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, Grüebl 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-
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-
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 ($\Phi_{ad}$) and local recruitment probabilities ($\Phi_{jrv}$) 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 (*), $[\Phi(\text{sex}*t)p(\text{sex}*t)]$, was not significant ($df = 127$, $\chi^2 = 110.22, p = 0.86$). However, the overall signed statistic for trap-dependence was significantly negative [$z = -2.859, p_{\text{two-tailed}} = 0.004$] indicating trap-happiness. This was due to trap dependence among males (test for differences in recapture probabilities, TEST2.CT; $df = 16, \chi^2 = 28.84, p = 0.03$) but not in females ($df = 16, \chi^2 = 17.63, p = 0.35$). TEST2.CL (test for differences in recapture probabilities) was not significant in either sex (males: $df = 15, \chi^2 = 16.79, p = 0.33$; females: $df = 13, \chi^2 = 11.46, p = 0.57$). 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: $df = 17, \chi^2 = 4.629, p = 0.99$; females: $df = 17, \chi^2 = 15.09, p = 0.59$) or later (test for differences in survival probabilities, TEST3.SM; males: $df = 18, \chi^2 = 6.9224, p = 0.99$; females: $df = 15, \chi^2 = 8.847, p = 0.89$). 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 \( \Phi(sex*t) p(sex*m*t) \). 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 \( \Phi(sex*t) p(sex*t) \) 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 \( \Phi(age*sex*t) p(sex*t) \) with tests 3.SM, 2.CT and 2.CL, which was nearly significant (\( df = 89, \chi^2 = 109.96, p = 0.066 \)). Because we wanted unbiased estimates of local recruitment we chose a global model that simultaneously considers age- and trap-dependence (Schmidt et al. 2002, Belda et al. 2007). In the first step, the goodness of fit for the original model was calculated by summing \( \chi^2 \) values and degree 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
(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; 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 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; Burnham & Anderson 2002). Recapture probabilities were considered as nuisance parameters. We report estimates as mean ± SE unless mentioned otherwise.

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models A1 and A2, $\beta_{\text{SEX}} = 0.247$, SE $\pm 0.095$, CI $= \{0.060, 0.434\}$). There was also strong temporal variation in survival (Table 1, $\Delta$AICc = 6; models A1 and A4). Sexes showed similar variation (Table 1, $\Delta$AICc = 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 ($\beta_{\text{TREND}} = -0.025$, 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: $\beta_{\text{TREND}} = -0.021$, CI $= \{-0.055, 0.012\}$). The mean recapture rate for year $i$ was higher (0.36 $\pm 0.017$) 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 $\pm 0.027$).

### 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 $\pm 0.013$) was similar to that of females (0.077 $\pm 0.013$). Adult survival after this first year was also similar between males (0.74 $\pm 0.036$) and females (0.72 $\pm 0.038$). 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 ($\chi^2 = 3.27$, df = 1, $p = 0.07$) and significant in females ($\chi^2 = 5.87$, df = 1, $p = 0.015$).

### 3.3. Natal and breeding dispersal

Breeding dispersal distances were significantly shorter for males (average 0.80 $\pm 0.231$ km, $n =$
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. We found no evidence of sex differences in local recruitment.

4. Discussion

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 Plovers 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 tenuirostris) 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 immi-
Pikkutyllin sukupuolikohtainen säilyvyys ja levittäytyminen

Sukupuolikohtaisen säilyvyyskien arvioiminen on tärkeää, koska koiraiden ja naaraiden väliset säilyvyyserot voivat vaikuttaa voimakkaasti mm. populatiodynamiikkaan ja sitä kautta esim. suojelubiologiaan. Linnuilla naaraan säilyvyys on usein matalampi kuin koiraiden, minkä yhtenä

pääsyyynä pidetään erilaista lisääntymispanosta sukupuolten välillä. Me tutkimme pienen yksiaiviosien kahlaajan, pikkutyllin, aikuissäilyvyyttä ja poikasten rekrytoitumista Etelä-Suomessa pesineestä populaatiosta kerätyyn 18 vuoden pituisen merkintä–takaismpyyntäaineiston avulla.

