

THE EFFECTS OF AGE AND SEX ON THE APPARENT SURVIVAL OF KENTISH PLOVERS BREEDING IN SOUTHERN TURKEY

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Abstract. Accurate estimates of annual survival are necessary for conservation of threatened species of migratory birds. We studied a large, stable population of Kentish Plovers (*Charadrius alexandrinus*) breeding in southern Turkey (36°43'N, 35°03'E) for five breeding seasons (1996–2000). Kentish Plovers of Eurasia and the conspecific Snowy Plover of North America are a species of conservation concern. We captured 2077 birds, and used time since marking models to estimate apparent survival (ϕ) and encounter rates (p) for juvenile and adult plovers. Return rates of young banded in their natal year were low (4%, 52 of 1176) and most philopatric young were recaptured as yearlings (69%, 36 of 52). Low return rates of shorebird young can be attributed to post-hatching mortality if apparent survival rates are ranked: chicks < fledglings = adults. We were unable to separate mortality from dispersal because apparent survival was ranked: chicks ($\hat{\phi}^1 = 0.08$) < fledglings ($\hat{\phi}^1 = 0.15$) < adults after banding ($\hat{\phi}^1 = 0.59$) < adults in later intervals ($\hat{\phi}^{2+} = 0.64$). Time since marking models gave improved estimates of the apparent survival of adults that were higher than return rates in other populations of Kentish Plovers, but lower than estimates of apparent survival for other *Charadrius* plovers. Sex-biased mating opportunities in Kentish Plovers were not explained by biased sex ratios at hatching or differential apparent survival among adults. Instead, male-biased adult sex ratios were explained, in part, by differential survival of juveniles and by higher encounter rates among adult males ($\hat{p} = 0.84$) than females ($\hat{p} = 0.74$). Our baseline estimates of apparent survival will assist assessments of population viability for Kentish and Snowy Plovers throughout their geographic range.

Key words: age at maturity, *Charadrius alexandrinus*, demography, mark-recapture, sex ratio, Snowy Plover.

Efectos de la Edad y del Sexo sobre la Supervivencia Aparente de *Charadrius alexandrinus* en Áreas de Cría en el Sur de Turquía

Resumen. Contar con estimaciones exactas de la supervivencia anual es necesario para la conservación de las aves migratorias amenazadas. Estudiamos una población grande y estable de *Charadrius alexandrinus* en un área de cría del sur de Turquía (36°43'N, 35°03'E) durante cinco épocas reproductivas (1996–2000). *Charadrius alexandrinus* es una especie con un estado de conservación preocupante tanto en Eurasia como en Norte América. En este estudio capturamos 2077 aves y empleamos modelos del tiempo transcurrido desde el marcado para estimar las tasas de supervivencia aparente (ϕ) y de encuentro (p) para individuos juveniles y adultos. Las tasas de regreso de juveniles anillados a su área de nacimiento fueron bajas (4%, 52 de 1176), y la mayoría de los individuos filopátricos fueron recapturados cuando tenían un año de edad (69%, 36 de 52). Las bajas tasas de regreso de los pichones de aves playeras pueden deberse a mortalidad post-eclosión si las tasas de supervivencia aparente son menores en los pichones que en los volantones y adultos, y si estos dos últimos tienen tasas de supervivencia similares. No estuvimos en capacidad de distinguir entre mortalidad y dispersión debido a que la supervivencia aparente fue mínima en los pichones ($\hat{\phi}^1 = 0.08$) y subsecuentemente mayor en volantones ($\hat{\phi}^1 = 0.15$), en adultos luego de ser marcados ($\hat{\phi}^1 = 0.59$) y en adultos en intervalos posteriores ($\hat{\phi}^{2+} = 0.64$). Los modelos basados en el tiempo transcurrido desde el marcado arrojaron mejores estimados de la supervivencia aparente de los adultos. Estos estimados fueron mayores que las tasas de regreso estimadas para otras poblaciones de *C. alexandrinus*, pero menores que la supervivencia aparente estimada para otras especies de *Charadrius*. Las oportunidades de apareamiento sesgadas de acuerdo al sexo observadas en *C. alexandrinus* no se explicaron

por cocientes de sexos sesgados al momento de la eclosión, ni por diferencias en la supervivencia aparente de individuos adultos. En cambio, los cocientes de sexos sesgados hacia los machos evidentes en los adultos se explicaron en parte por diferencias en la supervivencia de los juveniles y por tasas de encuentro mayores entre machos adultos ($\hat{p} = 0.84$) en comparación con las hembras ($\hat{p} = 0.74$). Nuestros estimados de la supervivencia aparente representan una base que contribuirá a examinar la viabilidad de las poblaciones de *C. alexandrinus* a través de su rango de distribución.

INTRODUCTION

Migratory shorebirds have life-history traits characterized by low productivity (clutch size ≤ 4 eggs, nest failure rates $>50\%$, 1 brood per year), delayed maturity, and a relatively high probability of adult survival (>0.7 per year, Evans and Pienkowski 1984, Piersma and Baker 2000). Of these three components of demography, adult survival frequently has the highest elasticity value and potentially the greatest impact on population growth rates, both in shorebirds (Hitchcock and Gratto-Trevor 1997, Larson et al. 2002) and other long-lived organisms (Crone 2001). Effective conservation of migratory birds requires robust estimates of juvenile and adult survival, but Cormack-Jolly-Seber (CJS) models for live encounter data have been applied to only 15 of 155 species of shorebirds worldwide (Sandercock 2003). CJS models correct for the probability of encounter (p), and yield estimates of apparent survival (ϕ) that are the product of the probabilities of true survival (S) and site fidelity (F).

