

# LOCAL SURVIVAL OF DUNLIN WINTERING IN CALIFORNIA<sup>1</sup>

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**Abstract.** We estimated local annual survival of 1,051 individually color-banded Dunlin (*Calidris alpina*) at Bolinas Lagoon, California from 1979 to 1992. Resighting rates for birds banded as adults varied significantly among years, and resighting rates for first-year birds varied by sex and year. No significant differences in local survival rates were found between males and females in any age classes. First-year birds had lower local survival rates than adults. We suspect that raptor predation accounted for much of this difference and other variation in survival rates. Adult Dunlin had lower local survival rates in the year of capture than in subsequent years. Variation in resighting of some groups of individuals including transient Dunlin may account for some differences. However, capture and release of Dunlin may induce short-term behavioral changes that increase the risk of depredation by avian predators within the first few days after capture.

**Key words:** *Dunlin*, *Calidris alpina*, local survival, shorebirds, predation, age and sex effects.

## INTRODUCTION

Demographic data are critical for assessing the status of avian populations (Lande 1988), but estimating these parameters and identifying factors that affect populations usually requires long-term studies of marked individuals (Lebreton and North 1993). During the breeding season, a number of parameters including fecundity and survival of adults influences the annual production of young, whereas for the nonbreeding period, over-winter survival of first-year and adult birds determines population status. Demographic data such as mortality estimates are the key to life-history theory. However, the relative importance of mortality during different periods of a birds' life-history cycle, and its influence on population dynamics, is poorly understood and difficult to study.

Research on breeding shorebirds has produced a wealth of data on population dynamics (Ryan et al. 1993, Thompson and Hale 1993,

Sandercock and Gratto-Trevor 1997). Away from the breeding grounds, where shorebirds spend the majority of their life cycle, quantitative demographic data are lacking, despite the contention that winter mortality limits many migratory bird populations (Evans and Pienkowski 1984, Conway et al. 1995). To understand life-history cycles of birds or predict how variables such as habitat loss due to global warming or human expansion will affect wintering shorebird populations (Goss-Custard et al. 1994), a better understanding of population dynamics during this winter period is required.

Dunlin (*Calidris alpina*) are one of the most widespread shorebird species in the world. They have been studied extensively on their breeding (Holmes 1966, Soikkeli 1967, Jönsson 1991) and wintering grounds (Ruiz et al. 1989, Warnock et al. 1995). Recent evidence suggests that Dunlin in Europe and North America are declining (Tucker and Heath 1994, Warnock and Gill 1996), and even though an estimated 76% of their total annual mortality is thought to occur during migration and on the wintering grounds (Evans 1991), there are no rigorous estimates of survival for Dunlin based on nonbreeding studies.

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Traditionally, return rates have been reported as minimum estimates of survival. Return rates are a composite of three rates: (1) the (true) rate of survival, (2) the rate of local site-fidelity, and (3) the rate of resighting (or recapturing). New statistical techniques based on mark-recapture data now allow estimation of (3) the rate of recapture ( $p$ ) (Burnham et al. 1987, Lebreton et al. 1992). Local survival ( $\phi$ ) is the product of rates (1) and (2), and as such is an improvement over return rates as it is a less biased measure of survival (Sandercock and Gratto-Trevor 1997). We used these improved mark-recapture analyses to obtain estimates of local survival and resighting rates of a color-banded population of Dunlin based on a 14-year study along the Pacific Coast of North America.

This race, *C. a. pacifica*, winters along the west coast of North America from southern Canada to Mexico (Warnock and Gill 1996) and exhibits strong fidelity to winter sites, including our study site, Bolinas Lagoon, California (Warnock et al. 1995). Previous work at this site demonstrated that first-year Dunlin are more likely to be depredated by raptors than adult birds (Kus et al. 1984). Weather also influences survival rates of shorebirds. In Lapwings (*Vanellus vanellus*) significant variation in adult survival rates could be explained by mean winter soil temperatures and winter rainfall (Peach et al. 1994). Therefore, we tested whether sex, age, or annual conditions affected the local survival and recapture rates of wintering Dunlin. We also investigated potential capture effects by testing the null hypothesis that newly banded Dunlin had the same local survival rates as returning, previously banded Dunlin. Testing these hypotheses elucidated variables influencing local survival of Dunlin during winter months. The conservation of shorebirds relies on identifying these factors because the winter period is a particularly sensitive and poorly understood segment of shorebirds' life-history cycle (Myers et al. 1987).

