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Estimating sex specific apparent survival and dispersal of Little Ringed Plovers (*Charadrius dubius*)

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Sex differences in survival have consequences to population dynamics making information on sex specific survival important. In birds, females often have lower survival than males, and one of the main mechanisms is considered to be differential reproductive investment. We studied apparent adult survival and local recruitment of a small monogamous shorebird, the Little Ringed Plover (*Charadrius dubius*), with 18 years of capture–recapture data collected from a population breeding in Southern Finland. We expected no sex differences in adult survival because parental care is shared and double-broods and excessive relaying are rare in this northern population. Because apparent survival is the product of true survival and site fidelity, we also estimated breeding and natal dispersal distances within the study area to examine bias in survival estimates caused by permanent emigration. We found higher apparent adult survival in males (0.660) than in females (0.609), but no sex differences in local recruitment (0.080). Breeding dispersal distances were longer in females than in males mainly due to lower breeding site fidelity of females (0.620) than that of males (0.808). Thus, the lower apparent survival of females likely resulted from permanent emigration. Interestingly, the philopatric portion of the population (from local recruitment analysis) had higher apparent adult survival than what was found from the analysis of all adults. These apparent survival estimates that are less likely to be biased by permanent emigration showed no sex differences (males 0.734; females 0.721), supporting our conclusion of no sex difference in true adult survival.

1. Introduction

Survival is one of the most influential life history stages affecting dynamics in vertebrate populations, especially in long lived species (Sæther & Bakke 2000, Oli & Dobson 2003). In birds, females often have lower survival than males, while the opposite occurs in mammals (Liker & Székely 2005). Sex-biased survival has implications for sex ratios, and consequently for breeding systems and population dynamics (Donald 2007, Grüebler *et al.* 2008, Liker *et al.* 2013, Székely *et al.* 2014). Therefore, information on variation in sex-specific survival in different taxa is important for gaining a better understanding of its causes, consequences and applications in conservation.

Sex-biased survival may result from differ-

† Deceased

ences in size, appearance, food, reproductive investment (e.g. parental care or mating competition) or susceptibility to predation or parasites (Promislow *et al.* 1992, Liker & Székely 2005, Donald 2007). In addition, members of the heterogametic sex (males in mammals, females in birds) may have higher mortality due to expression of deleterious alleles (Liker & Székely 2005). Alternative explanations of the observed differences in sex-specific survival are biased detection rates when return rates are used in studies (Sandercock *et al.* 2005) and different dispersal behaviour in open populations (Tavecchia *et al.* 2002). Either sex may have a higher probability to disperse outside the study area resulting in permanent emigration which is confounded with mortality when estimating apparent survival (Sandercock 2006). Sex specific natal dispersal is a common feature in animals where it probably functions to avoid inbreeding and kin-competition (Greenwood 1980, Clobert *et al.* 2001). The more dispersive sex usually depends on whether the breeding system is founded on resource or mate defence (Greenwood 1980). Birds usually have a resource defence system and females are more likely to change breeding sites after reproductive failure, divorce or death of a mate, whereas males benefit more from being faithful to their old territory (Clarke *et al.* 1997).

Shorebirds are an interesting group of birds in this respect because they have large variation in breeding systems, parental care, incubation patterns and dispersal behaviour (Oring & Lank 1984, Székely *et al.* 2006, Burns *et al.* 2013). Despite numerous studies on shorebirds, sex differences have rarely been observed with methods that control for recapture probabilities (Sandercock & Gratto-Trevor 1997, Stenzel *et al.* 2011, Colwell *et al.* 2013).

We used long-term (1980–1998) mark-recapture data collected from an apparently stable Little Ringed Plover (*Charadrius dubius curonicus*) population breeding in a large study area in Southern Finland to examine sex specific apparent adult survival and local recruitment. We provide the first estimates of apparent survival for this common yet rarely studied shorebird. Because sexes in this territorial and socially monogamous species are monomorphic in size, and share incubation and brood rearing duties (Cramp & Simmons 1983, Hedenström 1987), we hypothesize no differences in apparent survival. Because females may be more likely to permanently emigrate, we also assess sex differences in natal and breeding dispersal distributions within the study area.

2. Material and methods

2.1. The study species

Little Ringed Plover is a small (38 g) invertebrate feeding shorebird (Cramp & Simmons 1983). The species prefers the vicinity of fresh water but can also be found in saline inland pools and flats, brackish estuaries or lagoons. Humans have artificially created new but often temporary habitats at gravel pits, refuse dumps, sewage works, industrial wastelands, ports and opencast mining sites (Delany *et al.* 2009). Its breeding range extends across the main Western Palaearctic landmass through mild boreal, temperate, and Mediterranean zones (Delany *et al.* 2009). The European population is evaluated to be < 100,000 pairs and its overall trend suggests a small decline; currently the population is assigned to the "Least Concern" category in the IUCN classification (BirdLife International 2015). In Finland, the breeding distribution ranges from Southern Finland to Southern Lapland with a population size of 4,000–5,000 pairs (Valkama *et al.* 2011).