In this study, we used mark-recapture methods to estimate apparent survival rates for *Charadrius alexandrinus*. *C. alexandrinus* is a cosmopolitan shorebird that nests on coastal beaches and shores of inland alkali lakes. We studied a breeding population of the Eurasian subspecies *C.a. alexandrinus* (hereafter 'Kentish Plover'), in southern Turkey. Two subspecies are found in North America: *C.a. nivosus* west of the Rocky Mountains and *C.a. tenuirostris* in the southeastern U.S. (hereafter 'Snowy Plover'). Estimates of survivorship for Kentish and Snowy Plovers are of interest for three main reasons. First, *C. alexandrinus* populations worldwide are threatened by disturbance from beach recreation, predation by scavengers attracted to garbage and loss of breeding habitat to exotic plants (Lafferty 2001, Ruhlen et al. 2003). As a result, Kentish Plovers are a species of conservation concern throughout much of Europe and Asia (Wiersma 1996, Meininger and Székely 1997, Schmitz et al. 2001). Pacific coast populations of Snowy

Plovers have been listed as Threatened by the U.S. Fish and Wildlife Service since 1993. Southeast populations of Snowy Plovers are state-listed as threatened by at least five states and are under consideration for federal listing (Gorman and Haig 2002, Elliott-Smith et al. 2004). Our study site in Turkey supports a stable population of about 1000 pairs of plovers that breed in good quality habitat (Székely et al. 1999, A. Kosztolányi et al., unpubl. data). Baseline estimates of survival from this population will aid assessments of population viability for *C. alexandrinus* elsewhere.

Second, return rates of juvenile shorebirds banded at the nest are often low (<0.10 , Thompson et al. 1994, Sandercock and Gratto-Trevor 1997), which could be due to high mortality after the precocial young depart the nest, strong natal dispersal, or a combination of these two factors. Here, we calculate apparent survival separately for three groups: young banded at the nest, young known to have survived until fledging, and adults. Such estimates are rare because the precocial young of shorebirds are difficult to monitor after they depart the nest (Lukacs et al. 2004). Nonetheless, if survival rates are ranked: chicks $<$ fledglings = adults, then low return rates among juveniles can be attributed to pre-fledging mortality and not dispersal. If apparent survival is ranked: chicks \leq fledglings $<$ adults, then mortality and dispersal cannot be distinguished.

Third, sexual differences in the apparent survival of juveniles and adults are of interest as a possible explanation for male-biased sex ratios among breeding Kentish and Snowy Plovers. Population surveys frequently reveal a surplus of males in *C. alexandrinus*: Turkey (1.19 ± 0.10 [SD] males per female, $n = 4$ years; TS, unpubl. data), Sweden (1.39 ± 0.32 , $n = 10$ years, P. E. Jönsson, pers. comm.), and California (1.40 , $n = 2$ years, Warriner et al. 1986). Biased sex ratios affect mating opportunities, and experimental clutch and mate removals have shown that female Kentish Plovers locate and

pair with new mates faster than males (1.5 days vs. 12 days, Székely et al. 1999). Previously, we have also shown that the sex ratio is not biased towards males at hatching (Székely et al. 2004). Here, we test three alternative hypotheses; biased sex ratios may be due to: *i*) differential apparent survival among juveniles, *ii*) differential apparent survival among adults, or *iii*) differential encounter rates among adults. Biased sex ratios are of particular interest for Kentish Plovers because this species has an unusual mating system with flexible parental care. Both parents incubate the clutch, but shortly after hatching either parent may desert the brood (Székely and Lessells 1993, Fraga and Amat 1996, Kosztolányi et al. 2003). The incidence and timing of mate desertion are variable, but is usually by females who frequently pair with a new partner and lay another clutch during the same breeding season (Warriner et al. 1986, Székely and Williams 1995, Székely et al. 1999).

The objectives of this study were to: *i*) obtain baseline estimates of apparent survival for a large, stable population of Kentish Plovers breeding in good quality habitat, *ii*) assess whether pre fledging mortality accounts for low apparent survival rates among juvenile plovers, and *iii*) determine whether male-biased adult sex ratios were due to sexual differences in apparent survival or detection rates.

METHODS

FIELD METHODS

Kentish Plovers were studied at Tuzla Lake (36°43'N, 35°03'E), 2 km south of Tuzla village in the Çukurova Delta, southern Turkey. The study area was a saltmarsh bounded by arable land to the north and by the lake to the south. The habitat was open and the vegetation was dominated by halophytes such as *Salicornia europaea* and *Sueda prostrata*. Kentish Plovers are a migrant breeder at this site, and each year we monitored about half of the population of 1000 breeding pairs. We marked birds at three sites that totaled 1.6 km² in area, but resighted birds in an expanded area of 3.5 km². We also conducted periodic surveys of other breeding sites in the Çukurova Delta, but never resighted marked birds away from our study area at Tuzla Lake. Field work at Tuzla Lake was conducted during a 5-year period: between 13 April and 16 July 1996 (95 days), 15 April and 30 June 1997

(77 days), 8 April and 10 July 1998 (94 days), 14 April and 8 July 1999 (86 days), and 20 May and 19 June 2000 (31 days).

Plover nests were located by observing birds from a distance with spotting scopes and by walking at the study site. If a nest was found during egg laying, we revisited the nest until incubation commenced. If a nest was found during incubation, the number of days that the eggs had been incubated was estimated by floating the eggs in lukewarm water (J. Kis and T. Székely, unpubl. data). Nests were checked daily around the expected date of hatching. Plover young were captured and banded with a numbered metal leg band either on the day of hatching or within 1–2 days of departing the nest. Hatchling plovers have well-developed legs and received the same size of bands as adults. Each year, there were a few broods where the nest location was never found and date of hatching was unknown. Székely and Cuthill (1999) made repeated measurements of young from known-age broods, and found that tarsus length is a good indicator of chick age ($r^2 > 0.9$). Tarsus length was used to estimate the age of unbanded juveniles; all such broods were 0–6 days of age. Broods were checked at least every other day until the age of 25 days to count the number of surviving young, and less frequently after 25 days. Young were recaptured opportunistically during brood rearing to determine the minimum number of days that individual young survived post-hatching. Young recaptured close to fledging were uniquely marked with three colored bands.

