, Insley et al. 1997, Warnock et al. 1997, Yalden and Pearce-Higgins 1997, Dierschke 1998). In contrast to Europe, where freezing conditions can reduce food availability and lead to mortality, the weather in Hawaii is benign and unlikely to cause death of plovers. Discounting weather, the only identified source of mortality at our study site was accidents. Over the years, we were alerted to three banded birds reported dead in residential areas near BAFS. Upon examination, it appeared that each had collided (perhaps while flying at night) with overhead wires or other obstructions. Presumably, other plovers met the same fate, but either were not found or went unreported. Some birds probably were killed by predators, especially Barn Owls (*Tyto alba*) at nighttime roosts (Johnson and Connors 1996). It is impossible to know what caused losses away from the wintering grounds, but the list includes the vagaries of weather during migration and on the breeding grounds, availability of resources especially in springs with late snowmelt, and predation. Given the respective at-risk intervals of the breeding and nonbreeding seasons for Pacific

Golden-Plovers at BAFS (~4 months vs. 8 months), our findings of approximately equal mortality during those periods indicate that migrations and breeding were the most hazardous events on a time-relative basis.

Territorial plovers.—With a high degree of site-faithfulness and detection probability of 1.0, we considered the disappearance of a territorial bird to be an indicator of mortality. Alternative explanations for a missing bird are permanent emigration and establishment of a territory elsewhere, movement to a new territory at BAFS, or a shift to nonterritoriality. Although we think it unlikely, the first possibility cannot be discounted without further research. At BAFS, we have observed occasional expansion or contraction of an individual's territory as boundaries changed from one season to the next, but have seen no instance of a plover abandoning its known territory and establishing a new one. For a bird to shift from territoriality to nonterritoriality would be highly unusual unless it were relatively early in the wintering season when some of the juveniles have only temporary holds on territories. Our knowledge of events during that period is incomplete, but it appears that juveniles trying to establish territories are often evicted by resident adults (as in the Black-bellied Plover; Townshend 1985). Because we captured almost all of the territorial plovers in spring (when territory holders are well established), eviction was unlikely to affect any of our marked first-year birds. Furthermore, we have no evidence of Pacific Golden-Plovers switching from territoriality to nonterritoriality or vice versa after the first season. Our observations agree with Townshend's (1985) findings in Black-bellied Plovers that the pattern of behavior, either territorial or nonterritorial, becomes fixed during the first wintering season and does not change thereafter (Johnson and Connors 1996).

On the basis of the foregoing, we consider 80% survival and 20% mortality to be reasonable demographic estimates in the adult population at BAFS over the past two decades. Because our counts of territorial birds at BAFS have remained relatively stable over the years, 20% also represents an estimate of recruitment of young birds into this group. That 30% of territorial birds were in their first year when captured was inconsistent with 20% recruitment and its 95% CI of 0.16 to 0.23. The most likely

explanation for that disproportion is that young inexperienced birds were easier to catch than adults, and thus our age ratio was biased.

First-year shorebirds often show lower survival than adults (Evans and Pienkowski 1984, Insley et al. 1997, Dierschke 1998). The same is presumably true for Pacific Golden-Plovers, but we have no measure of the entire first season because our banding generally was done in late spring. Thus, the impressive apparent survival rate (0.90) of young territorial plovers at BAFS (also see Table 2) from their first season (when banded) through their second season (first postbanding season) probably has to do, at least in part, with the fact that they were well-established residents on the wintering ground when captured. Because first-year breeders were relatively common on nesting grounds in western Alaska (Johnson et al. 1993), high survival rates also suggest that young Pacific Golden-Plovers, despite inexperience, are well adapted to the risks of their first breeding season. However, further work is needed to assess the possibility that not all first-year migrants to the breeding grounds participate in reproduction (Johnson et al. 1993).