## METHODS

### STUDY SITE AND CAPTURE TECHNIQUES

Bolinas Lagoon is a 587-ha estuary on the north-central coast of California. Birds were captured in mist nets near nocturnal roosts. From 1979–1992, 1,051 individuals were uniquely color-banded, and each bird received a metal

U.S. Fish and Wildlife Service band. Dunlin were aged as either first-year birds (<1 year old) or adults. First-year birds were identified by the presence of buffy/chestnut-edges on the inner tertials or inner middle wing coverts. In adults, these feathers have white edges (Page 1974). We measured the length of the exposed culmen to the nearest 0.1 mm, and body mass to the nearest gram. Dunlin were sexed as male if their exposed culmen was  $\leq 37.7$  mm, female if it was  $\geq 39.8$  mm, and as unknown if it was 37.8–39.7 mm (Page 1974).

### RESIGHTING CRITERIA AND EFFORT

Resighting data were used to determine whether a specific bird was present at Bolinas Lagoon in a given year. We defined marking a bird as the event in which a Dunlin was initially caught, measured and color-banded. Subsequent recapture events of color-banded Dunlin were based on resightings where the bird was identified in the field by its unique color-band combination with a field scope, without physical recapture. All sightings were recorded as either positive or probable. Sightings were recorded as probable when the observer was not certain of one of the colors of the band combination. If the observer was unsure of more than one color, the bird was not recorded. Generally, no more than two observers resighted per year. From 1984 to 1992, the majority of resighting was done by the senior author. Daily effort usually entailed 1–5 hr scanning Dunlin flocks for color-banded Dunlin.

Color bands on Dunlin were small, faded with time, and bands were easily misread. In order to reduce resighting error, a bird was not recorded as being present at Bolinas Lagoon in a given year until it was either physically captured, positively resighted at least twice, positively resighted once with at least two probable resightings, or recorded at least four times as a probable resighting.

### SURVIVAL ANALYSIS

Local survival ( $\phi$ ) and resighting ( $p$ ) rates were estimated in two steps, following protocol outlined by Lebreton et al. (1992) and Cooch et al. (1996). Program RELEASE (Burnham et al. 1987) was used to calculate the goodness-of-fit to a time-dependent model ( $\phi$ ,  $p$ , or Cormack-Jolly-Seber model). The component statistics of RELEASE are efficient for detecting variation in capture probabilities of different individuals

(heterogeneity of capture), whether it is caused by trap dependence (Test 2) or transients (Test 3) (Cooch et al. 1996). In calculating the overall significance of the components of Test 2 (2.Ct and 2.Cm, which deal generally with recapture issues) and Test 3 (3.SR and 3.Sm, which deal generally with survival issues; see Cooch et al. 1996, Appendix, for fuller description and definitions of components), we included only those tests where data were sufficient to calculate a  $\chi^2$ -value. In the special case where 3 of the 4 components (3.Sm, 2.Ct, 2.Cm) are nonsignificant, the remaining 3.SR can be used as a goodness-of-fit test to an age model ( $\phi_{2ac^*t}$ ,  $p_t$ , Brownie and Robson 1983).

Next, we used program SURGE 4.1 (Pradel and Lebreton 1991) to model local survival and resighting rates. User-defined models and external constraints were used to supplement the model choices available in SURGE. Fit of a model was described by deviance (DEV) of the model and number of parameters (NP) of the model. The most parsimonious model was the one with the lowest value for Akaike's Information Criterion [ $AIC = DEV + 2(NP)$ ] (Cooch et al. 1996). Likelihood Ratio tests were used to contrast models; the difference in deviances between two nested models was compared to a  $\chi^2$ -distribution where the difference in number of parameters was used as the degrees of freedom. If the Likelihood Ratio Test was nonsignificant, the reduced model was accepted and tested against models with fewer parameters.

Factors tested in statistical models included sex (sex), year of study (t), age class (ac), and age at banding (grp). In modelling resighting and local survival rates, we started with fully saturated models that included sex, time and age class. We considered resighting rate first so that we had the best fit for  $p$  before we started modelling local survival. No effort was made to resight Dunlin in 1980, 1981, and 1989. The resighting rate was constrained to zero in those years, and these transitions were excluded from the totals of the number of parameters. We treated Dunlin banded as first-year and adult birds separately at first, and then compared them directly as different groups.

We followed conventional procedures outlined by Lebreton et al. (1992) in our modelling approach, but two points warrant further explanation. First, a two age-class term (2ac) was used to compare local survival in the year im-

mediately following banding with subsequent years. A significant effect of age-class on local survival may indicate age-specific mortality rates, but it may also be due to handling effects, transiency or heterogeneity of capture. Second, the difference between sexes (or groups) was sometimes constrained to be a constant difference in every year by using an additive model (sex+t). Comparing an additive and saturated model (sex\*t) is similar to testing whether the interaction term is significant in a two-way ANOVA.