Adults were captured on their nest using funnel traps and were banded with a numbered metal leg band and an individual combination of three colored bands. Kentish Plovers were aged and sexed by plumage characters: adult males have a rufous colored cap, a black eye-stripe, and a black frontal bar on the chest; the same areas are uniform brown in adult females. Plovers were aged as juveniles in their natal year by the presence of downy feathers or buff-fringed wing coverts. Starting in the second year of the study, a subset of juvenile plovers were sexed with a molecular technique (1997: 10%; 31 of 304, 1998: 88%; 246 of 280, 1999: 90%; 291 of 324). A droplet of blood was collected from the leg vein with a hypodermic needle and stored in 1 mL of Queen's lysis buffer. PCR reactions were then used to amplify two sex-

linked CHD genes to determine sex of the young (Székely et al. 2004).

STATISTICAL ANALYSES

We used mark-recapture methods to estimate annual probabilities of apparent survival (ϕ), corrected for the probability of encounter (p). Apparent survival was the probability that a plover survived and then returned to our study area between two consecutive years. The complement of ϕ included losses to mortality and to permanent emigration resulting from natal or breeding dispersal. Encounter histories were constructed for individual plovers from live encounter data where 0 = not detected during the field season, and 1 = captured or resighted on the study area (Appendix). In analyses of the apparent survival of juveniles, the first record in the encounter history was the year that the plover was banded as a juvenile. A few plovers marked as juveniles were philopatric and returned to the study area as adults. These birds were included in the analyses of apparent survival of adults, but capture and sighting records in the natal year were discarded from the encounter histories before pooling this sample with birds first marked as adults. In the first year of this study (1996), about a third of all adults (68 of 208) were temporarily held in captivity for 1–3 weeks as part of two other experiments (14 of each sex; Székely and Cuthill 1999, 20 of each sex; Székely et al. 1999). Birds that died in captivity or during handling were treated as not released on the last handling occasion. Adults held in captivity were included in the survival analyses because their behaviour after release was normal; most remated quickly with new partners before the end of the breeding season and bred successfully (Székely et al. 1999).

Sparse sample sizes precluded use of mark-recapture statistics to analyze sexual differences in the apparent survival of juvenile Kentish Plovers. Return rates of female and male juveniles were analysed as contingency data with Proc Freq of Program SAS (SAS Institute 2000). Return rates were analysed separately for two different groups of plovers: the subset of juveniles sexed with the CHD genetic markers and all juveniles. In the latter analysis, the expected number of males and females that were marked as hatchlings was estimated separately for equal and observed sex ratios (M:F = 0.85:1, Székely

et al. 2004). Philopatric juveniles were sexed by plumage when they returned as breeding adults.

Mark-recapture analyses were implemented in Program Mark (White and Burnham 1999), following procedures discussed by Burnham and Anderson (1998). First, we selected factors to include in the global model for the probabilities of apparent survival (ϕ) and encounter (p). Mortality rates in precocial birds are often high immediately after nidifugous young depart the nest. We modeled apparent survival of juveniles separately for four independent groups of young (*grp*): birds banded as hatchlings on day 0 and not recaptured during the same breeding season, young that survived at least 1–14 days, young that survived at least 15–28 days, and young that survived until fledging at ≥ 29 days. These groups were defined by stages of development for Kentish Plover young: hatchlings leave the nest at 0–2 days of age, start to thermoregulate independently at 14–15 days, and fledge at 28–30 days of age (Visser and Ricklefs 1993, Page et al. 1995, Székely 1996). We included sex (*sex*) and time-dependence (*t*) in models of apparent survival for adults because these factors affect ϕ and p in many birds. Apparent survival of both juveniles and adults was modeled with time since marking models that separated the interval after first capture (ϕ^1) from all subsequent transitions (ϕ^{2+}). This model design is sometimes denoted as a '2 age-class' model (ϕ_{2ac}). Lower rates of apparent survival after first capture are common in bird populations, and may be due to several nonexclusive factors (Sandercock and Jaramillo 2002, Sandercock 2003). For these reasons, the starting global models were $\phi_{grp*ts}^1, \phi_t^{2+}, p_t$ for juveniles and $\phi_{sex*t}^1, \phi_{sex*ts}^{2+}, p_{sex*t}$ for adults.

Second, we used a parametric bootstrap goodness-of-fit test (hereafter, GOF test) to examine the fit of the starting global models to the plover encounter histories (Appendix). A bootstrap distribution of expected deviances was generated by simulation ($n = 1000$ replicates) and a variance inflation factor (\hat{c}) was calculated as the observed deviance divided by the mean expected deviance. Moderate amounts of overdispersion are common in analyses of mark-recapture data and values of $\hat{c} = 1$ to 3 indicate that the global model is acceptable. We corrected for overdispersion by using \hat{c} -values to adjust model selection and the variance of our parameter estimates.

Third, we proceeded with model testing by fitting reduced models with fewer parameters. All models were constructed with design matrices and the logit-link function. Starting with our global model, we applied constraints to the probabilities in the following order: encounter rates (p), apparent survival of returning birds (ϕ^{2+}), and apparent survival after first capture (ϕ^1). Each probability was modeled by dropping parameters from a factorial model ($sex*t$) to create an additive model ($sex + t$), and then single factor (sex or t) and constant models (c). Model fit was assessed with quasi-Akaike's Information Criterion (QAIC_c):

$$QAIC_c = (\text{Dev } \hat{c}^{-1}) + 2k + 2k(k + 1) (n - k - 1)^{-1},$$

where Dev = the deviance or $-2 \ln [\mathcal{L}(\hat{\theta})]$, \hat{c} = the variance inflation factor, k = the number of parameters, and n = sample size. Model selection was based on the difference in QAIC_c values between models ($\Delta QAIC_c$). By definition, the best-fit model had a $\Delta QAIC_c$ of zero, and other models were equally parsimonious if $\Delta QAIC_c \leq 2$. Akaike weights (w_i) were used to determine the relative likelihood of a model within the set of candidate models:

$$w_i = \exp(-0.5\Delta_i) \left[\sum_{r=1}^R \exp(-0.5\Delta_r) \right]^{-1},$$

where Δ_i is the difference in QAIC_c between model i and the best-fit model. The ratio of Akaike weights between two candidate models ($w_i w_j^{-1}$) was used to quantify the relative degree that a particular model was supported by the data relative to another model(s).