Nonterritorial plovers.—Lacking close association with defended spaces, these birds were more difficult to study than were territorial plovers. During intraseason monitoring, individuals were not always present, suggesting that BAFS was only one of a number of feeding or loafing sites. Of the birds observed in postbanding seasons, approximately one-third (12/37) went undetected for one to three seasons between sightings. In a shorter-duration study, most of those missing individuals would have been presumed dead. However, over a series of wintering seasons we observed a situation similar to Townshend's (1982) "Lazarus syndrome" in which "dead" birds reappeared. Compared with territorial plovers, nonterritorial birds had lower apparent survival rates, but whether that was an accurate index of true survival is uncertain. At least some of that difference could have resulted from permanent emigration. Given the mobility of Pacific Golden-Plovers, permanent relocations may have been at considerable distances from BAFS (even removed from Oahu) making it almost impossible to find banded individuals. We suspect that territoriality is advantageous for plovers at BAFS but conclusive data are lacking, and we

can only point out that there may be a correlation between nonterritoriality and lower survival rates.

Longevity.—Although maximum longevity has little to do with estimates of survival rate (Krementz et al. 1989), we have included our findings for general interest and to update records for Pacific Golden-Plovers. The oldest bird in our study (minimum age of 18 years 10 months) was the same individual previously accorded record status at an age of at least 15 years 5 months (Johnson and Connors 1996). Other published records eclipsed by many in our sample of territorial birds and by a few among nonterritorial birds are 4 years 6 months (McClure 1998), 4 years 10 months (Klimkiewicz and Futcher 1989), and 6 years 6 months (Piersma and Wiersma 1996). Whether all four members of the genus *Pluvialis* share similar longevity parameters is unknown. Current records for the other three species are: American Golden-Plover (*P. dominica*), 8 years (Johnson et al. 1997b); Eurasian Golden-Plover *P. apricaria,* 12 years 2 months (Rydzewski 1978); and Black-bellied Plover, 20 years 4 months (Holland 1992).

Comparisons with Bristle-thighed Curlews.— The only other survival data for a winter resident shorebird in the tropical Pacific come from Marks and Redmond's (1996) studies of the Bristle-thighed Curlew at Laysan Island. Comparing our respective findings is complicated by differences in sampling and in the biology of the two species. Marks and Redmond's measurements were based on fewer seasonal cohorts (two for adults, and three for first-year birds) and relatively short-term monitoring. In the next season after banding, they found survival of 90–95% for first-year curlews and 86% for adults. Our similar measurements in territorial plovers (we have disregarded nonterritorial birds because of the previously mentioned uncertainties about their survival) were 91% (31/34) for first-year birds, and 86% (67/78) for adults (Table 2). Marks and Redmond tracked one cohort of first-year curlews over three subsequent seasons, and at the end of that time 83% (39/47) of the birds were still alive. Comparable three-year survival of first-year territorial plovers was much lower at 62% (21/34, Table 2). Three important differences in wintering biology suggest that young Bristle-thighed Curlews are predisposed to higher survival rates than young Pacific Golden-Plovers. Unlike plovers, Bristle-thighed Curlews (1) do not defend feeding territories and adults tolerate the settling-in of juveniles when the latter arrive in the fall, (2) winter mostly on predator-free islands, and (3) usually defer their first northward migration until at least three years of age (Marks and Redmond 1996). The current record for the oldest known Bristle-thighed Curlew is a bird collected at an age of at least 23 years 10 months (Marks 1992). Whether Pacific Golden-Plovers have the same potential for long life awaits continued study.

Concluding remarks.—Territorial Pacific Golden-Plovers wintering at BAFS clearly demonstrated high rates of survival and site-faithfulness along with adaptability for life amidst an urban environment. The latter trait suggests a relatively bright future for plovers on Hawaiian wintering grounds. Although we were unable to provide solid evidence, it seems probable that territorial plovers had a survival advantage over nonterritorial plovers. We judge the habitat at BAFS to be of excellent quality, and to what extent our findings there apply to other wintering sites in Hawaii is unknown. The demographics of *Pluvialis* plovers are not well understood (Piersma et al. 1997, Byrkjedal and Thompson 1998). This treatment is the first of its kind for the Pacific Golden-Plover, and we hope our findings will lead to comparative studies of the species elsewhere on its nonbreeding range. Such information may be critical in future conservation issues and practices affecting this bird.

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