To examine potential effects of handling birds, we looked at the proportion of body mass that captive Dunlin lost over time by weighing some birds immediately upon capture and then again at the time of release. We tested the relationship between body mass loss and time in captivity (both variables log transformed) using linear regression analysis. Unless otherwise noted, means are given  $\pm$  SD, confidence limits (CL) are 95% CL, and all tests are considered significant at the 0.05 level.

## RESULTS

### BANDING AND RESIGHTING SUMMARY

In the fourteen years of this study (1979–1992), 609 first-year (females,  $n = 177$ ; males,  $n = 252$ ; unknown sex,  $n = 180$ ) and 432 adult Dunlin (females,  $n = 108$ ; males,  $n = 211$ ; unknown sex,  $n = 113$ ) were color-banded at Bolinas Lagoon. Ten birds that were not aged were not used in the survival analysis. Ninety percent of birds were captured between October–January (October, 14%; November, 45%; December, 18%; January, 13%; February, 6%; March, 3%; April, 1%). Resighting effort varied by year (Table 1,  $\bar{x} = 58 \pm 35$  days,  $n = 10$  years), and averaged  $12 \pm 7$  resightings bird<sup>-1</sup> year<sup>-1</sup>.

### SURVIVAL ANALYSIS

*Goodness-of-fit tests.* All components of RELEASE (3.Sm, 2.Ct, 2.Cm) were nonsignificant in both first-years ( $\chi^2_3 = 4.1$ ,  $P > 0.25$ ) and adults ( $\chi^2_5 = 6.1$ ,  $P > 0.25$ ), with the exception of 3.SR (first-years  $\chi^2_{14} = 92.3$ ,  $P < 0.001$ ; adults  $\chi^2_{11} = 29.1$ ,  $P < 0.01$ ). The 3.SR transitions were consistently skewed in the same direction (i.e., a bird was more likely to be seen again if it had been seen before). We subsequently pooled females, males and unsexed birds in order to compare first-years with adults (see below), and the 3.SR components were

TABLE 1. Yearly totals of cumulative October to December rainfall, number of days in the field with more than one Dunlin resighted, and number of Dunlin banded at Bolinas Lagoon, California.

	Rainfall (cm)	Number of days spent resighting	Number of Dunlin banded
1979	17.8	0	202
1980	5.7	0	22
1981	19.6	0	43
1982	18.6	46	98
1983	21.7	63	130
1984	19.5	110	77
1985	14.0	78	56
1986	4.3	111	153
1987	14.7	73	96
1988	13.3	22	42
1989	4.2	0	0
1990	3.4	25	76
1991	8.6	38	109
1992	12.7	12	0

again significant ( $\chi^2_{18} = 165.1, P < 0.001$ ), as were the other three components ( $\chi^2_{12} = 25.4, P < 0.03$ ). This latter test was considered weak evidence for overall heterogeneity because the test was nonsignificant if only one transition of one of the test components (2.Ct5) was not included ( $\chi^2_{11} = 15.2, P > 0.10$ ). Although the Cormack-Jolly-Seber model ( $\phi, p_t$ ) was rejected in the three cases above, the test statistics were consistent with age-dependence in survival ( $\phi_{2ac \times t}, p_t$ ). For this reason, we did not use a variance inflation factor (Lebreton et al. 1992) to adjust the Likelihood Ratio tests.

*Variation in local resighting rate (p).* There

was no difference in the local resighting rate between first and subsequent age classes in either first-year (Table 2, models 2a vs. 1a) or adult (Table 3, models 2b vs. 1b) Dunlin. There was an interaction between time and sex in the resighting rate of first-year birds: the additive model (where resighting rate was held to be a constant difference) was significantly different from the unconstrained model (Table 2, models 3a vs. 2a, see also 4a vs. 2a). Overall, first-year females had resighting rates that were higher than males (model 5a). Resighting rates were not significantly different between females and males banded as adults (Table 3, models 3b vs. 2b, 4b vs. 3b). We pooled the sexes in order to compare Dunlin banded as first-year birds and as adults; resighting rate was not significantly affected by age at banding (Table 4, models 2c vs. 1c, 3c vs. 2c). There was significant annual variation in resighting rates (Tables 1–3, first-year birds, models 5a vs. 2a; adults, models 5b vs. 4b; pooled, models 4c vs. 3c) that was not explained by annual rainfall (models 12c vs. 8c) or effort (i.e., number of days afield; models 13c vs. 8c). Mean annual resighting rates ranged from 0.38 to 0.98 (Table 5, from model 8c).