Annual estimates of apparent survival ($\hat{\phi}$) and encounter rates (\hat{p}) were calculated using the model averaging procedure of Program Mark, where parameter estimates were weighted by the Akaike weight of the model from which they were derived. Standard errors of the weighted averages were unconditional and include variance associated with model uncertainty. Overall estimates were calculated by taking the arithmetic average of the annual estimates calculated by model averaging. Variance components procedures were not used to separate sampling and process variance because the duration of our study was relatively short. Data are presented as means \pm SE.

RESULTS

In the first four years of this study, a total of 2077 Kentish Plovers were captured and individually marked. The majority were juvenile plovers captured in their natal year ($n = 1176$), and the remainder were adult males ($n = 432$) and females ($n = 469$). The sample of juveniles was 25% male (292 of 1176, 277 sexed by blood samples and 15 sexed by plumage upon return), 26% female (310 of 1176: 291 by blood and 19 by plumage), and 49% birds of unknown sex (574 of 1176).

APPARENT SURVIVAL OF JUVENILES AND AGE AT FIRST BREEDING

Overall return rates of juveniles were low; only 4% of juveniles (52 of 1176) were recaptured on the study site at least once after their natal year (Table 1). In the sample of juveniles that were sexed using genetic markers, the percentage of males (4%, 10 of 277) and females (5%, 13 of 291) that were philopatric to the study site was not significantly different (Fisher's Exact Test, $P = 0.15$). Similarly, the percentage of returning males (4%, 25 of 588) and females (5%, 27 of 588) was not different among all juveniles, whether the number of hatchlings per sex was estimated from an equal sex ratio (M:F = 1:1, $P = 0.11$) or the observed sex ratio at hatching (M:F = 0.85:1, $P = 0.11$). Among philopatric juveniles of known sex, the percentage of males (80%, 8 of 10) and females (85%, 11 of 13) that were first recaptured as 1-year old birds was not significantly different ($P = 0.40$). Similarly, the percentage of males (72%, 18 of 25) and females (67%, 18 of 27) first captured as 1-year old birds was not different in the sample of all juveniles ($P = 0.22$). As there was little evidence of sexual differences in juvenile return rates, we pooled juveniles of known and unknown sex in subsequent mark-recapture analyses.

The global model $\phi_{grp*t}^1, \phi_t^{2+}, p_t$ was a good fit to live encounter data for plovers marked as juveniles (GOF test, $\hat{c} = 1.06$). In juveniles, the best-fit model was one where the apparent survival of juveniles differed among groups and years in an additive manner (Table 2). However, models with only group effects, time-dependence and constant juvenile survival were equally parsimonious (i.e., $\Delta QAIC_c \leq 2$). The parameters ϕ^{2+} and p collapsed to time dependence and a constant, respectively, in all of the top-

TABLE 1. Sexual and annual variation in the number of juvenile Kentish Plovers first recaptured as either 1-year and ≥ 2 -year old birds.

Sex	Interval ^a	Juveniles of known sex			All juveniles		
		<i>n</i>	1 year	≥ 2 years	<i>n</i> ^b	1 year	≥ 2 years
Males	1996	–	–	–	134	5	3
	1997	16	2	2	152	7	4
	1998	114	6	0	140	6	0
	1999	147	0	–	162	0	–
	All	277	8	2	588	18	7
Females	1996	–	–	–	134	2	2
	1997	15	0	2	152	4	7
	1998	132	6	0	140	7	0
	1999	144	5	–	162	5	–
	All	291	11	2	588	18	9

^a Starting year of interval (e.g., 1996 = 1996–1997).

^b Total number of banded juveniles multiplied by 0.5. The observed sex ratio of Kentish Plovers at hatching is not significantly different from a 1:1 ratio (Székely et al. 2004).

ranked models. The top two models with group effects in juvenile survival had roughly equal support ($w_i w_j^{-1} = 1.1$) and both had >1.5 – 1.9 times the support of the other two parsimonious models. As might be expected for a sample of juvenile birds, a standard Cormack-Jolly-Seber (CJS) model that did not control for time since marking (ϕ_{grp*tr, p_t}) was a poor fit to the encounter histories of juvenile plovers ($\Delta QAIC_c > 39$, $w_i < 0.001$).

Apparent survival of juveniles varied little among years (Table 3). Apparent survival among juveniles was lowest in the last interval (1999–2000), possibly because field effort was reduced in the final year of this study. Mean estimates of juvenile survival were similar among young plovers incapable of flight that survived 0, 1–14 or 15–28 days. Juveniles that survived until fledging (≥ 29 days) had apparent survival rates that were almost double the rates of plovers

TABLE 2. Mark-recapture modeling to estimate apparent survival in the interval immediately after first banding (ϕ^1), apparent survival in later transitions (ϕ^{2+}), and encounter rates (*p*) for juvenile and adult Kentish Plovers.