Koska pikkutyllit jakavat jälkeläisiä hoidon ja koska tutkimuspopulation pikkutyllit pesivät vuosittain vain kerran, odotimme, että aikuisten pikkutyllien säilyvyydessä ei ole eroa sukupuolten välillä. Säilyvyys estimaatti on todellisen säilyvyysten ja paikkauskollisuuden tulo. Tästä johtuen arvioimme tutkimusalueen ulkopuolelle johtaneen emigraation säilyvyyskiä väärentävää vaikutusta estimoimalla myös pesimä- ja nuoruuslevittäytyminen etäisyyksiä tutkimusalueen sisällä. Koiraiden säilyvyys (0.660) oli korkeampi kuin naaraiden (0.609), mutta poikasten rekrytoituminen ei riippunut sukupuolten välillä (0.080). Naarailla pesimälevittäytyminen etäisyydet olivat pitempiä johtuen erittäin heikommaista pesimäpaikkauskollisuudesta (koiraat 0.808, naaraat 0.620). Naaraat siis vaihtoivat pesimäpaikkaa vuosien välillä noin kaksi kertaa niin usein kuin koirat. Naaraiden matalampi säilyvyys estimaatti selittyyneen emigraation avulla.

Paikkauskollisten tutkimusalueella syntyni den ja sinne rekrytoituneiden lintujen säilyvyys olivat korkeampia kuin koko aikuisten keskuudessa. Tämä estimaatit ovat todennäköisesti vähemmän emigraation vääristämiä, ja ne eivät osoittaneet minkäänäisen sukupuolten välistä emigraation avulla. Naaraiden ja koiraiden säilyvyys ei eroonut ja emigraatio oli pääsyy matalampaan säilyvyysarvioon.

Acknowledgements. The data were collected by the late wader ringer Heikki Arppe. The Ringing Centre of the Finnish Museum of Natural History provided the archived ringing data. The study was funded by the Kone foundation (JV; SL) and the Finnish Academy project 278759 (VMP). The work complies with the current laws of Finland. We thank peer number 1100 from Peerage of Science, one anonymous reviewer, Kari Koivula, Antti Rönkä and Robert Thomson for valuable comments on the manuscript.

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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 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 \(i+2\)?

References


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 \( (\lambda) \) 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

\[
A = \begin{bmatrix}
F_1 & F_2 \\
S & S
\end{bmatrix},
\]

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: \( F_i = \frac{1}{2} \times \text{breeding probability at age } i \times \text{hatching success} \times \text{number of hatched chicks} \times \text{local recruitment} \)

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

<table>
<thead>
<tr>
<th>Transition</th>
<th>Parameter</th>
<th>Value</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>Female survival</td>
<td>0.61</td>
<td>This study</td>
</tr>
<tr>
<td>F</td>
<td>Local recruitment</td>
<td>42216</td>
<td>This study</td>
</tr>
<tr>
<td>F</td>
<td>Hatching success</td>
<td>100%</td>
<td>Assumed</td>
</tr>
<tr>
<td>F</td>
<td>Number of hatched chicks</td>
<td>4</td>
<td>Assumed</td>
</tr>
<tr>
<td>F</td>
<td>Hatching sex ratio</td>
<td>0.0424</td>
<td>Assumed</td>
</tr>
<tr>
<td>F</td>
<td>Breeding probability age1</td>
<td>0.5 (1)</td>
<td>Assumed</td>
</tr>
<tr>
<td>F</td>
<td>Breeding probability age2</td>
<td>1</td>
<td>Hölzinger et al. 1972: Cramp &amp; Simmons 1983</td>
</tr>
</tbody>
</table>

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

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

<table>
<thead>
<tr>
<th>Transition</th>
<th>Parameter</th>
<th>Value</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>S</td>
<td>Female survival</td>
<td>0.72</td>
<td>This study</td>
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<tr>
<td>F</td>
<td>Local recruitment</td>
<td>0.0125</td>
<td>Stenzel et al. 2007</td>
</tr>
<tr>
<td>F</td>
<td>Hatching success</td>
<td>100%</td>
<td>Assumed</td>
</tr>
<tr>
<td>F</td>
<td>Number of hatched chicks</td>
<td>4</td>
<td>Assumed</td>
</tr>
<tr>
<td>F</td>
<td>Hatching sex ratio</td>
<td>0.0424</td>
<td>Assumed</td>
</tr>
<tr>
<td>F</td>
<td>Breeding probability age1</td>
<td>0.5 (1)</td>
<td>Assumed</td>
</tr>
<tr>
<td>F</td>
<td>Breeding probability age2</td>
<td>1</td>
<td>Hölzinger et al. 1972: Cramp &amp; Simmons 1983</td>
</tr>
</tbody>
</table>
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 ($\lambda = 1.080$).

References