*Variation in local survival rate (phi).* Our minimum estimate of band loss was 1.1% (12/1,051), so no adjustments were made for band loss. Infrequently, foot injuries associated with banding have been reported for shorebirds (Reed and Oring 1993), and this could affect resighting and survival rates. We only found three color-banded Dunlin with injured feet or legs, and two

TABLE 2. Summary of model testing for Dunlin banded as first-year birds (females  $n = 177$ , males  $n = 252$ ) at Bolinas Lagoon, California. The fit of each model is described by the deviance (DEV) and the number of parameters (NP); a low value for Akaike's Information Criterion [ $AIC = DEV + 2(NP)$ ] indicates a parsimonious model. Likelihood ratio tests (LRT:  $\chi^2 = \Delta DEV, DF = \Delta NP$ ) are used to compare nested models. The local survival model that best fits the data is outlined in bold. Model subscripts include: 2ac = two age classes, sex = sex-dependent, t = time-dependent. Model numbers are referred to in text.

Model	DEV	NP	AIC	LRT	$\chi^2$	DF	P
<b>Modelling resighting rate (p)</b>							
(1a) $\phi_{2ac \times sex \times t}, p_{2ac \times sex \times t}$	947.0	86	1,119.0				
(2a) $\phi_{2ac \times sex \times t}, p_{sex \times t}$	958.1	66	1,091.1	2a-1a	11.1	20	>0.90
(3a) $\phi_{2ac \times sex \times t}, p_{sex \times t}$	975.8	57	1,089.8	3a-2a	17.7	9	<0.05
(4a) $\phi_{2ac \times sex \times t}, p_t$	984.5	56	1,096.5	4a-2a	26.4	10	<0.005
(5a) $\phi_{2ac \times sex \times t}, p_{sex}$	1,008.4	52	1,112.4	5a-2a	50.3	14	<0.001
<b>Modelling local survival (phi)</b>							
(6a) $\phi_{2ac \times t}, p_{sex \times t}$	970.6	41	1,052.6	6a-2a	12.5	25	>0.95
<b>(7a) <math>\phi_{2ac \times t}, p_{sex \times t}</math></b>	<b>980.4</b>	<b>32</b>	<b>1,044.4</b>	<b>7a-6a</b>	<b>9.8</b>	<b>9</b>	<b>&gt;0.25</b>
(8a) $\phi_t, p_{sex \times t}$	1,082.3	31	1,144.3	8a-7a	101.9	1	<0.001
(9a) $\phi_{2ac}, p_{sex \times t}$	1,018.3	22	1,062.3	9a-7a	37.9	10	<0.001

TABLE 3. Summary of model testing for Dunlin banded as adults (females  $n = 108$ , males  $n = 211$ ) at Bolinas Lagoon, California. Model subscripts include: 2ac = two age classes, c = constant, sex = sex-dependent, t = annual variation. See caption of Table 2 and text for explanation of other terms.

Model	DEV	NP	AIC	LRT	$\chi^2$	DF	P
<b>Modelling resighting rate (<math>p</math>)</b>							
(1b) $\phi_{2ac^{*}sex^{*}t}, P_{2ac^{*}sex^{*}t}$	961.2	86	1,133.2				
(2b) $\phi_{2ac^{*}sex^{*}t}, P_{sex^{*}t}$	971.5	66	1,103.5	2b-1b	10.3	20	>0.95
(3b) $\phi_{2ac^{*}sex^{*}t}, P_{sex^{*}t}$	981.5	57	1,095.5	3b-2b	10.0	9	>0.25
(4b) $\phi_{2ac^{*}sex^{*}t}, P_t$	984.5	56	1,096.5	4b-3b	3.0	1	>0.05
(5b) $\phi_{2ac^{*}sex^{*}t}, P_c$	1,035.1	51	1,137.1	5b-4b	50.6	5	<0.001
<b>Modelling local survival (<math>\phi</math>)</b>							
(6b) $\phi_{2ac^{*}t}, P_t$	1,000.6	33	1,066.6	6b-4b	16.1	23	>0.75
(7b) $\phi_{2ac^{*}t}, P_t$	1,016.2	23	1,062.2	7b-6b	15.6	10	>0.10
<b>(8b) <math>\phi_{2ac^{*}}, P_t</math></b>	<b>1,031.7</b>	<b>12</b>	<b>1,055.7</b>	<b>8b-7b</b>	<b>15.5</b>	<b>11</b>	<b>&gt;0.10</b>
(9b) $\phi_c, P_t$	1,044.7	11	1,066.7	9b-8b	13.0	1	<0.001

of them were seen in years after the foot injury was first noticed. Local survival rates of females and males were not significantly different for first-year (Table 2, models 6a vs. 2a) or adult (Table 3, models 6b vs. 4b) Dunlin. In first-years, the most parsimonious model (model with lowest AIC value) for local survival was one where  $\phi$  was constrained to be a constant difference between the two age classes (Table 2, model 7a). In adults, the best model was one without significant annual variation in local survival rate (Table 3, models 7b vs. 6b, 8b vs. 7b),

but with a significant effect of year of first capture (models 9b vs. 8b).