Fennoscandian Little Ringed Plovers winter from sub-Saharan Africa to India (Hedenström *et al.* 2013). They arrive to the breeding grounds in southern Finland in late April. Little ringed plovers normally start breeding as yearlings but often not until two years old (Cramp and Simmons 1983). Egg laying starts in May. A clutch of four eggs is laid in an open nest cup with little or no vegetation surrounding the nest (Cramp & Simmons 1983). Little Ringed Plovers usually tend one brood per season in Fennoscandia, but commonly renest after failure (Arppe 2000).

2.2. Study population and data collection

Breeding adult Little Ringed Plovers and their chicks were marked with uniquely numbered steel rings during 1978–2005 mostly in made-made habitats including 177 different breeding sites (sand pits, train yards etc.) in the city of Helsinki and surrounding municipalities in southern Fin-

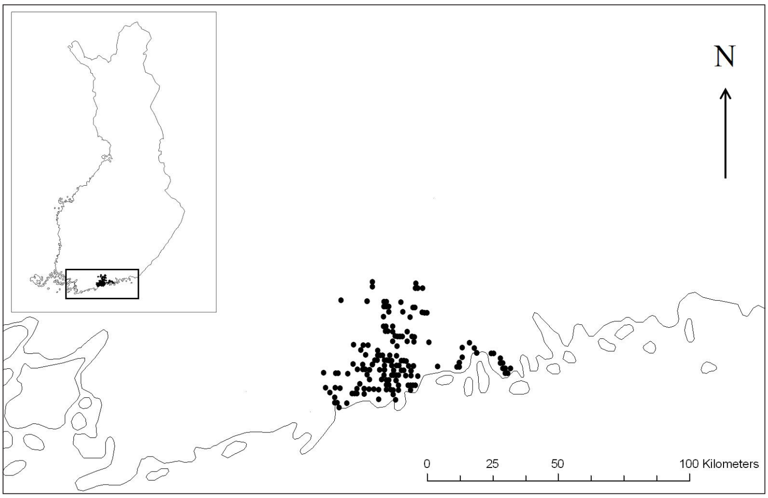

Fig. 1. Location of the study area in Southern Finland. The black circles represent the breeding sites where Little Ringed Plovers were studied.

land (Fig. 1; Arppe 2000, Saurola *et al.* 2013). Breeding site contained one or more territories. Both unmarked and marked adults were captured at the breeding sites with cages while incubating a nest or when brooding chicks. Hence, recaptures involved capturing the bird multiple times. We used only data from 1980 to 1998 when the sampling effort was fairly similar across years. These data consist of 4,135 chicks and 1,386 adults (639 males, 747 females). Adults were sexed based on plumage characteristics, which is relatively easy with breeding birds when sexes can be compared (Meissner 2007). Due to uncertainty or missing information, we removed 33 adults from the data. Because we did not have sex information on juveniles, we assigned the sex of non-returning individuals with the method described in Szép (1999), where an equal sex ratio is assumed among ringed chicks each year. While sex ratios may part from equality, most hatching sex ratios are balanced (Donald 2007). This is the case also for a close relative, the Kentish Plover (*Charadrius alexandrinus*; Székely *et al.* 2004), a fact supporting our assumption. However, due this uncertainty in sex of the non-recruiting juveniles, results from this comparison should be viewed with caution.

2.3. Modelling approach and goodness-of-fit tests

We used live encounter data to examine annual apparent adult survival (Φ_{ad}) and local recruitment probabilities (Φ_{juv}) using capture–recapture models developed for open populations (Lebreton *et al.* 1992). Local recruitment is a function of first-year survival and natal philopatry. Survival was modelled in program MARK 8.0 (White & Burnham 1999). The goodness-of-fit tests were performed with U-CARE 2.3.2 (Choquet *et al.* 2009).

The goodness of fit test for our starting model for modelling apparent adult survival that included effects of sex and time (t) and their interaction (*), [Φ(sex*t) p(sex*t)], was not significant (df = 127, χ^2 = 110.22, p = 0.86). However, the overall signed statistic for trap-dependence was significantly negative [z = –2.859, p(two-tailed) = 0.004] indicating trap-happiness. This was due to trap dependence among males (test for differences in recapture probabilities, TEST2.CT; df = 16, χ^2 = 28.84, p = 0.03) but not in females (df = 16, χ^2 = 17.63, p = 0.35). TEST2.CL (test for differences in recapture probabilities) was not significant in either sex (males: df =15, χ^2 = 16.79, p = 0.33; females: df = 13, χ^2 = 11.46, p = 0.57). There was no evidence of heterogeneity in survival during the first year after being marked (test for differences in survival probabilities, i.e. transience, TEST3.SR; (males: df = 17, χ^2 = 4.629, p = 0.99; females: df =17, χ^2 = 15.09, p = 0.59) or later (test for differences in survival probabilities, TEST3.SM; males: df=18, χ^2 = 6.9224, p = 0.99; females: df = 15, χ^2 = 8.847, p = 0.89). See Appendix 1 and Choquet *et al.* (2009) for more information on the above tests.