Age-class	Model structure ^a			Model statistics ^b			
	ϕ^1	ϕ^{2+}	<i>p</i>	Dev	<i>k</i>	$\Delta QAIC_c$	W_i
Juveniles	<i>grp+t</i>	<i>t</i>	<i>c</i>	55.0	10	0.0	0.33
	<i>grp</i>	<i>t</i>	<i>c</i>	61.3	7	0.2	0.30
	<i>c</i>	<i>t</i>	<i>c</i>	68.2	4	1.0	0.20
	<i>t</i>	<i>t</i>	<i>c</i>	62.5	7	1.4	0.16
	<i>grp*<i>t</i></i>	<i>t</i>	<i>c</i>	49.0	18	10.4	<0.01
	<i>grp*<i>t</i></i>	<i>t</i>	<i>t</i>	44.3	21	11.9	<0.01
	<i>grp*<i>t</i></i>	<i>t</i>	<i>t</i>	76.0	19	39.4	<0.01
Adults	<i>t</i>	<i>t</i>	<i>sex</i>	48.7	9	0.0	0.59
	<i>sex+t</i>	<i>t</i>	<i>sex</i>	48.4	10	1.8	0.24
	<i>sex*<i>t</i></i>	<i>t</i>	<i>sex</i>	44.5	13	4.0	0.08
	<i>sex*<i>t</i></i>	<i>sex+t</i>	<i>sex</i>	44.3	14	5.8	0.03
	<i>sex*<i>t</i></i>	<i>sex*<i>t</i></i>	<i>sex</i>	40.8	16	6.4	0.02
	<i>sex*<i>t</i></i>	<i>sex*<i>t</i></i>	<i>sex*<i>t</i></i>	35.9	20	9.7	0.01
	<i>sex*<i>t</i></i>	<i>sex*<i>t</i></i>	<i>sex*<i>t</i></i>	47.5	15	11.1	<0.01
	<i>sex*<i>t</i></i>	<i>sex*<i>t</i></i>	<i>sex*<i>t</i></i>				

^a Model factors included: *c* = constant, *grp* = group (0, 1–14, 15–28, or ≥ 29 days of age), *sex*, *t* = time or annual variation, * = a factorial model, and + = a main effects or ‘additive’ model.

^b Model fit is described by the deviance (Dev), number of parameters (*k*), and the difference in quasi-Akaike’s Information Criterion from the best-fit model ($\Delta QAIC_c$). $QAIC_c$ values were calculated using a variance inflation factor (\hat{c}) of 1.06 for juveniles and 1.47 for adults. Models are presented if they were a starting global model or had moderate support (Akaike weight $w_i \geq 0.002$).

TABLE 3. Apparent survival rates (mean ± SE) of juvenile Kentish Plovers in the interval after first capture (ϕ^1). Juveniles were separated into four independent groups based on the number of days that young were known to have survived after departing the nest (day 0 = day of hatching). Annual estimates were calculated by model averaging. Overall means are the arithmetic average of the first three intervals (1996–1999).

Interval ^a	0 days (<i>n</i> = 444)	1–14 days (<i>n</i> = 395)	15–28 days (<i>n</i> = 268)	≥29 days (<i>n</i> = 66)
1996	0.08 ± 0.02	0.06 ± 0.02	0.09 ± 0.03	0.13 ± 0.07
1997	0.10 ± 0.03	0.07 ± 0.03	0.11 ± 0.04	0.16 ± 0.09
1998	0.09 ± 0.03	0.06 ± 0.03	0.10 ± 0.04	0.15 ± 0.08
1999	0.06 ± 0.03	0.04 ± 0.03	0.07 ± 0.04	0.10 ± 0.07
Overall mean	0.09 ± 0.01	0.06 ± 0.004	0.10 ± 0.01	0.15 ± 0.01

^a Starting year of interval (e.g., 1996 = 1996–1997).

surviving 0–28 days ($\hat{\phi} = 0.15$ vs. pooled $\hat{\phi} = 0.08$). Pooling all four groups of young, the overall rate of apparent survival for juvenile plovers was 0.09 ± 0.01 and the overall encounter rate was 0.41 ± 0.08 .

APPARENT SURVIVAL OF ADULTS

Return rates of adult Kentish Plovers were moderate: 41% (176 of 432) of males and 39% (184 of 469) of females were captured in more than one year. Minor overdispersion was detected when fitting the global model $\phi_{sex^*t}^1, \phi_{sex^*t}^{2+}, P_{sex^*t}$ to the encounter histories of adult plovers (GOF test, $\hat{c} = 1.47$). The apparent survival of adults in the interval after first banding differed from that in subsequent years because the global model had > 2.5 times the support of a standard CJS model $\phi_{sex^*t}, P_{sex^*t}$ that did not control for time since marking. The best-fit model was one with time-dependence in apparent survival after first capture, time-dependence in apparent survival in subsequent intervals and sexual differences in encounter rates (Table 2). A model with annual variation but a constant difference between the sexes in apparent survival after first capture was equally parsimonious ($\Delta QAIC_c = 1.80$), but the

best-fit model had >2.4 times the support of this and all other candidate models.

Estimates of apparent survival from model averaging showed considerable annual variation but only small differences between the sexes (Table 4). Apparent survival rates during the first three intervals of the study were 2–3 times greater than our estimate for the interval between 1999–2000. Low apparent survival in the last interval was likely the result of reduced resighting effort in the final year of the study. Accordingly, estimates of apparent survival for 1999–2000 are presented for comparison but are not included in the overall means. Apparent survival rates of adults were greater in later intervals ($\hat{\phi}^{2+}$) than immediately following first capture ($\hat{\phi}^1$), but the difference between these rates ($\hat{\phi}^{2+} - \hat{\phi}^1$) was more pronounced in some years (1997–1998: 0.15 to 0.16) than others (1998–1999: 0.06 to 0.07). Based on the subset of breeding birds that returned to the study area at least once, our best overall estimate of apparent survival for adult Kentish Plovers was $\hat{\phi} = 0.64$. Encounter rates (\hat{p}) averaged 0.84 ± 0.04 in males and 0.74 ± 0.05 in females.

TABLE 4. Apparent survival rates (mean ± SE) of adult Kentish Plovers in the interval after first capture (ϕ^1) and later intervals (ϕ^{2+}). Annual estimates were calculated by model averaging. Overall means are the arithmetic average of the first three intervals (1996–1999).