We found no effect of sex on local survival rates, so all Dunlin were pooled. We detected a significant age-dependent effect on local survival (Table 4, models 5c vs. 3c), so we modelled factors within each age class separately (models 5c–13c). Dunlin banded as first-years and adults had significantly different local survival rates during the year after banding (a1, the first age-class; models 9c vs. 8c, 10c vs. 8c). However, age at initial banding had no effect on local sur-

TABLE 4. Summary of model testing for all Dunlin (first-year  $n = 609$ , adults  $n = 432$ ) at Bolinas Lagoon, California. Model subscripts include: a1( ) and a2( ) = factors affecting local survival in first and second age classes, respectively, c = constant, grp = group (banded as first-year or adult), t = annual variation. See caption of Table 2 and text for explanation of other terms.

Model	DEV	NP	AIC	LRT	$\chi^2$	DF	P
<b>Modelling resighting rate (<math>p</math>)</b>							
(1c) $\phi_{2ac^{*}grp^{*}t}, P_{grp^{*}t}$	2,662.0	66	2,794.0				
(2c) $\phi_{2ac^{*}grp^{*}t}, P_{grp^{*}t}$	2,669.2	57	2,783.2	2c-1c	7.2	9	>0.50
(3c) $\phi_{2ac^{*}grp^{*}t}, P_t$	2,670.6	56	2,782.6	3c-2c	1.4	1	>0.10
(4c) $\phi_{2ac^{*}grp^{*}t}, P_c$	2,779.1	51	2,881.1	4c-3c	108.5	5	<0.001
<b>Modelling local survival (<math>\phi</math>)†</b>							
(5c) $\phi_{grp^{*}t}, P_t$	2,856.6	34	2,924.6	5c-3c	186	22	<0.001
(6c) $\phi_{a1(grp^{*}t), a2(grp^{*}t)}, P_t$	2,678.7	46	2,770.7	6c-3c	8.1	10	>0.50
(7c) $\phi_{a1(grp^{*}t), a2(t)}, P_t$	2,678.8	45	2,768.8	7c-6c	0.1	1	>0.75
<b>(8c) <math>\phi_{a1(grp^{*}t), a2(c)}, P_t</math></b>	<b>2,684.8</b>	<b>35</b>	<b>2,754.8</b>	<b>8c-7c</b>	<b>6.0</b>	<b>10</b>	<b>&gt;0.75</b>
(9c) $\phi_{a1(grp^{*}t), a2(c)}, P_t$	2,716.3	24	2,764.3	9c-8c	31.5	11	<0.001
(10c) $\phi_{a1(t), a2(c)}, P_t$	2,740.0	23	2,786.0	10c-8c	55.2	12	<0.001
(11c) $\phi_{a1(grp), a2(c)}, P_t$	2,777.0	13	2,803.0	11c-8c	92.2	22	<0.001
<b>Further models</b>							
(12c) $\phi_{a1(grp^{*}t), a2(c)}, P_{rainfall}$	2,774.7	29	2,832.7	12c-8c	89.9	6	<0.001
(13c) $\phi_{a1(grp^{*}t), a2(c)}, P_{effort}$	2,795.2	29	2,853.2	13c-8c	110.4	6	<0.001

† In this notation,  $\phi_{2ac^{*}grp^{*}t}$  is rewritten as  $\phi_{a1(grp^{*}t), a2(grp^{*}t)}$ . For example, comparing models 10c vs. 8c tests whether the local survival of first-years and adults is significantly different during the year after banding. Comparing models 7c vs. 3c tests whether local survival of the two groups is different in subsequent years.

TABLE 5. Yearly resighting rates ( $p$ ) of Dunlin banded at Bolinas Lagoon (model 8c,  $\phi_{a1(\text{grp}^*t),a2(c),p1}$ ), and local survival rates ( $\phi$ ) of first-year and adult Dunlin banded at Bolinas Lagoon in year after capture (model 8c,  $\phi_{a1(\text{grp}^*t),a2(c),p1}$ ). Local survival rate of both adult and first-year Dunlin in subsequent years = 0.73 (95% Confidence Interval 0.70–0.76).