Because not considering trap-dependence leads to biased estimate of survival, we modelled trap-dependence with the traditional approach outlined in Pradel (1993). The data were arranged so that each capture history was terminated after each recapture, and the individual was marked as removed from the analysis ("loss on capture"). Then new encounter histories were created starting from each recapture (Pradel 1993). This was repeated until the last recapture. This data manipulation was done with U-CARE (Choquet *et al.* 2009). We note that this approach does not replicate new data, and does not lead to pseudo-replication. The amount of data does not change. Importantly, this arrangement of data together with an age structure in recapture rates allows the modelling of recapture probabilities in relation to whether or not an individual was captured in the previous encounter occasion (i.e. year). Our final global model thus included immediate trap-dependence (m) on capture probabilities [Φ(sex*t) p(sex*m*t)]. The goodness-of-fit test for this model calculated with tests 3.SR + 3.SM + 2.CL indicated good fit with the data ($df = 95$, $\chi^2 = 63.7$; $p = 0.994$).

The overall goodness of fit of our starting model for local recruitment [Φ(sex*t) p(sex*t)] indicated poor fit with the data ($df = 123$, $\chi^2 = 415.59$, $p < 0.0001$) due to both transience (signed statistic for transience, $z = 15.99$, $p < 0.0001$) and trap-dependence (signed statistic for trap-dependence, $z = 2.345$, $p = 0.019$). Transience is caused by a genuine age effect in juvenile data, and we considered it with an age effect (Sandercock 2006). We then excluded TEST 3.SR and assessed goodness of fit for model [Φ(age*sex*t) p(sex*t)] with tests 3.SM, 2.CT and 2.CL, which was nearly significant ($df = 89$, $\chi^2 = 109.95$, $p = 0.066$). Because we wanted unbiased estimates of local recruitment we chose a global model that simultaneously considers age- and trap-dependence (Schmidt *et al.* 2002, Doligez *et al.* 2004). Thus, a similar splitting of data was performed as for the adult data. When the individuals were inserted back to the data after splitting their capture histories, individuals were grouped by age (first year- and older birds). The starting model [Φ(a2*sex*t) p(m*sex*t)] included two age classes (a2), sex and time (t) dependence. Recapture probabilities included trap-dependence (m) in interaction with time (t) and sex. Because our focus was on local recruitment, and because goodness of fit tests for a three age class survival structure together with trap-dependence are not available, we only examined survival with two age classes.

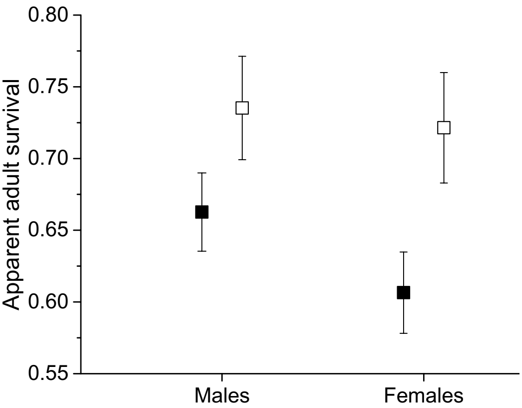

Fig. 2. Average apparent adult survival (± SE) of male and female Little Ringed Plovers breeding in Finland during 1980–1998 estimated from all adult data (filled symbols) and from juvenile data (philopatric individuals, open symbols). Survival rates were calculated by model averaging (ΔAICc = 4).

The goodness of fit for this new global model was done in three steps (Schmidt *et al.* 2002, Belda *et al.* 2007). In the first step, the goodness of fit for the original model was calculated by summing χ^2 values and degreed of freedom for elements 3.SM + 2.CT + 2.CL (df = 89, $\chi^2 = 109.96$). Second, the differences in deviance and the deviance degrees of freedom were calculated for models differing in their recapture probability with respect to trap-dependence, p(sex*m*t) and p(sex*t), i.e. deviance: 2011.39 – 1969.03 = 42.4, *df*: 51 – 34 = 17. In the third step, goodness of fit of the model was evaluated by comparing this difference to the original goodness of fit test ($df = 72$, $\chi^2 = 67.59$, $p = 0.63$), which suggested that the new model is a suitable starting model. We estimated overdispersion by comparing models p(sex*m*t) and p(sex*t), ($\hat{c} = 42.4 / 17 = 2.49$).

2.4. Model selection

We fitted a set of *a priori* models containing structures that tested for time dependence, linear and quadratic trends and sex in both survival and recapture rates. Akaike's information Criterion corrected for a small sample (AICc) or after correcting for over-dispersion the Quasi-AICc were used in the model selection. A difference between the

Table 1. Results of modelling apparent adult survival (A) and local recruitment (B) of Little Ringed Plovers breeding in Southern Finland. # = model number, Model = model structure, (Q)AICc = (Quasi-)Akaike's information criterion corrected for small sample size, Δ(Q)AICc = difference in (Q)AIC compared to the best fitting model, Weight = Akaike weight, *k* = number of parameters. Φ = apparent survival probability; p = recapture probability; t = time effect; sex = sex effect; m = trap dependence; trend = linear trend; Qtrend = quadratic trend; * = interaction; + = additive effect, a2= two age classes;. = constant. In local recruitment models, $\hat{c}$ = 2.49.