Interval ^a	Males (<i>n</i> = 456)		Females (<i>n</i> = 491)	
	Interval after first capture	Later intervals	Interval after first capture	Later intervals
1996	0.71 ± 0.05	–	0.73 ± 0.06	–
1997	0.48 ± 0.05	0.64 ± 0.06	0.50 ± 0.05	0.64 ± 0.06
1998	0.56 ± 0.07	0.63 ± 0.05	0.56 ± 0.07	0.63 ± 0.06
1999	0.18 ± 0.21	0.34 ± 0.28	0.17 ± 0.42	0.33 ± 0.48
Overall mean	0.58 ± 0.07	0.63 ± 0.01	0.60 ± 0.07	0.64 ± 0.01

^a Starting year of interval (e.g., 1996 = 1996–1997).

DISCUSSION

We used mark-recapture statistics to estimate annual rates of apparent survival for juvenile and adult Kentish Plovers at a breeding site in southern Turkey. Our estimates of apparent survival (ϕ) are an improvement over return rates because the probability of encounter (p) was < 1 for both age classes (Tables 3 and 4). However, apparent survival remains a conservative measure of annual survival because ϕ is the product of true survival and site fidelity. Site fidelity appeared to be high among Kentish Plovers in Turkey because we did not observe marked birds in surveys of breeding sites elsewhere in the Çukurova Delta. However, Snowy Plovers in California are known to move long distances between breeding attempts (up to 1140 km, Stenzel et al. 1994), and permanent emigration could have been an undetected feature of our study population. We discuss the implications of our apparent survival estimates for understanding the demography of *Charadrius* plovers.

APPARENT SURVIVAL OF JUVENILES AND AGE AT FIRST BREEDING

Apparent survival rates in the interval after first capture were ranked: young incapable of flight ($\hat{\phi}^1 = 0.08$) $<$ young surviving until fledging ($\hat{\phi}^1 = 0.15$) $<$ adults ($\hat{\phi}^1 = 0.59$). In *Charadrius* plovers, mortality rates are greatest when chicks are less than 6–10 days old (Warriner et al. 1986, Loegering and Fraser 1995, Ruhlen et al. 2003, Lukacs et al. 2004). We found that nest departure and development of homeothermy did not confer a substantial survival advantage in Kentish Plovers because apparent survival rates were similar among groups of young last sighted at 0, 1–14, and 15–28 days of age. A roughly twofold increase in apparent survival after fledging indicates that flight ability helps plover young to evade predators, and that mortality rates were highest for young during the first four weeks after hatching. The apparent survival of fledgling Kentish Plovers was less than one quarter of the apparent survival rate of adults.

Two previous studies of shorebirds have reported separate estimates of survival for chicks, fledglings and adults. In a 7-year study of Ringed Plovers (*C. hiaticula*), Pienkowski (1984) reported return rates of 0.29 for chicks, 0.57 for fledglings, and 0.80 for adults. In a 3-year study of Common Redshanks (*Tringa totanus*), Thompson and Hale (1989) found that

return rates of redshank young increased with age at banding: 0.01 for young banded at the nest, 0.05 for young banded at 1–15 days, and 0.14 among young banded at 16–30 days. However, return rates of these young were lower than return rates of adults (0.36–0.40, Thompson and Hale 1989) and apparent survival rates of adults during a 15-year study at the same study site ($\phi = 0.72$ –0.75, Thompson and Hale 1993). Thus, our results for Kentish Plovers were consistent with previous work in that apparent survival was ranked: chicks \leq fledglings $<$ adults. Estimates of apparent survival are unlikely to be adequate for separating the effects of mortality and permanent emigration on low rates of juvenile survival, except in the rare circumstance where survival of fledglings is high and natal philopatry is strong.

Our overall estimate of apparent survival for Kentish Plover chicks ($\phi = 0.08$) was higher than return rates and apparent survival rates of *Charadrius* plovers marked as young: Killdeer *C. vociferus* (0.0, Lenington and Mace 1975), Mountain Plovers (0.01, *C. montanus*, Graul 1973), Ringed Plovers (0.04, Laven 1940), Piping Plovers (0.05, Wilcox 1959), Kentish Plovers in Germany (0.06, Rittinghaus 1956), Semipalmated Plovers (0.16, *C. semipalmatus*, Flynn et al. 1999), and Piping Plovers ($\phi = 0.32$, Larson et al. 2000). On the other hand, our estimate of apparent survival for fledgling Kentish Plovers ($\phi = 0.15$) was low compared to return rates and apparent survival rates of fledglings in other plover species: Great Plains Piping Plovers (0.12, Haig and Oring 1988a), Mountain Plovers ($\phi = 0.47$, Dinsmore et al. 2003), Atlantic Piping Plovers ($\phi = 0.48$, Melvin and Gibbs 1996), and Snowy Plovers (0.64, Page et al. 1983). Comparisons are challenging because interspecific variability could be due to differences in true survival, site fidelity, or encounter rates. In the present study, we suspect that our estimates of juvenile survival are conservative because our study area was set within a larger region of contiguous saltflats that was also suitable breeding habitat. Moderate rates of natal dispersal would have reduced apparent survival if juvenile plovers permanently emigrated from our study population. Better estimates of pre-fledging and juvenile survival for *Charadrius* plovers may require use of radio-telemetry (Miller and Knopf 1993), improved brood survey methods (Lukacs et al. 2004), or joint mark-recapture models that

combine live encounter and dead recovery information (L. E. Stenzel et al., unpubl. data).