	All Dunlin		First-year Dunlin		Adult Dunlin	
	$p$	95% Confidence Interval	$\phi$	95% Confidence Interval	$\phi$	95% Confidence Interval
1979	0	—	0.43	0.26–0.61	0.58	0.37–0.78
1980	0	—	0.55	0.22–0.84	1.00	0.00–1.00
1981	0	—	0.16	0.05–0.40	0.57	0.31–0.80
1982	0.59	0.46–0.71	0.26	0.15–0.42	0.63	0.43–0.79
1983	0.38	0.28–0.48	0.38	0.27–0.50	0.70	0.53–0.82
1984	0.77	0.68–0.83	0.02	0.00–0.09	0.36	0.12–0.71
1985	0.74	0.64–0.83	0.44	0.29–0.60	0.25	0.11–0.49
1986	0.96	0.90–0.99	0.53	0.42–0.63	0.50	0.37–0.64
1987	0.98	0.92–0.99	0.15	0.06–0.33	0.45	0.30–0.60
1988	0.70	0.60–0.79	0.32	0.13–0.59	0.17	0.04–0.51
1989	0	—	0.50	0.12–0.88	0.50	0.12–0.88
1990	0.81	0.68–0.89	0.29	0.15–0.49	0.59	0.33–0.81
1991	0.71	0.56–0.83	0.17	0.04–0.52	0.59	0.19–0.90
1992	0.48	0.32–0.64	—	—	—	—

vival rate in any of the following years (a2, the second age-class; models 6c vs. 3c, 7c vs. 6c). There was significant annual variation in local survival rate in the year after banding (models 11c vs. 8c), but not in following years (8c vs. 7c).

Mean local survival rates (from model 11c) in the year after banding were lower (first-years  $\phi = 0.33$ , CL = 0.28–0.37; adults  $\phi = 0.53$ , CL = 0.47–0.59) than in following years ( $\phi = 0.74$ , CL = 0.71–0.77). The range of annual estimates of local survival (Table 5, from model 8c) during the year after banding was  $\phi = 0.02$ –0.55 in first-years and  $\phi = 0.17$ –1.00 in adults.

#### EFFECTS OF BANDING AND PREDATION

Newly captured Dunlin lost an average of 4% of their body mass in the first two hours of captivity ( $> 2 \text{ g hr}^{-1}$  in some cases). Hours in captivity ranged from 30 min to  $> 4 \text{ hr}$  (Warnock 1994). The proportion of body mass loss was significantly related to time in captivity, although there was much unexplained variation in this model ( $r_{218} = 0.20$ ,  $P < 0.01$ ). We used data from 33 radiomarked Dunlin at Bolinas Lagoon to examine the timing of predation on marked birds. Nine of the 33 radiomarked Dunlin were depredated by raptors during the two months the radios were active. Seventy-eight percent (7/9) of predation on the radiomarked Dunlin occurred in the first 4 days of release. Between 1986–1992, Peregrine Falcon (*Falco peregrinus*)

and Merlin (*F. columbarius*) were commonly observed ( $0.55 \pm 0.14$  sightings day $^{-1}$ ,  $n = 6$  years).

#### DISCUSSION

##### RESIGHTING RATES

Among first-year birds, we resighted females significantly more than males. Male Dunlin are more prone to temporarily leave their winter grounds at Bolinas Lagoon for sites in the interior of California, especially in wet years (Warnock et al. 1995). First-year birds are generally less efficient foragers than adults and are often displaced from feeding areas (Goss-Custard 1987a, 1987b). It is plausible that first-year, male Dunlin are forced from Bolinas Lagoon in some years.

Spatial segregation of cohorts of birds and biased resighting efforts can lead to erroneous resighting rates and subsequent conclusions about survival of cohorts (Pradel et al. 1995). Spatial segregation of first-year and adult birds does exist between microhabitats within Bolinas Lagoon (Warnock 1990). However, within the estuary, it is unlikely that cohorts of Dunlin were differentially resighted. Bolinas Lagoon is not a large estuary and during falling high tides all Dunlin concentrate at one area within the lagoon and begin feeding as tides recede (Warnock 1990). Our resighting efforts centered on these sites and visibility was excellent. Furthermore, as part of

a separate study, we made an effort to equally sample areas used by first-year birds and areas used by adults (Warnock 1990).