#	Model		AICc	ΔAICc	Weight	*k*
A1	Φ(sex+t)	p(m+trend)	4111.67	0.00	0.807	22
A2	Φ(t)	p(m+trend)	4116.25	4.59	0.081	21
A3	Φ(sex+trend)	p(m+trend)	4117.04	5.38	0.055	6
A4	Φ(sex)	p(m+trend)	4117.70	6.04	0.039	5
A5	Φ(trend)	p(m+trend)	4120.91	9.24	0.008	5
A6	Φ(.)	p(m+trend)	4121.64	9.97	0.006	4
A7	Φ(Qtrend)	p(m+trend)	4122.68	11.01	0.003	6
A8	Φ(sex*t)	p(m+trend)	4138.94	27.27	0.000	39
#	**Model**		**QAICc**	**ΔQAICc**	**Weight**	***k***
B1	Φ(a2)	p(m)	1049.391	0.00	0.61	4
B2	Φ(a2+sex)	p(m)	1050.872	1.48	0.29	5
B3	Φ(a2*sex)	p(m)	1052.873	3.48	0.11	6
B4	Φ(a2+time)	p(m)	1071.704	22.31	0.00	21
B5	Φ(a2+sex+t)	p(m)	1073.177	23.79	0.00	22
B6	Φ(a2*time)	p(m)	1090.618	41.23	0.00	32

(Q)AICc values (ΔAICc) of two or more units was considered to show a difference in explanatory values of the models (Burnham & Anderson 2002). Model selection uncertainty was considered by model averaging (AICc ≤ 4; Burnham & Anderson 2002). Recapture probabilities were considered as nuisance parameters. We report estimates as mean ± SE unless mentioned otherwise.

2.5. Dispersal

We measured site fidelity of adults and juveniles (philopatry) as the probability of changing breeding sites (see description of study area, not territories) between successive years. In adult data, there were many movements that occurred with more than one year between observations but these were not used because they would have biased the estimates as there would have been higher probability of movement compared to those with only one year in between. Dispersal distances were measured as the distance between breeding sites. Each site had an average point that was used. This method was used because our data is based on the ringing records and hence we do not have nest location data with the accuracy of meters. Thus, short distance dispersal e.g. territory changes within sites are included as zeros in the data and may slightly underestimate dispersal distances. These measures were calculated by considering only the first observation from each individual. However, we also describe all observed breeding dispersal movements to show how extensive it was. When testing for differences between sexes, both site fidelity and dispersal distances were measured only from observations occurring within the study area. However, we also report dispersal distances that resulted from permanent emigration of individuals that were caught or found outside the study area. These data result from random trapping by other ringers or dead birds found by people (e.g. not collected by us) and were retrieved from the Finnish Ringing Scheme.

3. Results

3.1. Apparent adult survival

Males had higher apparent survival (0.66 ± 0.027) than females (0.61 ± 0.028; Fig. 2; Table 1, ΔAICc

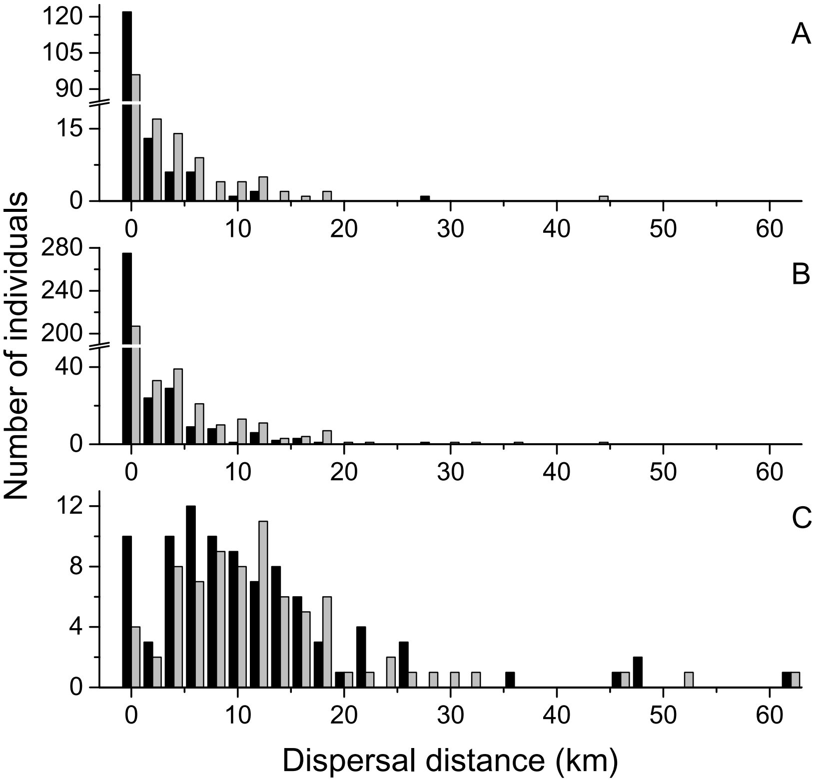

Fig. 3. Dispersal distributions of male (black) and female (grey) Little Ringed Plovers breeding in Southern Finland. Breeding dispersal A) observed between first capture and recapture in the following year, B) all observations of breeding dispersal without reference to individuals or elapsed time between observations, and C) natal dispersal. Note the breaks in the Y axis in panels A and B.