Philopatric Kentish Plover young were usually recaptured as breeding yearlings (69%), and the remainder were first observed breeding as 2-year olds or older (31%, $n = 52$, Table 1). Similar age distributions have been reported in Ringed Plovers (yearlings: 94% and ≥ 2 -year olds: 6%, $n = 36$, Pienkowski 1984) and Northern Lapwings (*Vanellus vanellus*, yearlings: 67%, 2-year olds: 27%, and ≥ 3 -year olds: 6%, $n = 103$, Thompson et al. 1994). In Semipalmated Plovers, no philopatric young were captured as yearlings, 14% were captured as 2-year olds, 71% as 3-year olds and 14% as ≥ 4 -year olds ($n = 7$, Flynn et al. 1999). Distributions of age of first capture are sometimes interpreted as variation in age at first breeding, which is reasonable if the probability of encounter is close to unity. In this study, the probability of encounter was lower among Kentish Plovers banded as juveniles ($\hat{p}_{\text{juv}} = 0.41$) than adults ($\hat{p}_{\text{adt}} > 0.74$). Similar differences have been reported in Snowy Plovers ($\hat{p}_{\text{juv}} = 0.21$ and $\hat{p}_{\text{adt}} > 0.52$, Patton 1994) and Piping Plovers ($\hat{p}_{\text{juv}} = 0.26$ and $\hat{p}_{\text{adt}} = 0.44$, Larson et al. 2000). If all Kentish Plovers started breeding as yearlings, and if $\hat{p} = 0.41$ for yearlings and 0.79 thereafter, the expected distribution of age at first capture would be: 41% as yearlings, 47% as 2-year olds, and 12% as ≥ 3 -year olds. However, our observed distribution of age at first capture was skewed towards yearlings (Table 1, $\chi^2_2 = 19.4$, $P < 0.001$). We conclude that a majority of Kentish Plovers in Turkey start breeding at 1 year of age, and that birds first captured as ≥ 2 -year olds were probably overlooked for one or more years.

ADULT SURVIVAL

Time since marking was an important source of heterogeneity in the apparent survival rates of adult Kentish Plovers in Turkey. We found greater support for models that separated the interval after first banding from later transitions (Table 2), although the relative difference in apparent survival of adults was large in only a subset of years (Table 4). Time since marking models control for animals that are never detected after the year of banding, which can be evidence of age or handling effects on survival or site fidelity, presence of transient breeders, or heterogeneity of capture (Sandercock and Jaramillo 2002). For example, breeding dispersal follow-

ing nest failure occurs in both Snowy (Stenzel et al. 1994) and Semipalmated Plovers (Flynn et al. 1999). Transient breeders have not been reported in *Charadrius* plovers but are a feature of other migratory birds (Francis and Cooke 1993). Heterogeneity of capture was unlikely to be important in our study because plovers were resighted in an expanded zone around our core study sites. We were unable to evaluate the relative importance of these alternatives, but our results join growing evidence that time since marking models are a preferred starting global model for analyses of live encounter data (Sandercock and Jaramillo 2002, Sandercock 2003).

Controlling for encounter rates and time since marking yielded estimates of apparent survival for adults that were higher than return rates for 4 of 5 populations of Kentish Plovers in Europe, but lower than 4 of 5 populations of Snowy Plovers in North America (Table 5). It is unclear at present if subspecific differences in return rates are due to variation in true survival, but caution is warranted if these estimates are used to parameterize population models for *C. alexandrinus*. Overall, the apparent survival of adult Kentish Plovers in Turkey ($\phi = 0.64$) was lower than the apparent survival rates reported for five other species of *Charadrius* plovers: $\phi = 0.68$ in Mountain Plovers (Dinsmore et al. 2003), $\phi = 0.74$ in Piping Plovers (Larson et al. 2000), $\phi = 0.75$ in Double-banded Plovers (*C. bicinctus*, Barter 1991), $\phi = 0.77$ in Semipalmated Plovers (Badzinski 2000), and $\phi = 0.87$ in Ringed Plovers (Wallander and Andersson 2003). Variation in apparent survival among plovers may be due, in part, to interspecific differences in body size: Kentish Plovers are smaller than the other five species of plovers (41 g vs. 46–110 g, Dunning 1993).

SOURCES OF BIAS IN ADULT SEX RATIOS

A surplus of adult males is a common feature of *C. alexandrinus* populations and at least four hypotheses may explain such bias in adult sex ratio: *i*) a biased sex ratio at laying or hatching, *ii*) sexual differences in the apparent survival of juveniles, *iii*) greater apparent survival among adult males, or *iv*) higher encounter rates among adult males. We reject the first hypothesis because the hatching sex ratio among Kentish Plovers in Turkey was not significantly different from a 1:1 ratio, and is actually biased towards females (M:F = 0.85:1, $n = 454$ chicks in 158

TABLE 5. Estimates of annual survival for Kentish Plovers (*Charadrius alexandrinus alexandrinus*) and western Snowy Plovers (*C. a. nivosus*) based on live encounter data.

Species	Sex ^a	Age ^b	Locality	Type ^c	Estimate ± SE ^d	Number of			Source
						esti- mates ^e	years ^f	birds ^g	
Kentish Plovers	MF	C	Germany	Ret-S	0.06 ± 0.02	9	10	1220	Rittinghaus 1956
	MF	C	Turkey	CMR- CJS	0.08 ± 0.01	3	5	1107	This study
	MF	F			0.15 ± 0.01			66	
	MF	A	Spain	Ret-S	0.51	1	6	80	Amat et al. 1999
	MF	A	Germany	Ret-S	0.55 ± 0.04	9	10	410	Rittinghaus 1956
	F	A	Hungary	Ret-A	0.57	1	7	37	Székely and Williams 1995
	MF	A	Denmark	Ret	0.59 ± 0.13	1	4	108	Boyd 1962
	M	A	Turkey	CMR- TSM	0.63 ± 0.01	2	5	456	This study
	F				0.64 ± 0.01			491	
	M	A	Sweden	Ret-S	0.82 ± 0.04	9	10	178	P. E. Jönsson, unpubl. data
F				0.78 ± 0.04			134		
Snowy Plovers	MF	CF	UT, USA	CMR- CJS	0.39 ± 0.30	1	4	171	Paton 1994
	MF	F	CA, USA	Ret-S	0.64	1	2	14	Page et al. 1983
	M	A	UT, USA	Ret-S	0.58 ± 0.06	3	4	224	Paton and Ed- wards 1996
	F				0.51 ± 0.06			278	
	MF	A	UT, USA	CMR- CJS	0.73 ± 0.09	3	4	361	Paton 1994
	M	A	Monterey CA, USA	Ret-S	0.77	1	3	47	Page et al. 1983
	F				0.72			54	
	M	A	Mono Lake, CA, USA	Ret-S	0.78	1	2	18	Page et al. 1983
	F				0.45			49	
	M	A	Pajaro, CA, USA	Ret-S	0.79	1	6	56	Warriner et al. 1986
F				0.73			73		

^a M = male, F = female.