#### LOCAL SURVIVAL OF FIRST-YEAR BIRDS

First-year shorebirds frequently suffer higher mortality rates than adults (Evans and Pienkowski 1984, Cresswell and Whitfield 1994). Local survival of first-year Dunlin at Bolinas Lagoon was significantly lower than local survival of newly-banded and returning adult Dunlin, and was within the range of reported return rates (0.25–0.56) to natal sites for first-year Dunlin (Boyd 1962, Jönsson 1991). Our first-year local survival rate is lower than mean return rates of two slightly smaller, but similar calidrid species, Western Sandpiper (*Calidris mauri*) and Semipalmated Sandpiper (*C. pusilla*), to a wintering site in Puerto Rico (Rice 1995).

Low local survival in first-year birds may be partly an artifact of age-related differences in site-fidelity (Pradel et al. 1995). If, after banding, first-year Dunlin fail to return to Bolinas Lagoon in future years, they are presumed dead even though they may have wintered elsewhere. The process by which first-year birds establish fidelity to wintering sites is poorly understood, but it does seem to occur sometime during their first year. In Italy, establishment of winter site fidelity by first-year Dunlin occurs soon after birds arrive at their wintering sites (Baccetti et al. 1995); however, at Bolinas Lagoon, these patterns are still unknown.

Within a 50 km radius of Bolinas Lagoon lie several estuaries that support populations of Dunlin equal in size to the Bolinas population (up to 5,000 birds, Shuford et al. 1989), including Tomales Bay, California (ca. 20 km north of Bolinas) and Bodega Harbor, California (ca. 50 km north of Bolinas). These estuaries were censused frequently for color-banded Dunlin during at least three years of this study as part of another project (Ruiz et al. 1989), and only a few Bolinas Lagoon Dunlin were recorded, all in the fall and spring when birds were migrating (S. Warnock, per. comm.). Likewise, of 500–1,000 Dunlin color-marked at Tomales Bay and Bodega Harbor, < 4 were seen at Bolinas Lagoon, only for a few days in the spring (N. Warnock, unpubl. data). Part of San Francisco Bay, California, a site that supports over 100,000 Dunlin in winter months (Stenzel and Page 1988), lies within 14 km of Bolinas Lagoon, and Dunlin are

known to commute daily to the bay (Warnock et al. 1995). Occasional searches of the bay failed to yield any birds not also seen at Bolinas Lagoon that year. Extensive resighting efforts at suitable habitat within a 50 km radius of the lagoon suggests that the rate of permanent dispersal from Bolinas Lagoon is low. Furthermore, during this study period, the senior author spent considerable time throughout California to the border of Mexico looking for color-banded shorebirds and never sighted banded Dunlin outside the Point Reyes–San Francisco area. These findings of low permanent dispersal rates are consistent with the results of a study of dispersal of Sanderling (*C. alba*) at nearby Bodega Bay (Myers et al. 1988). Seventy-five percent of Sanderling banded at Bodega Bay were seen only at that site (among years), and only 7% of the birds banded there were seen elsewhere in other years and not at Bodega Bay.

Other factors may lead to different survival rates between first-year and adult birds, perhaps most importantly, predation. In Europe and North America, raptors have been estimated to kill 5–34% of Dunlin populations in a single year (Page and Whitacre 1975, Cresswell and Whitfield 1994). There is strong evidence that first-year Dunlin suffer higher predation rates than adult Dunlin, especially by raptors (Evans and Pienkowski 1984, Cresswell and Whitfield 1994). Research at Bolinas Lagoon has shown that compared to adult birds, first-year Dunlin feed in areas where they are more likely to be attacked by raptors (Warnock 1994), are more likely to be found on the exterior of feeding flocks (Kus 1985), and are significantly more likely to be preyed on by raptors (Kus et al. 1984). These data all support the notion that raptors account for some of the difference in survival between first-year and adult Dunlin at Bolinas Lagoon.

#### LOCAL SURVIVAL OF ADULT BIRDS

Local survival of returning, adult Dunlin at Bolinas Lagoon ( $\phi = 0.74$ ) is within the range of return rates (0.66–0.89) reported in other studies of adult Dunlin (Boyd 1962, Warnock and Gill 1996). This local survival rate is higher than similarly calculated local survival rates for breeding adult Semipalmated Sandpipers (male  $\phi = 0.61$ , female  $\phi = 0.56$ ; Sandercock and Gratto-Trevor 1997) and Snowy Plovers (*Charadrius alexandrinus*,  $\phi = 0.69$ ; Paton 1994),

and confirms strong winter-site fidelity of Dunlin (Warnock et al. 1995). Site fidelity of shorebirds may be stronger to wintering sites than to breeding areas. Alternatively, body size is an indicator of mortality in shorebirds (Boyd 1962, Bèlisle and Giroux 1995), with smaller species having lower survival rates than larger species. Smaller-bodied shorebirds may suffer higher mortality from a greater range of avian predators (Bèlisle and Giroux 1995), accounting for some of the observed variability in return rates to migratory and wintering sites by adult shorebirds.