= 4.6; models A1 and A2, β_{SEX} = 0.247, SE ± 0.095, CI = {0.060, 0.434}). There was also strong temporal variation in survival (Table 1, ΔAICc = 6; models A1 and A4). Sexes showed similar variation (Table 1, ΔAICc = 27; models A1 and A8) with annual estimates ranging widely (males: 0.41–0.85; females 0.35–0.82). A trend in survival was included in the third best model, but the 95% confidence intervals for the coefficient overlapped zero (β_{TREND} = –0.025, CI = {–0.054, 0.004}). Recapture rates also tended to decline during the study, but the 95% confidence interval of the coefficient overlapped zero (from model A1: β_{TREND} = –0.021, CI = {–0.055, 0.012}). The mean recapture rate for year i was higher (0.36 ± 0.017) for individuals captured in the previous encounter occasion (i.e. year $i – 1$) than for those not captured in the previous encounter occasion (0.27 ± 0.027).

3.2. Local recruitment

Out of 78 returning juvenile females, 30% were caught in their first year and 49% were caught in their second year of age for the first time as breeders (Appendix 2). It seems that most females breed for the first time by the age of two years. The distribution for males (n = 92) was similar (Appendix 2). These results do not reflect true age of first breeding because of the low recapture probabilities. For example, it is unlikely that three years old or older Little Ringed Plovers bred for the first time. Local recruitment did not show strong time dependence and did not differ by sex (Table 1). Model averaged local recruitment of males (0.082 ± 0.013) was similar to that of females (0.077 ± 0.013). Adult survival after this first year was also similar between males (0.74 ± 0.036) and females (0.72 ± 0.038). These estimates of adult survival were higher than those estimated in the apparent adult survival analysis (Fig. 2). The difference was nearly significant in males (χ^2 = 3.27, df = 1, p = 0.07) and significant in females (χ^2 = 5.87, df = 1, p = 0.015).

3.3. Natal and breeding dispersal

Breeding dispersal distances were significantly shorter for males (average 0.80 ± 0.231 km, n =

152) than females (average 2.17 ± 0.397 km, n = 156; Wilcoxon test, W = 9336.5, p = 0.0001; Fig. 3a). This was mostly due to breeding site fidelity between two successive years which was lower in females (0.620, n = 156) than in males (0.808, n = 152; $\chi^2 = 12.35$, $df = 1$, $p < 0.001$). When translated into dispersal propensity, females (0.38 = 1 – fidelity) were twice as likely to change breeding sites compared to males (0.192). Distances moved between breeding sites were shorter for males (average 4.1 km, median 2.1 km) than females (average 5.7 km, median 3.4 km) when considering only birds that were not faithful to their previous breeding site but the difference was not statistically significant (Wilcoxon test, W = 697, p = 0.16; Fig 3a). The longest recorded breeding dispersal distances were 28 km for adult males and 43 km for females, and these longer movements were more frequent among females when all movements were considered (Fig 3b). Furthermore, out of those birds emigrating outside the study area, three adult females were observed to have dispersed distances of 98 km, 108 km and 210 km, further supporting sex-biased dispersal distances. Natal philopatry to the site of birth was low in both males (0.11, n = 92) and females (0.05, n = 78). Average distances for males (11.1 ± 1.19 km, n = 92) and females (12.5 ± 1.30 km, n = 78) were similar (Wilcoxon test, W = 3159, p = 0.18). They did not change much after removing philopatric individuals (males: 12.4 ± 1.30 km, n = 82; females 13.2 ± 1.32 km, n = 74; t = 0.855, df = 154, p = 0.394, Fig 3c). The maximum recorded natal dispersal distance was 333 km.

4. Discussion

Contrary to our expectations, apparent adult survival of the Little Ringed Plover was different between sexes, being higher in males than females. While we cannot exclude the possibility that lower apparent survival of adult females is partly true, results on dispersal suggest that our survival estimates are affected by permanent emigration, and that the observed difference is caused by female-biased dispersal, which has been shown for some shorebirds (Rönkä *et al.* 2008, Rönkä *et al.* 2012, Küpper *et al.* 2012). We found no evidence of sex differences in local recruitment.

Few studies have shown sex differences in apparent or true survival among *Charadrius* plovers (*alexandrinus*: Foppen *et al.* 2006, *hiaticula*: Wallander & Andersson 2003, *nivosus*: Mullin *et al.* 2010, Stenzel *et al.* 2011, Colwell *et al.* 2013), while most studies show no effects (*alexandrinus*: Sandercock *et al.* 2005, *hiaticula*: Foppen *et al.* 2006, *melodus*: Cohen *et al.* 2006; Ledee *et al.* 2010, Cohen & Gratto-Trevor 2011, *montanus*: Dinsmore 2008; *nivosus*: Paton 1994, Saalfeld *et al.* 2013, *semipalmatus*: Badzinski 2000). The polyandrous Kentish and Snowy Plovers (*alexandrinus / nivosus*) show the greatest variation in sex specific survival (see above). The lack of consistency within species suggests that local conditions or other population specific attributes affect sex specific survival and/or site fidelity. Stenzel *et al.* (2011) is the only study that has shown a sex difference in true survival by separating site fidelity when estimating survival. In this Californian population, the most likely cause for lower survival of females was the large reproductive investment of females that laid up to six clutches in one breeding season (Stenzel *et al.* 2011). Interestingly, such high laying investments are probably less likely in monogamous species and in populations that have shorter breeding seasons such as our study population, which also exhibit less evidence for sex-biased survival (e.g. Lishman *et al.* 2010, Cohen & Gratto-Trevor 2011).