^b C = chicks incapable of flight, F = fledglings, A = adults ≥1 year of age.

^c CMR-TSM = estimate based on a capture-mark-recapture model that controls for time since marking (ϕ_t^1 , ϕ_t^{2+} , p_t), CMR-CJS = estimate based on a time-dependent Cormack-Jolly-Seber model (ϕ_t , p_t), Ret-S = return rate in the year immediately following banding, and Ret-A = return rate in all years following banding.

^d Arithmetic mean of annual survival rates (number of estimates >1) or return rate based on pooled years (number of estimates = 1).

^e Number of annual estimates of apparent survival.

^f Duration of study in years.

^g Sample size of birds or bird-years.

broods, Székely et al. 2004). The second hypothesis received mixed support. We found no evidence of sexual differences in juvenile return rates, but our test was relatively weak because most disappearances were unexplained ($1 - \hat{\phi} > 0.85$). Sex differences in the true survival of juvenile Kentish Plovers remain plausible because juvenile females have lower growth rates than males, and because late season broods contain more females (Székely et al. 2004). It is

possible that we were unable to detect seasonal effects on juvenile survival because a majority of the surviving young eventually dispersed.

We found no support for the third hypothesis: apparent survival did not differ between males and females and was 0.58–0.64 among all adults (Table 4). Previous studies have found little evidence of sexual differences in the reproductive effort of Kentish Plovers. Amat et al. (2000) found that body condition, metabolic rates, and

daily energy expenditure of males and females are similar throughout the breeding season. Moreover, males and females responsible for uniparental care of broods do not differ in their attendance behavior or subsequent chick survival and growth, at least for our study site in Turkey (Székely and Cuthill 1999, but see Székely 1996). Nevertheless, equivalent rates of apparent survival for males and females are surprising because males have higher return rates than females in most *Charadrius* plovers: Kentish and Snowy Plovers (Table 5), Piping Plover (males and females: 0.75 and 0.56, Haig and Oring 1998b), Semipalmated Plover (0.60 and 0.41, Flynn et al. 1999) and Killdeer (0.56 and 0.20, Lenington and Mace 1975).

The fourth hypothesis was supported: sexual differences in encounter rates (p) may explain both male-biased sex ratios, and also higher return rates among male plovers. In at least three species of plovers, sexual differences have been found in encounter rates of adults but not their apparent survival: Kentish Plovers (males: $p = 0.84$; females: $p = 0.74$, this study), Snowy Plovers ($p = 0.68$; $p = 0.52$, Paton 1994) and Semipalmated Plovers ($p = 0.85$; $p = 0.64$, Badzinski 2000). Ratios of these sex-specific encounter rates yield predicted sex ratios ($\hat{p}_m \hat{p}_f^{-1} = 1.13$ – 1.33) that are comparable to the observed sex ratios of Kentish Plovers based on count data (1.19–1.40). Encounter rates of male plovers may be higher because male behavior and plumage coloration makes them conspicuous to human observers, especially during daylight hours when population surveys are conducted. Female Kentish Plovers spend more time incubating and attend the clutch during daylight hours, whereas males incubate mainly at night (Kosztolányi and Székely 2002), an incubation schedule shared with other *Charadrius* plovers (Thibault and McNeil 1995, Warnock and Oring 1996, Blanken and Nol 1998). Moreover, off-duty male Kentish Plovers are gregarious and form flocks at feeding areas (TS, pers. obs., Paton and Edwards 1996). Sexual differences in p are not a complete explanation for the male-biased sex ratio of Kentish Plovers in Turkey, however, because females were able to remate faster than males (Székely et al. 1999). In the future, better estimates of juvenile survival will improve our understanding of sex ratio variation in plover populations, as well as the implications of biased

sex ratios for the evolution of mating and parental behavior.

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APPENDIX. Encounter histories and numbers of Kentish Plovers banded as juveniles or as adults. Age in days is the minimum age to which the juvenile survived, where 0 = hatchlings and ≥ 29 = fledglings. Numbers in brackets indicate the number of birds that were not released upon last capture.

Encounter history	Juveniles (age in days)				All	Adults	
	0	1–14	15–28	≥ 29		Females	Males
11111	1	0	0	0	1	4	4
11110	0	0	0	0	0	7 (1)	11
11101	0	0	0	0	0	1	1
11100	1	0	0	0	1	18	14
11010	0	0	0	0	0	7	0
11001	0	0	0	0	0	1	0
11000	1	2	1	1	5	27	23
10110	0	0	1	0	1	2	3
10100	0	1	0	0	1	2	4
10011	0	0	1	0	1	0	0
10010	0	0	1	1	2	4	1
10001	0	0	0	0	0	1	0
10000	87	93	60	16	256	33 (1)	38
01111	0	0	0	0	0	2	15
01110	2	2	0	0	4	26 (2)	16
01101	1	0	0	0	1	2	1
01100	2	2	2	0	6	23	25
01011	0	0	0	0	0	0	1
01010	5	1	3	1	10	5 (1)	2
01001	0	0	1	0	1	0	1
01000	75	121	77	9	282	73	83
00111	1	0	2	1	4	8	9
00110	2	2	4	1	9	23	25
00101	0	0	0	0	0	4	5
00100	90	93	61	23	267	48	36
00011	3	1	1	0	5	16 (1)	24
00010	176	77	54	12	319	143 (5)	114
Total	444	395	268	66	1176	491	456