Soikkeli (1967, 1970b), who studied breeding Dunlin in Finland, failed to find evidence of sex differences in survival, as did our study. However, in Sweden, Jönsson (1991) found significant differences in return rates of breeding adult, male (0.89) and female (0.77) Dunlin, and he suggested predation may be a factor. Our survival results do not support the differential predation hypothesis. The probability of resighting breeding birds may be biased (consequently, so will the survival rates), because site-fidelity of breeding birds is influenced by mating systems, avoidance of inbreeding, and nest success (Greenwood 1980). Male Dunlin typically exhibit stronger breeding site fidelity than females (Soikkeli 1970a) which could account for greater resightings of males than females in some studies.

#### LOCAL SURVIVAL IN YEAR AFTER CAPTURE

Our findings of lower rates of local survival of adult Dunlin in their first capture year than in subsequent years is consistent with studies of other birds. This result may be caused by effects of heterogeneity in capture rates (Francis and Cooke 1993), or it could indicate a banding effect (Pradel et al. 1995). Handling and marking birds affects behavior and sometimes survival (Calvo and Furness 1992). In Snow Geese (*Anser caerulescens*), this effect appears to be caused by differential dispersal in response to banding (Pradel et al. 1995). Few studies have looked at the effects of capture on shorebirds. Lank (1980) found that Semipalmated Sandpipers with patagial wing tags were more likely to be preyed on by raptors than were unbanded birds; but, using the same data set, Brownie and Robson (1983) failed to find a difference in survival estimates between the day after trapping with subsequent days.

Dunlin lose significant mass in captivity (Da-

vidson 1984, this study). We observed numerous avian predators attempting to catch newly-released Dunlin, and the remains of two newly color-banded Dunlin were found in a Long-eared Owl (*Asio otus*) pellet. We suspect that newly released birds, especially those losing the most body mass during captivity, are at higher risk of raptor predation in the few days immediately after capture as has been shown for radiomarked Dunlin and Western Sandpipers (Warnock and Takekawa 1996, this study).

Some of the difference in local survival rates the year after capture appear to be due to this handling effect, but the difficulty in separating permanent emigration from true mortality (Brownie and Robson 1983) confounds a definitive conclusion. Non site-faithful Dunlin (transients) that are captured while passing through Bolinas Lagoon and then permanently emigrate are for the purposes of survival analyses "dead." If transient birds are included in our capture histories, this will cause a decrease in mean local survival rates in the year after capture. The frequency of transient birds in our population is currently unknown but thought to be low (see discussion of dispersal above).

#### POTENTIAL SOURCES OF MORTALITY IN DUNLIN

Few quantitative data have been collected on factors contributing to mortality in shorebirds. Freezing weather makes it difficult for shorebirds to reach their invertebrate prey, and cold conditions have caused mortality in shorebird populations (Peach et al. 1994), including Dunlin (Clark et al. 1993). In North America, no data exist for breeding or nonbreeding grounds to suggest cold weather is a factor in Dunlin mortality. Abundance of food and food quality will affect body condition of birds and consequently their survivorship if body condition decreases too much, but this relationship is poorly understood in shorebirds. Due to the tremendous variability in most invertebrate populations at coastal estuaries (Sewell 1996), relating shorebird survivorship to the variance of their invertebrate prey populations is difficult, except perhaps in cases where birds are relying on single prey species. Ruiz et al. (1989) found lower lipid levels in resident Dunlin at a wintering site where their invertebrate prey populations had crashed locally, but survivorship of these birds was not measured. Parasites may decrease



shorebird survivorship (McNeil et al. 1994), but parasite levels found in Dunlin in North America have generally been low (Warnock and Gill 1996). In some bird populations, pesticides and other contaminants have had a tremendous negative effect. Levels of contaminants have not been found to be high enough to significantly impact Dunlin populations (Warnock and Gill 1996). Predation, mostly by raptors, appears to be the major source of mortality at breeding and nonbreeding grounds for Dunlin in North America (Warnock and Gill 1996) and in Europe, and this appears to hold true for many other species of shorebirds (Cresswell and Whitfield 1994, Peach et al. 1994). Identifying the critical factors affecting survivorship of shorebirds while implementing well designed mark-recapture studies to obtain rigorous estimates of survival will lead to a better understanding of how and why shorebird populations change spatially and temporally. Overall, these data will improve our ability to conserve shorebird populations worldwide.

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