Sex differences in apparent survival are often caused by permanent emigration of females (e.g. Wallander & Andersson 2003). This was most likely the case also in our study. The propensity of adult females to disperse was twice as high as that of males. Females also tended to have longer dispersal distances than males within our study area. Furthermore, dispersal distances and dispersal propensities may have been biased low because long distance dispersal is not recorded (Koenig *et al.* 1996). Even from the observable distances, the frequencies of distances longer than the radius of the study area will be biased low because long distance dispersal can occur only from edge to another, whereas most of the recorded distances come from the center of the study area and are short (van Noordwijk 2011). Maximum possible distances within our study area were ca. 70 km, while the observed maximum dispersal distances from individuals originating from our study were

210 km in adult females (only 28 km in males). Females may be more sensitive and have stronger responses to changes in the environment (e.g. nest predation risk) whereas males benefit more from fidelity to their territory (Clarke *et al.* 1997), but we lack data to test this.

Permanent emigration is also visible from our low estimates of apparent survival for juveniles. Our estimate of apparent juvenile survival (8%) is typical for a small shorebird (Sandercock *et al.* 2005, Koivula *et al.* 2008, Nol *et al.* 2010). However, it is low when compared to true juvenile survival (separated from site fidelity) of the Snowy Plover, 0.18 (Stenzel *et al.* 2007). The propensity of juveniles to move from their natal site was high (males: 0.89, females: 0.95) and their movements were longer than those recorded from adults. Undetected large scale movements (up to 333 km in juvenile females) may have prevented us from finding differences in natal dispersal distances or local recruitment between the sexes (see above). Natal dispersal patterns in the Little Ringed Plover are similar to those described for Kentish Plovers (Foppen *et al.* 2006) and Snowy Plovers (Stenzel *et al.* 2007).

Our mean estimate of adult survival (65%) falls in the low end of the range 65%–74% derived from return rates or dead recoveries of Little Ringed Plovers (Boyd 1962, Hölzinger 1972). This estimate is also rather low compared to other *Charadrius* plovers, but as the Little Ringed Plover is one of the smallest plover species, this low survival estimate fits the general pattern of correlation between body size and survival in *Charadrius* plovers (Boyd 1962, Sandercock *et al.* 2005). However, some evidence suggest that our estimate can be biased by permanent emigration.

Adults of northern temperate *Charadrius* species mostly exhibit 0.72–0.99 site fidelity between years when measured on a within-site scale (Pienkowski 1984, Haig & Oring 1988, Wiens & Cuthbert 1988, Jackson 1994, Lloyd 2008, Cohen *et al.* 2006; note that site fidelity can be reported in relation to territory, breeding site or the whole study area), while the Snowy Plover has shown lower rates (0.26–0.40; Paton & Edwards 1996). We found the mean within-site fidelity of the Little Ringed Plovers to be 71%. We do not have data on site fidelity on the territory scale which would probably be lower. Historically, Little Ringed Plovers bred mainly in ephemeral sites such as river flood plains and continue to do so in man-made sites that also have low predictability in habitat quality (Delany *et al.* 2009). They are often forced to find new breeding areas when their old sites deteriorate (Cramp & Simmons 1983). Thus, their site fidelity reflects heterogeneity between and unpredictability within quality of territories that favour dispersal (Ronce 1997).

The influence of permanent emigration of females especially is evident when population growth rates are estimated for this apparently stable population. With average adult survival of females (0.61) and average local recruitment (0.08), a projected population growth rate would be only ca. 0.76–0.77 even with a hatching success of 100% (Appendix 3). With such population growth rates, the population would disappear quickly. But if adult survival is set to that of the philopatric females (0.72) and juvenile survival is given a value of 0.18 (true survival from Stenzel *et al.* 2007), the population growth rate would be above unity (1.03–1.08; Appendix). As a comparison, other small shorebirds, the Temminck's stint (*Calidris temminckii*) and the Dunlin (*Calidris alpina*), species that breed in more or less stable coastal meadow environments, have higher average adult survival rates from 0.70 to 0.83 (Jönsson 1991, Koivula *et al.* 2008), despite that these estimates were derived from declining populations.

There was trap-dependence in our data. In addition to a genuine response to catching an individual, trap-dependence may result from extrinsic features that cause heterogeneity in recapture probabilities, e.g. sampling design. It may also arise from non-random temporary emigration (Pradel 1993), behaviour that can be related biologically relevant unconsidered features (Crespin *et al.* 2008). One possible factor is sex, which was considered in our analyses. Another natural source of intrinsic heterogeneity in recapture rates could be different dispersal strategies (Frederiksen *et al.* 2014). In line with this, we found apparent adult survival estimated from all adults to be lower than that of locally produced philopatric adults (from local recruitment analysis). This suggests a difference in apparent survival between immigrants and philopatric individuals (Nol *et al.* 2010, Pakanen *et al.* 2010, 2011), a difference that is likely to be caused by a higher emigration propensity of immigrants (Doligez & Pärt 2008, Chernetsov *et al.* 2009, Pakanen *et al.* 2011, Stenzel *et al.* 2011) or possible unconsidered age-specific variation in survival.

Our results suggest that apparent adult survival studies on shorebirds should pay attention to permanent emigration, especially when examining sex-specific rates. In shorebirds, permanent emigration is often encountered as transience in the data, i.e. lowered apparent survival after first capture (Sandercock 2003), with the older age classes representing more accurate survival (Foppen *et al.* 2006, Sandercock *et al.* 2005). We found no evidence of transience despite the strong implications of permanent emigration, suggesting that emigration occurred also at older ages. Clearly, other measures may be needed. If the data do not allow separating site fidelity (e.g. Stenzel *et al.* 2011), survival information on the more site faithful portion of the population, the philopatric individuals, may give more reliable estimates of adult survival (Pakanen *et al.* 2011). Interestingly, the sex difference in survival disappeared in this site faithful portion of our data (females: 0.721, males: 0.735). Unless there were sex specific costs of dispersal to the immigrants, this result gives further proof that the observed sex difference in the main apparent adult survival analysis was caused by a higher rate of permanent emigration by females.

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Pikkutyllin sukupuolikohtainen säilyvyys ja levittäytyminen

Sukupuolikohtaisten säilyvyyksien arvioiminen on tärkeää, koska koiraiden ja naaraiden väliset säilyvyyserot voivat vaikuttaa voimakkaasti mm. populaatiodynamiikkaan ja sitä kautta esim. suojelubiologiaan. Linnuilla naaraiden säilyvyys on usein matalampi kuin koiraiden, minkä yhtenä pääsyynä pidetään erilaista lisääntymispanosta sukupuolten välillä. Me tutkimme pienen yksiavioisen kahlaajan, pikkutyllin, aikuissäilyvyyttä ja poikasten rekrytoitumista Etelä-Suomessa pesineestä populaatiosta kerätyn 18 vuoden pituisen merkintä–takaisinpyyntiaineiston avulla.

Koska pikkutyllit jakavat jälkeläisten hoidon ja koska tutkimuspopulaation pikkutyllit pesivät vuosittain vain kerran, odotimme, että aikuisten pikkutyllien säilyvyydessä ei ole eroa sukupuolten välillä. Säilyvyysestimaatti on todellisen säilyvyyden ja paikkauskollisuuden tulo. Tästä johtuen arvioimme tutkimusalueen ulkopuolelle johtaneen emigraation säilyvyyksiä väärentävää vaikutusta estimoimalla myös pesimä- ja nuoruuslevittäytymisen etäisyyksiä tutkimusalueen sisällä. Koiraiden säilyvyys (0.660) oli korkeampi kuin naaraiden (0.609), mutta poikasten rekrytoituminen ei riippunut sukupuolesta (0.080). Naarailla pesimälevittäytymisen etäisyydet olivat pitempiä johtuen erityisesti heikommasta pesimäpaikkauskollisuudesta (koiraat 0.808, naaraat 0.620). Naaraat siis vaihtoivat pesimäpaikkaa vuosien välillä noin kaksi kertaa niin usein kuin koiraat. Naaraiden matalampi säilyvyysestimaatti selittyneekin emigraation avulla.

Paikkauskollisten tutkimusalueella syntyneiden ja sinne rekrytoituneiden lintujen säilyvyydet olivat korkeampia kuin koko aikuisaineiston säilyvyysestimaatit. Nämä estimaatit ovat todennäköisesti vähemmän emigraation vääristämiä, ja ne eivät osoittaneet minkäänlaista sukupuolieroa paikkauskollisten aikuisten keskuudessa. Tämä tukee johtopäätöstä, että naaraiden ja koiraiden säilyvyys ei eronnut ja emigraatio oli pääsyy matalampaan säilyvyysarvioon.

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Appendix 1. Description of what the separate the goodness of fit tests used in program U-CARE specifically test for (Choquet *et al.* 2009).

TEST3.SR: Does the probability that an individual known to be alive at occasion (*i*) is ever seen again depend on whether it was marked at or before occasion (*i*)?

TEST3.SM: Does when individuals were recapture depend on whether they were marked on or before occasion (*i*)?

TEST2.CT: Is the probability of being seen at occasion (*i* + 1) a function of whether or not the individual was seen at occasion (*i*), conditional on surviving from (*i*) to (*i* + 1)?

TEST2.CL: Is there is a difference in the expected time of next recapture between the individuals captured and not captured at occasion i conditional on presence at both occasions i and i + 2?

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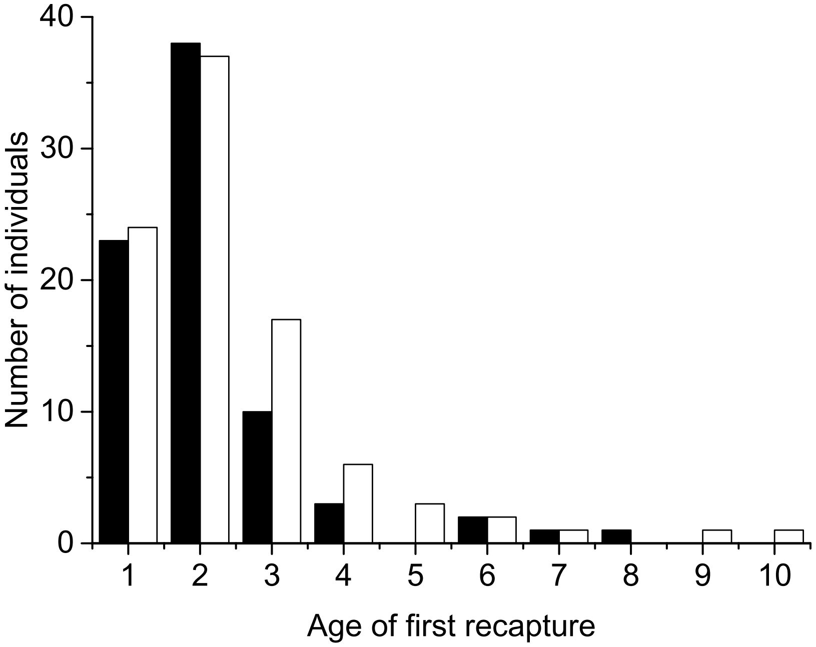
Appendix 2. Age of first recapture as breeding adults for recruiting juvenile Little Ringed Plovers ringed as chicks at the study site in Southern Finland.



Appendix 3

We examined population growth rates (l) that result from our estimates of apparent adult survival and local recruitment with a population matrix model that accounts for only adult survival and fecundities and assumes no immigration or emigration (Caswell 2001).

The matrix was based on a pre-breeding census and describes female dynamics with two stages that represent ages 1 year old and two or older. The matrix is written as

$$A = \begin{bmatrix} F1 & F2 \\ S & S \end{bmatrix},$$

where S express survival of females and F(i) express age (i) dependent fecundities, i.e. the mean number of recruits produced per females which were calculated as: Fi = ½ * breeding probability at age i * hatching success * number of hatched chicks * local recruitment

Hatching sex ratios were assumed to be even.

In order to make a point about the influence of permanent emigration, we assumed that hatching success was 100%. Then we made two different parameterizations of the model. In A, we used our average results on apparent survival and local recruitment. In B, we replaced them with estimates that were more likely to reflect true survival (i.e. where permanent emigration was removed). Apparent survival of females was replaced with that of philopatric females (this study) and local recruitment rate was taken from Stenzel *et al.* (2007). Because there is uncertainty on age of first breeding, we calculated the population growth rates also assuming that all females breed at age one.

Parameterization A

Transition	Parameter	Value	Reference
S	Female survival	0.61	This study
F	Local recruitment	42216	This study
F	Hatching success	100%	Assumed
F	Number of hatched chicks	4	Assumed
F	Hatching sex ratio	0.0424	Assumed
F	Breeding probability age1	0.5 (1)	Assumed
F	Breeding probability age2	1	Hölzinger *et al.* 1972: Cramp & Simmons 1983

$$A = \begin{bmatrix} 0.08 & 0.16 \\ 0.61 & 0.61 \end{bmatrix}$$

The projected population growth rate ($\lambda = 0.755$) suggested that the population would decline 24% each year even though hatching success was 100%. This result is not sensible and such a decline did not take place during the study. Little Ringed Plovers did not decline in a large scale either suggesting that there was balanced dispersal such that emigration and immigration may have been similar per capita.

If all females would start to breed a one year old, the population growth rate would be slightly higher ($\lambda = 0.770$).

Parameterization B

Transition	Parameter	Value	Reference
S	Female survival	0.72	This study
F	Local recruitment	0.0125	Stenzel *et al.* 2007
F	Hatching success	100%	Assumed
F	Number of hatched chicks	4	Assumed
F	Hatching sex ratio	0.0424	Assumed
F	Breeding probability age1	0.5 (1)	Assumed
F	Breeding probability age2	1	Hölzinger *et al.* 1972: Cramp & Simmons 1983

$$A = \begin{bmatrix} 0.18 & 0.36 \\ 0.72 & 0.72 \end{bmatrix}$$

The projected population growth rate ($\lambda = 1.026$) suggested that the population is stable or in slight increase. Even though the assumption of 100% hatching success is not realistic, this result is more sensible as the population was more or less stable during the study years. Furthermore, it shows that even with higher and perhaps more accurate values of survival, the population growth rate is only slightly over 1 when hatching success is unrealistically high.

If all females would start to breed a one year old, the population growth rate would be slightly higher ($\lambda = 1.080$).

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